In Focus – Managing Forests in Europe

Introduced tree species in European forests:

opportunities and challenges

Frank Krumm and Lucie Vítková (eds.)

Introduced tree species in European forests: *opportunities and challenges*

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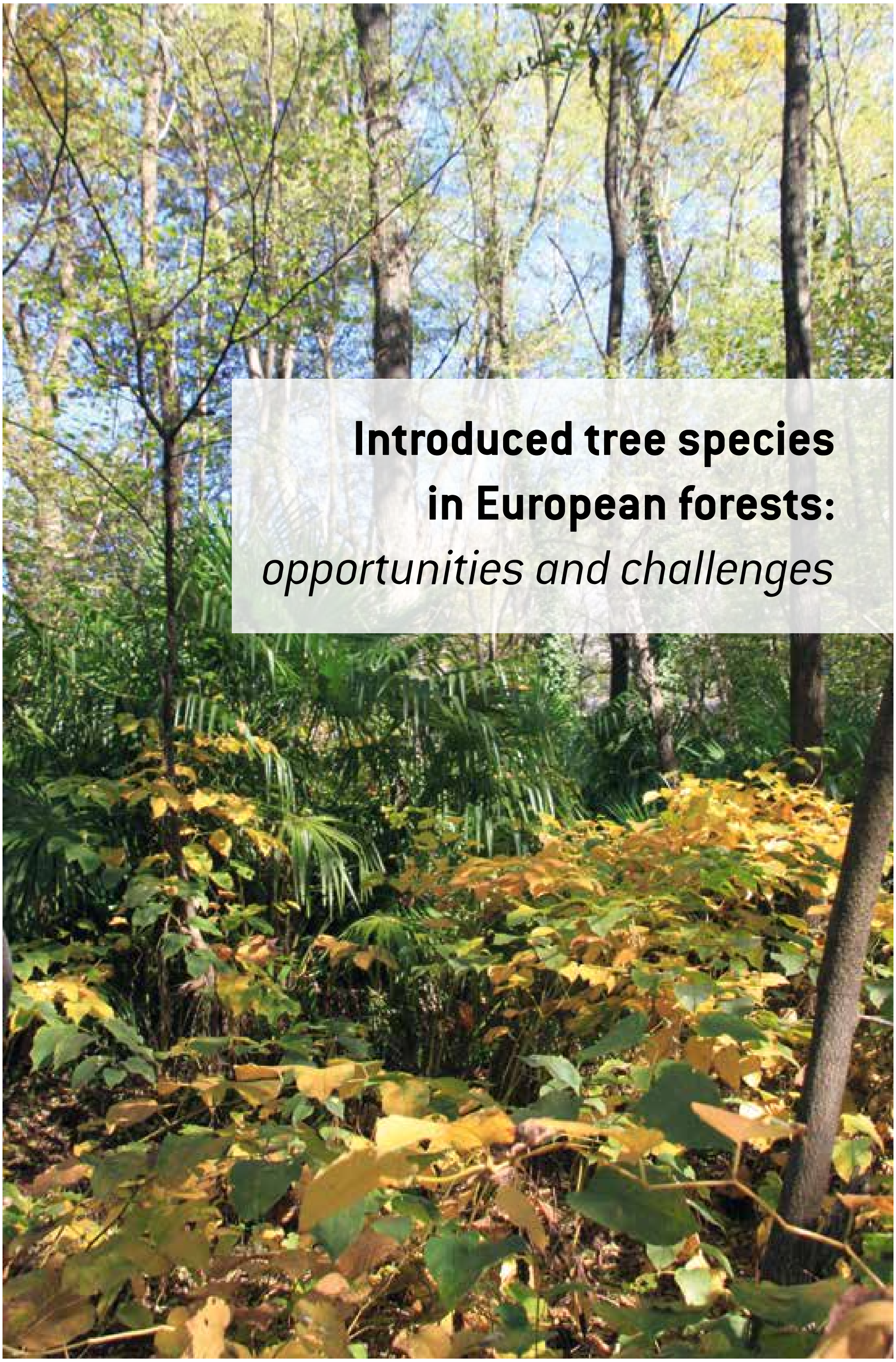

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Authors

Ignacio Barbeito, AgroParisTech and INRA, Nancy, France
Annemarie Bastrup-Birk, European Environmental Agency (EEA), Denmark
Pieter Bas van der Lei, Wageningen University, The Netherlands
Pavel Bednář, The Czech Academy of Sciences - Global Change Research Institute, Czech Republic
Anja Bindewald, Forest Research Institute Baden-Württemberg (FVA), Germany
H. John B. Birks, Bergen University, Norway and University College London, United Kingdom
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Andreas Bolte, Thünen Institute of Forest Ecosystems, Germany
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Isabel Cañellas, INIA-CIFOR Madrid, Spain
Paul Cavaillé, Université Grenoble Alpes and Irstea, UR EMGR, Centre de Grenoble, France
Raffaele Cavalli, Department of Land, Environment, Agriculture and Forestry, University of Padova, Italy
Laura Celesti-Grapow, University of Rome, Italy
Marco Conedera, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Cadenazzo, Switzerland
Owen Davies, FSC UK, United Kingdom
Bram D'hondt, Ghent University, Belgium
Romina D. Dimarco, INTA-CONICET, Argentina
Tuğba Doğmuş, Suleyman Demirel University, Isparta, Turkey
Fanny Dommanget, Université Grenoble Alpes and Irstea, UR EMGR, Centre de Grenoble, France
Yann Dumas, Irstea, Nogent-sur-Vernisson, France
Uta Eser, Office for Environmental Ethics, Germany
André Evette, Université Grenoble Alpes and Irstea, UR EMGR, Centre de Grenoble, France
Linda Feichtinger, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, Switzerland
Anna Gazda, University of Agriculture, Krakow, Poland
Arthur Gessler, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, Switzerland
Martin M. Gossner, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, Switzerland and TU Munich, Germany
Daniela Gurtner, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, Switzerland
Marc Hanewinkel, University of Freiburg, Germany
Tina Heger, University of Potsdam and TU Munich, Germany
Alexander Held, European Forest Institute (EFI), Central European Office EFICENT, Germany
Laura Hernández, INIA-CIFOR Madrid, Spain
Rolf Holderegger, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf and Swiss Federal Institute of Technology ETH, Zurich, Switzerland
Anke Höltermann, Federal Agency for Nature Conservation (BfN), Germany
Marion Karmann, FSC International, Germany
Jorie Knook, Business School of the University of Edinburgh and Scottish Rural College (SRUC), Scotland
Simon Knüsel, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, Switzerland
Ingo Kowarik, TU Berlin, Germany
Daniel Kraus, European Forest Institute (EFI), Central European Office EFICENT, Germany
Frank Krumm, European Forest Institute (EFI), Central European Office EFICENT, Germany
Sabrina Kumschick, Centre for Invasion Biology, Stellenbosch University and Kirstenbosch National Botanical Gardens, South Africa
François-Marie Martin, Université Grenoble Alpes and Irstea, UR EMGR, Centre de Grenoble, France
Franco Mason, National Centre for the Study and Conservation of Forest Biodiversity Bosco Fontana, Italy
Eliane Meier, Agroscope, Institute for Sustainability Sciences, Switzerland
Fabio Meloni, University of Turin, Italy
Bernhard Mettendorf, Ortenaukreis, ForstBW and IG Alternative Baumarten, Germany
Hans-Gerhard Michiels, Forest Research Institute Baden-Württemberg (FVA), Germany

Emma Minari, National Centre for the Study and Conservation of Forest Biodiversity Bosco Fontana, Italy
Renzo Motta, University of Turin, Italy
Bart Muys, KU Leuven University, Belgium and EFIMED, Spain
Stefan Nehring, Federal Agency for Nature Conservation (BfN), Germany
Áine Ní Dhubháin, University College Dublin, Ireland
Martin A. Nuñez, INIBIOMA-CONICET, Universidad Nacional del Comahue, Bariloche, Argentina
Bart Nyssen, Bosgroep Zuid Nederland, The Netherlands
Gerald Oitzinger, Austrian Federal Forests (ÖBf AG) and National Park Donau-Auen, Austria
Pádraig O'Tuama, Coillte Teo., Ireland
Jan den Ouden, Wageningen University, The Netherlands
Jan Pergl, Institute of Botany, The Czech Academy of Sciences, Czech Republic
Nahuel Policelli, INIBIOMA-CONICET, Universidad Nacional del Comahue, Bariloche, Argentina
Paddy Purser, PTR Ltd., Ireland
Petr Pyšek, Institute of Botany, The Czech Academy of Sciences and Charles University, Czech Republic
Patrick Pyttel, University of Freiburg, Germany
Verena Quadt, European Forest Institute (EFI), Central European Office EFICENT, Germany
Valentin Queloz, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, Switzerland
David M. Richardson, Centre for Invasion Biology, Stellenbosch University, South Africa
Andreas Rigling, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, Switzerland
Jiří Sádlo, Institute of Botany, The Czech Academy of Sciences, Czech Republic
Joaquim S. Silva, Coimbra College of Agriculture and University of Lisbon, Portugal
Alberto Santini, CNR Firenze, Italy
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Willy Tinner, Institute of Plant Sciences and Oeschger Centre for Climate Change Research, University of Bern, Switzerland
Margarida Tomé, Forest Research Centre, School of Agriculture, University of Lisbon, Portugal
Brian van Wilgen, Centre for Invasion Biology, Stellenbosch University, South Africa
Giorgio Vacchiano, University of Turin, Italy
Sonia Vanderhoeven, Belgian Biodiversity Platform, Belgium
Petr Vaněk, Faculty of Forestry and Wood Technology Brno, Czech Republic
Margot Vanhellemont, Ghent University, Belgium
Kris Verheyen, Ghent University, Belgium
Daniela Vetter, Ortenaukreis and ForstBW, Germany
Lucie Vítková, European Forest Institute (EFI), Central European Office EFICENT, Germany
Michaela Vítková, Institute of Botany, The Czech Academy of Sciences, Czech Republic
Torsten Vor, University of Göttingen, Germany
Faith Wilson, Ecological Consultancy, Ireland
Thomas Wohlgemuth, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, Switzerland
Steve Woodward, University of Aberdeen, Scotland, United Kingdom
Jan Wunder, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, Switzerland
Livia Zapponi, Institute of Agroenvironmental and Forest Biology, National Research Council and National Centre for the Study and Conservation of Forest Biodiversity Bosco Fontana, Italy
Niklaus Zimmermann, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, Switzerland
Karoline Zsak, National Park Donau-Auen, Austria

Drafting committee

Annemarie Bastrup-Birk, European Environment Agency (EEA), Denmark
Jürgen Bauhus, University of Freiburg, Germany
Etienne Branquart, Directorate General for Agriculture, Natural Resources and Environment, Service Public de Wallonie, Belgium
Marco Conedera, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Cadenazzo, Switzerland
Franz Essl, University of Vienna and Austrian Environment Agency, Austria
Frank Krumm (coordinator), European Forest Institute (EFI), Central European Office EFICENT, Germany
Hans-Gerhard Michiels, Forest Research Institute of Baden-Württemberg FVA, Germany
Andreas Rigling, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, Switzerland
Lucie Vítková (coordinator), European Forest Institute (EFI), Central European Office EFICENT, Germany
Jan Wunder, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, Switzerland

Reviewers

Annemarie Bastrup-Birk, European Environmental Agency (EEA), Denmark
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Petr Pyšek, Institute of Botany, The Czech Academy of Sciences and Charles University, Czech Republic
Patrick Pyttel, University of Freiburg, Germany
Albert Reif, University of Freiburg, Germany
David M. Richardson, Centre for Invasion Biology, Stellenbosch University, South Africa
Andreas Schuck, European Forest Institute (EFI), Central European Office EFICENT, Germany
Beatrice Senn-Irlet, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, Switzerland
Vincent Upton, Galway Institute of Technology, Ireland
Giorgio Vacchiano, University of Turin, Italy
Kris Vandekerkhove, INBO, Belgium
Andrea Vannini, University of Tuscia, Italy
Brian van Wilgen, Centre for Invasion Biology, Stellenbosch University, South Africa
Pau Vericat, CTFC, Spain
Torsten Vor, University of Göttingen, Germany
Susanne Winter, WWF Germany and University of Applied Sciences for Sustainable Development Eberswalde (HNEE), Germany
Tom Wohlgemuth, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, Switzerland
Jan Wunder, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, Switzerland

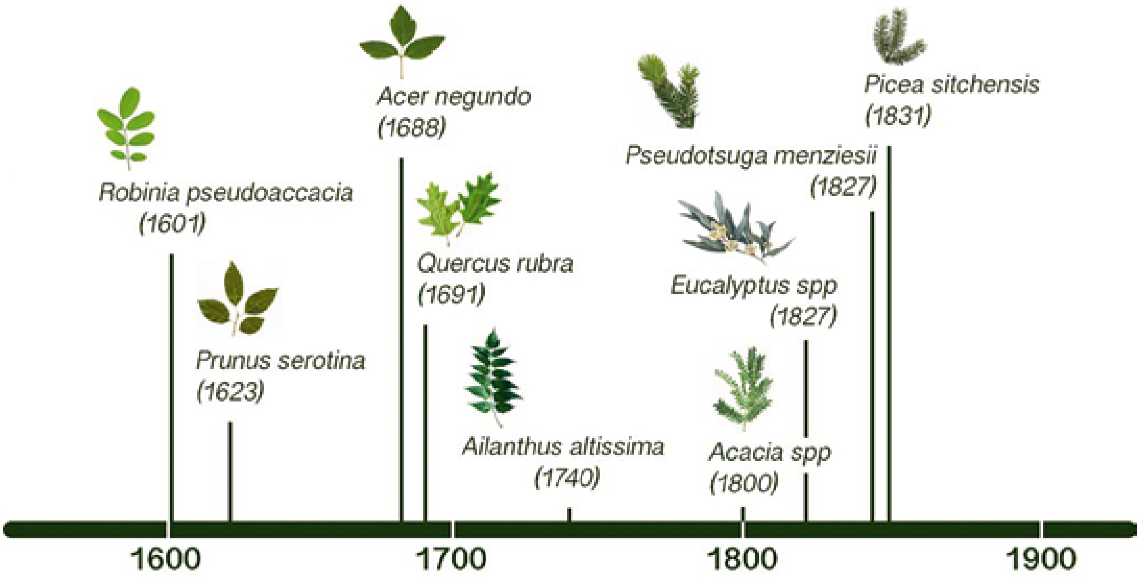

Figure 1: Time line of introductions of some of the important non-native tree species introduced to Europe.

Preface

Invasive species have the potential to seriously threaten biodiversity. They can eliminate native species or endanger them by introducing diseases, and they can even drive populations of rare species to extinction. Therefore the Convention on Biological Diversity commits its Parties to take action against invasive alien species; on 1 January 2015 the EU Regulation on invasive alien species entered into force and national legislation also contains provisions against invasive alien species.

We all know examples of invasive species in flora and fauna. It is, however, not always clear whether a species introduced from another continent should be classified as invasive and is a real threat to indigenous flora and fauna. Furthermore, economic, social and cultural aspects need to be considered as well. Many crops do not originate from Europe. Yet are they "invasive"? Cultivated apple trees (*Malus domestica*) are a threat to our native wild apple trees (*Malus sylvestris*) due to genetic introgression. Yet nobody will seriously ask for cultivated apple trees to be banned for this reason. On the contrary: the many varieties of *Malus domesticus* not only contribute to our healthy diets; they have also become part of our natural and cultural heritage; they are themselves worthy of protection, and conservation programmes are carried out for this purpose. We have become accustomed to some tree and shrub species that have been introduced; they have become an integral part of our cultivated landscape.

As far back as Roman times, tree species were transferred within Europe to regions where they did not naturally occur. For instance, we owe the presence of chestnuts (*Castanea sativa*) in wine-growing areas north of the Alps to the Romans. "Exotic" tree species have been added to many tree plantations and parks over the last few centuries to make them a more attractive and enhance them as recreational areas. The European forestry sector has been integrating tree species from outside Europe into its forest management system for more than two hundred years. This has been mostly successful, but some attempts failed. *Pinus strobus*, for example, turned out to be too susceptible to infection with *Cronartium ribicola*. The American black cherry (*Prunus serotina*), introduced with the best of intentions to areas almost exclusively dominated by pine trees, has spread widely and in many areas has now formed an impenetrable undergrowth. Foresters and forest owners spend a lot of money on combatting it to successfully re-introduce native broadleaved trees.

Foresters are now hoping that some tree species introduced from other areas will cope better with the challenges of climate change than our native spruce (*Picea abies*) and will safeguard forest productivity.

But all of a sudden the presence of these alien tree species is being questioned: aren't they invasive? Do they harm biodiversity? A publication by the Federal Agency for Nature Conservation (BfN), which classified some alien tree species as "invasive", created a stir in Germany and beyond, at least in our German-speaking neighbouring countries. The German Association of Forest Research Institutes (DVFF) joined leading German and Swiss forest scientists in arguing against this BfN publication by publishing their own paper. Since then, the debate between nature conservationists and the forestry sector has continued unabated.

Against this backdrop, the Federal Ministry of Food and Agriculture (BMEL) funded this study by the European Forest Institute (EFI). As an institute operating at European level, I believe the EFI is perfectly suited to contribute independent research findings to what is sometimes a very emotional debate. The study now offers a comprehensive description of current knowledge, not only on invasive species, but also on the broader issue of introducing species into a new environment. The present book provides a broad range of recent scientific findings and assessments, by both nature conservationists and foresters, and it includes economic and social aspects. It is rounded off by contributions and case studies from other continents, allowing us to learn from others. We hope that this very accomplished work will help place the debate on a more objective footing and develop good solutions for policy makers.

Dr Axel Heider
Deputy Director General Directorate Forestry
Federal Ministry of Food and Agriculture

Introduction

Lucie Vítková and Frank Krumm

Introductions of species outside of their natural range have occurred for as long as humans migrated and explored new areas. The first deliberate introductions may be considered as those taking place in Mesolithic time by hunter-gatherers (ca. 10 000–5 000 BC). However, the discovery of the Americas and the consequent colonial era and the global exploration are generally thought of as the onset of greater introduction efforts in modern history (e.g. Preston et al. 2004).

Although the introduction of tree species was relatively low until the 19th century, demographic changes and modern agriculture resulted in substantial changes to most ecosystems. The era of industrial revolution led to a considerable increase in global trade as new means of transport and novel technologies were developed. This era also resulted in some irreversible changes to our environment, similarly as to numerous (deliberate as well as accidental) introductions of species outside of their natural ranges. Nonetheless, there has been a radical increase in biological introductions worldwide over the last few decades, mainly as a result of the increase in trade, changes in geographical ranges due to climate change and expanding propagule pressure (Hulme 2009) with the concept of species introductions starting to be considered as a part of global change by some.

Some introduced tree species became significant contributors to some countries' forestry sectors while others turned out to be problematic. This is mainly since some of the ecological characteristics of certain species developed pressure on some of the native ecosystems spreading rather extensively. Such introduced tree species are therefore referred to as *invasive* tree species; i.e. those species whose introduction, and consequent spread, have caused socio-cultural, economic and/or environmental harm disrupting some of the key functions of forest ecosystems. However, it is important to note that invasive tree species were used to define some of the modern concepts of ecology and evolution that were presented by e.g. Charles Darwin (1859) who discussed the revolutionary idea of evolution and natural selection driven by competition or by Eugen Warming (1895) who considered abiotic factors when shaping the idea of ecological niche. Such ideas subsequently had an impact on important developments with regards to ecology addressed by e.g. Arthur Tansley, Frederic Clements or Henry Cowles, to mention a few, with Charles Elton (1958) dealing specifically with the ecology of invasions by both plants and animals.

The amount of literature produced on the topic of invasiveness is vast and has been increasing over the last 20 years or so (Figure 2). However, there is still a lack of long-term empirical data on the ecology and evolution of invasive species of trees in particular. Although this is not considered as novel information, it is striking to see how much research has been done, and yet, how little has been considered on policy level considering the importance of the topic involving numerous stakeholders. The topic of invasion ecology has developed rapidly (e.g. Williamson 1996, Pyšek et al. 2004), which has simultaneously created confusion in terminology with regards to invasion process and this fact has been recognised by e.g. Pyšek et al. (2004), Hulme et al. (2013) or Jeschke et al. (2014). Richardson et al. (2000) and Blackburn et al. (2011) proposed graphic schemes conceptualising the introduction process leading to invasion that helps visualise this process, which includes key aspects such as management actions and barriers to this development (Figure 3).

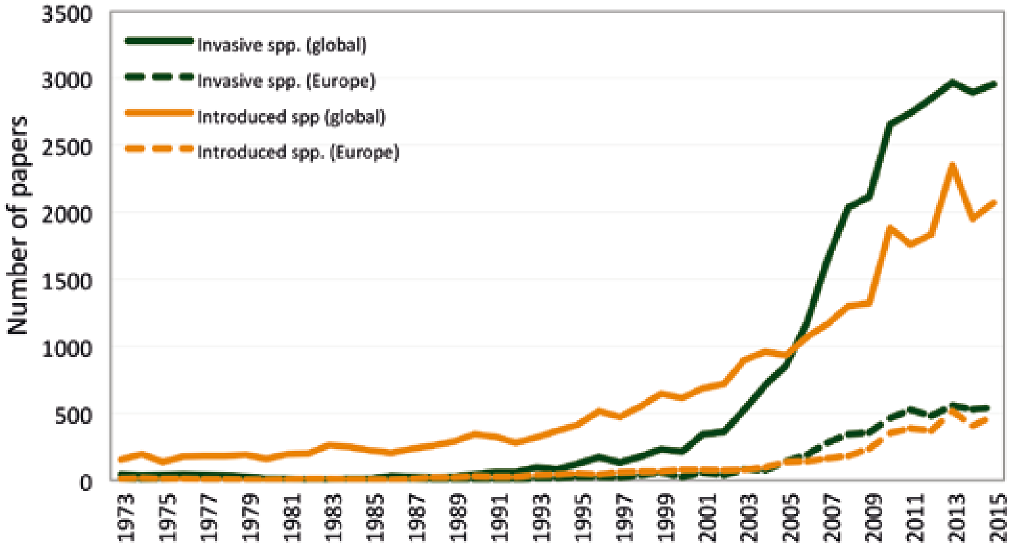

Figure 2. The number of scientific papers on introduced and invasive tree species published since 1973 on both European and global levels (including European papers) is shown. The literature search was conducted on 13th October 2016 using the CAB Abstracts database (records for scientific papers abstracted by CAB International since 1973). The search strategy used combined the CABI subject headings 'invasive species' OR 'invasive alien species' OR 'invasion' OR 'invasions'. Terms related to 'invasive species' were also selected from the CAB Thesaurus – 'invasive species', 'invasive organisms', 'invasive alien species'; combining the initial search with these index terms resulted in a total of 30 537 scientific papers.

Terms and definitions on the topic of introduced and invasive species are often used in contradictory form and often leading to misunderstanding.

The topic of introduced and invasive tree species is rather broad and complex and involves many concepts that need to be defined. Various definitions of terms available are often interpreted in different ways. For the sake of clarity, bearing in mind the same (or at least similar) sense of a particular term, Table 1 presents some of the key terms that are frequently used throughout this book along with their definitions that were agreed on with the drafting committee and the authors of the various chapters of this publication.

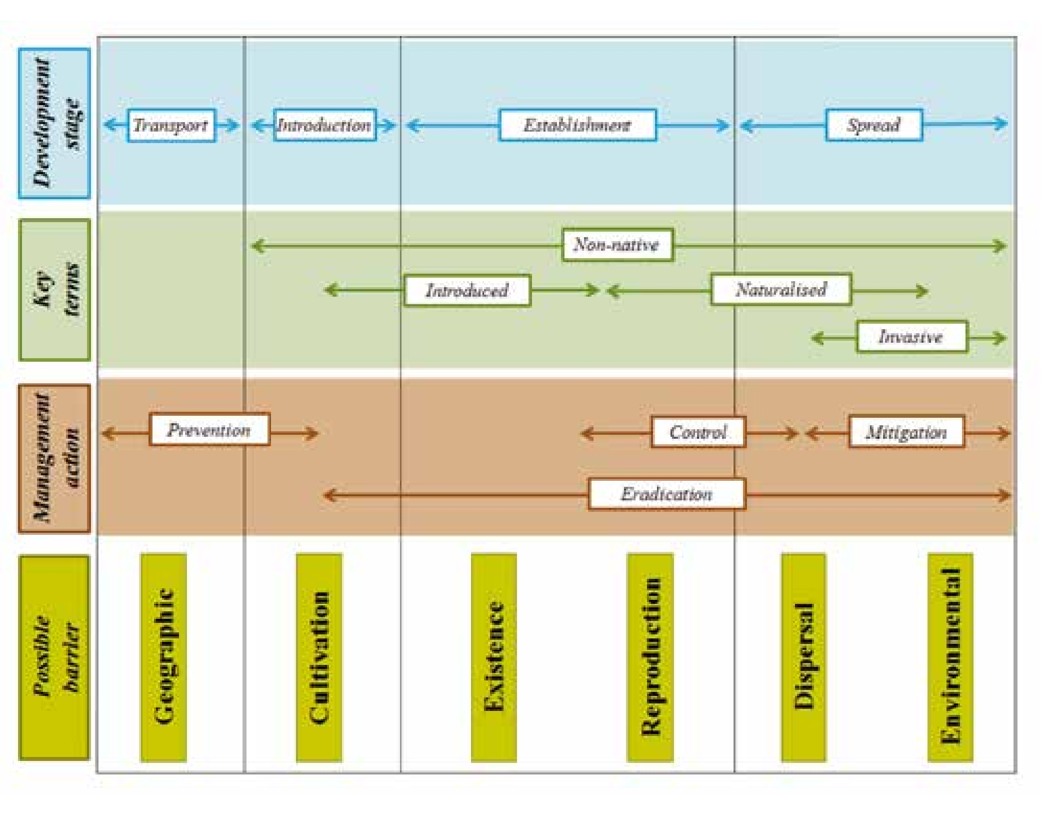

Figure 3. The process of species introductions where the distinctive developmental stages are shown; the key terms relating to introduced tree species along with the management actions and the major barriers limiting the spread of introduced tree species are also presented (adapted from Blackburn et al. 2011).

Table 1. Key terms and their definitions.

Term	Definition	Source
Introduction	A process (or an action) that enables a species (or its propagule) to overcome, through a human agency, a major geographical barrier.	Amended from Richardson et al. (2000)
Introduced species (non-native, alien, non-indigenous, exotic)	A species in a given area whose presence there is due to intentional or accidental introduction as a result of human activity.	Gassmann and Weber (2006)
Invasion	A process whereby a species must overcome a series of barriers to be able to spread into novel areas in which it becomes dominant.	Amended from Valéry et al. (2008)
Invasive species	A species that has overcome a series of barriers to be able to spread into novel areas in which it becomes dominant.	
Naturalisation	Process whereby the species establishes new self-perpetuating populations, undergoes widespread dispersal and becomes incorporated within the resident flora.	Richardson et al. (2000)
Native species	Species that have evolved in a given area or that arrived there by natural means without the intentional or accidental intervention of humans from an area where they are (or had been) native.	Amended from Pyšek et al. (2004)
Invasiveness	The features of an organism (e.g. life history traits and modes of reproduction) that define their capacity to overcome various barriers to invasion.	Amended from Richardson et al. (2011)
Invasibility	The properties of a community, habitat or ecosystem that determine its inherent vulnerability to invasion.	Lonsdale (1999)

> *The discussion on biological invasions and forestry has been often dominated by prejudice and emotions.*

The reasons for tree species introductions are described in some of the chapters in this book along with the underlying processes leading to particular species becoming invasive. There are two distinct types of tree introductions: (i) *accidental* (e.g. escapes from gardens, by-product of trade etc.); and (ii) *intentional* (done for a specific deliberate purpose). Although both introduction types are relevant to forestry, intentional introductions may be considered of particular importance. Setting aside introduction of individual trees for ornamental purposes, planting introduced tree species for forestry purposes have resulted in large areas being planted with high numbers of trees; this translates into a high propagule pressure, which has been recognised as a major factor in a tree species becoming invasive (e.g. Lonsdale 1999, Chytrý et al. 2005).

Deliberate efforts to match environmental conditions of the introduced range with conditions in the native range of a species (or provenance) resulted in situations that have led to invasions by some species (e.g. Lambdon et al. 2008, Pyšek et al. 2009, Křivánek et al. 2006, Richardson 2011). It is therefore no surprise that the combination of intensive forest plantation management (large scale, high density, re-establishing populations), high propagule pressure and species traits has made forestry an efficient pathway for invasion (e.g. Křivánek et al. 2006, Pyšek et al. 2009, Wilson et al. 2009, Essl et al. 2010). However, we must also consider that the introductions used in plantation forestry have contributed substantially towards providing jobs and income in rural areas that would otherwise be rather scarce in such areas in some countries.

The growing need for timber supply for various purposes, the necessity to produce biomass for energy, and the obligation to retain carbon in forests to mitigate climate change, etc. have led to inevitable expansion of forests comprising, entirely or partially, of introduced tree species. Climatic change is influencing our ecosystems and there is a need to be better prepared for further changes as well as to increase the resilience of forests. In order to fulfil the increasing demand for multiple services from forests, it is important to consider the various demands on a large scale. This is clearly a policy task and there are efforts to tackle the various challenges in distinct initiatives. For example, the Convention on Biological Diversity (CBD) states in the Article 8h, that each party to the convention shall as far as possible "prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species." Target no. 9 of the Aichi Biodiversity Targets (CBD 2010) mentions that "By 2020, invasive alien species and pathways are identified and prioritised, priority species are controlled or eradicated, and measures are in place to manage pathways to prevent their introduction and establishment." In 2004, the Council of Europe published a strategy on how to deal with invasive species, based on the work of the Bern Convention which was started in 2003 (Genovesi and Shine 2004). The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) further forms the basis for the convention on import restrictions with an ecological danger on native species. In 2016, the European Commission published the first list on Invasive Alien Species, which was a result of the convention on the management and prevention of invasive alien species (EC 2016).

About this book

The major aim of this book is to create a compilation of chapters highlighting some of the major aspects of the topic of introduced tree species within a European context. There has been a request for such a publication on this topic as the discussions on introduced species are often not objective and are often driven by emotions. The presented findings are based on sound scientific studies as well as on reliable examples from practice. It is also important to state that the development of invasion biology is rapid and certain processes have already reached a 'point of no return', which triggered the necessity to develop adaptive management approaches to satisfy the multiple functions that society requests from forests.

The chapters included in this book do not exhaustively cover the topic of introduced and invasive tree species across the European continent as it is a very complex topic including multiple themes and subjects. However, we aim to present a selection of issues of current importance, as well as to provide an overview on available knowledge that can be applied or adapted elsewhere. In order to ensure a concise volume of the book, individual chapters are brief focusing only on the major features of the topic they cover. In addition, the book contains Boxes that are short inserts focusing on specific issues that provide supplementary information on particular topics.

The readers should keep in mind that there is a considerable variation in the professional background of different authors – some are forestry practitioners actively engaged in forest management, while others are researchers, others are civil servants, and others work for non-governmental agencies focusing on natural sciences. The variety of expertise amongst the authors ranges from nature conservation to forestry, but authors from social sciences and invasion ecology have also contributed.

Last, but definitely not least; the book is aimed at readers from a variety of backgrounds. The chapters within this book were written in a style that is accessible to lay persons with an interest in nature, but also that the chapters are interesting, bringing new insights for those with a professional interest in the subject.

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Figure 4: Two Lebanon cedars in the Physic Garden by John Fuge (copyright Royal Borough of Kensington and Chelsea)

1 History of introduced and invasive tree species

The introduction of tree species has a long history and especially throughout Europe, activities on the introduction of species for various purposes have started a long time ago. Chapter 1.1 provides a background on natural shifts and movements of species in pre-human times, and on the human influences during early human history. Chapter 1.2 focuses at the deliberate introductions of tree species by humans across Europe.

1.1. European tree dynamics and invasions during the Quaternary
H. John B. Birks and Willy Tinner

1.2. History of introduced tree species in Europe in a nutshell
Bart Nyssen, Uwe Eduard Schmidt, Bart Muys, Pieter Bas van der Lei and Patrick Pyttel

1.1 European tree dynamics and invasions during the Quaternary[1]

H. John B. Birks and Willy Tinner

Introduction

The abundance and distribution of terrestrial organisms vary in space and time over a wide range of scales from a single 25x25 m plot to whole continents and from days to millennia. Trees are no exception but the relevant temporal and spatial scales are naturally different from those for a small annual forest herb because of the long life-span and large size of trees.

European trees have varied in their abundance and geographical distribution over the last 5 million years or more in response to major global climate changes (Birks and Tinner 2016). They have also undergone similarly striking changes due to the alternating glacial–interglacial cycles within the Quaternary period (last 2.6 million years). Tree dynamics have also been greatly modified in the last 5 000–6 000 years by human activities in the current Holocene epoch (plus the 'Anthropocene') in which we live. Documenting and understanding these dynamics and changes provide us with ecological 'lessons from the past' about tree dynamics (including invasions) and responses to environmental changes in the past (Birks and Tinner 2016).

The problem with studying tree dynamics is that many trees are long-lived and their life-spans greatly exceed those of ecologists, foresters, and woodland historians. As we cannot directly record tree dynamics in space and time at the relevant scales, we need to reconstruct past tree dynamics indirectly using the palaeobotanical record.

Box 1. Reconstructing past tree dynamics and invasions

Palaeobotany involves the study of seeds, fruits, leaves, wood, and charcoal ('macrofossils') (Birks 2013) and of microscopic pollen grains, spores, cells (e.g. stomata), and charred particles (microfossils) deposited in lake, bog, alluvial, and other sediments or ice where organic material is preserved (Birks and Birks 1980). Other emerging and rapidly developing approaches such as ancient DNA, phylogeography, and back-cast dynamic vegetation modelling (Henne et al. 2015) have the potential to enhance greatly our studies of past tree dynamics.

Methodological considerations

Pollen analysis as a tool for the reconstruction of past forests and changing tree abundances in space and time was invented 100 years ago in 1916 by the Swedish geologist Lennart

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[1] Parts of this review are reproduced from Birks and Tinner (2016) in the recently published European Atlas of Forest Tree Species

Figure 5. Lennart von Post (1884–1951), the Swedish Quaternary geologist who was the main inventor of pollen analysis in the early 20th century and demonstrated the power of pollen analysis as a tool in reconstructing forest and climate history.

von Post (Figure 5). It is still the dominant technique for studying tree and vegetation dynamics at decadal to centennial scales in the Quaternary, especially the last 15 000 years of the late-Quaternary. Von Post had the brilliant idea of expressing fossil pollen assemblages in a single sample of peat as percentages of the sum of pollen grains counted, and of presenting these percentages as stratigraphical pollen diagrams with pollen assemblages plotted against their stratigraphical position (depth or age) through the sediment sequence (Figure 6). He showed strong similarities in pollen diagrams from a small area, and striking differences between different areas. He was thus able to provide the fourth dimension of time to the study of tree dynamics and vegetation and forest history.

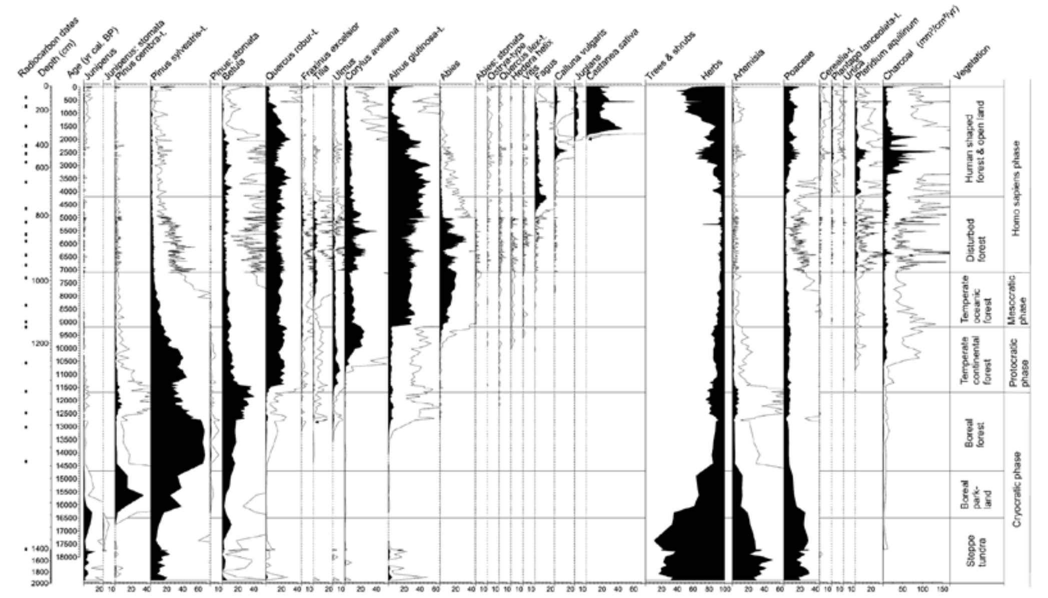

Figure 6. Summary pollen diagram from Lago di Origlio, a small lake in Ticino, southern Switzerland covering the last 19 000–18 000 years (only selected taxa shown). The vegetation history of this site is representative for northern Italy (including the northern Apennines) with exception of the Po-Plain lowlands. The horizontal lines represent partitions of the pollen stratigraphy into main pollen-assemblage zones, which reflect different vegetation types. The phases of the glacial-interglacial cycle (see Box 3) and the *Homo sapiens* phase are also indicated. The vertical axes are depth of sediment (0 cm = water-sediment interface) and age is in calibrated years before present (cal. BP). The chronology is based on 25 radiocarbon dates which were calibrated with the program calib 7.1. The taxa are ordered according to their temporal expansion. The local presence of conifers can be inferred from stomata, a proxy for macrofossils (e.g. for *Juniperus* at ca. 17 800 cal. BP, *Pinus* at ca. 16 000 cal. BP). Macrofossil and pollen evidence (see Figure 7) can be used to infer the first establishment of populations, e.g. for *Tilia* and *Castanea* sativa at the 'empirical pollen limit' (see arrows in diagram). All the pollen and spore types are expressed as percentages of the total number of terrestrial pollen counted (generally >600 per sample, spores and aquatic pollen excluded), the microscopic charcoal influx is a proxy for fire activity, mainly regional fire frequency.

The results of a pollen analysis of a site are most commonly presented as a pollen diagram, showing how the relative percentages of different pollen types change with depth, and hence age, in the sedimentary sequence (Figure 6). Besides calculating relative percentages that have the limitation that if pollen type A increases then other types will decrease as a result of the constraints of 'closed' data, it is now possible at some sites to estimate pollen-accumulation rates (PARs) or 'influx' (grains cm–^{2} yr–^{1}), so-called absolute pollen frequencies. PARs are not susceptible to the closure problem and they can, in many instances, be viewed as a long-term record of past tree populations within the site's pollen-source area (generally within a 5–10 km radius).

Limitations of PARs are that their estimation requires very accurate chronologies such as those provided by annually laminated (varved) sediments (which are very rarely found), and that they can be influenced by various processes occurring during sedimentation such as resuspension and focusing (which are not uncommon) that can introduce 'noise' into the PAR signal (Birks and Birks 1980).

Box 2. Basic principles of pollen analysis

There are ten basic principles of pollen analysis (Birks and Birks 1980, Lang 1994, Birks and Tinner 2016).

1. Pollen grains and spores are produced in great abundance by plants
2. A minute fraction of these fulfil their natural reproductive function of transferring the male gamete to the female ovary: the vast majority fall to the ground
3. Pollen and spores decay more or less rapidly, unless the processes of biological decomposition are inhibited by a lack of oxygen, such as in bogs, lakes, the ocean floor and ice where pollen is preserved
4. Before reaching the ground, pollen is well mixed by atmospheric turbulence, which results in a more or less uniform pollen rain within an area of similar vegetation and landform
5. The proportion of each pollen type depends on the number of parent plants and their pollen productivity and dispersal. Hence the pollen rain is a complex function of the composition of the vegetation. A sample of the pollen rain is thus an indirect record of the regional vegetation at that point in space and time
6. Different pollen grains and spores can be identified to various taxonomic levels (e.g. species, genus, family)
7. In vegetated areas pollen is ubiquitous in lake and bog sediments. Very high concentrations (usually around 100 000 cm–^{3}) in lake sediments permit efficient analyses and statistically robust results (standard pollen counts are usually ca. 500–1 000 grains per sample).
8. If a sample of the pollen rain is examined from a peat or lake-mud sample of known age (dated by annual layers or radiometric dating), the pollen assemblage is an indirect record of the regional and local vegetation surrounding the sampled site at that point of time in the past

9. If pollen assemblages are obtained from several levels through a sediment sequence, they provide a record, admittedly an indirect record, of the regional and local vegetation and their development near the sampled site at various times through the time interval represented by the sedimentary record (Figure 6)

10. If two or more series of pollen assemblage are obtained from several sites, it is possible to study changes in past pollen assemblages and in geographical distributions, and hence in the regional and local vegetation through both time and space (Figure 7)

When many pollen sequences have been studied and dated (e.g. by radiocarbon dating), their pollen data can be mapped for a particular time interval (e.g. 5 000 years ago) to produce a so-called ‘isopollen’ map for particular pollen types where the contours represent different pollen values (e.g. 2.5 %, 5 %) (Figure 7) (Huntley and Birks 1983). Such maps provide a snap-shot view of spatial variation in the pollen values at one point in time, one aspect of past tree dynamics. Alternatively, when interest is centred on the spatial dynamics and the directions and rates of spatial spread, so-called ‘isochrone’ maps can be constructed where the contours represent ages established by radiocarbon dating (e.g. 5 000, 6 000 years ago). When the value of a particular pollen type exceeds a certain threshold value, that point can be interpreted as reflecting the first expansion at different sites (Figures 8 and 9) (Birks 1989). The first arrival of a taxon is much more difficult to determine, because the absence of pollen may not reflect a true absence of the taxon in the landscape, the so-called ‘false absence’ problem (Birks 2014). The study of plant macrofossils such as bud-scales or conifer needles in conjunction with pollen (Figure 9) can help pinpoint when a taxon appeared locally near the study site (Lang 1994).

Pollen stratigraphical data when expressed as PARs can be viewed as palaeo-population records to which specific population growth models can be fitted for the time intervals (generally 250–1 000 years) of presumed tree arrival and subsequent population expansion to asymptotic pollen (and assumed tree population) values (Watts 1973). Bennett (1983, 1986) developed this approach in Europe and fitted exponential and logistic population models to several British pollen-stratigraphical data (Bennett 1983). From r, the intrinsic rate of population growth per unit of time, estimated from the gradient in a regression of loge PAR against age, doubling times can be estimated for each taxon (Table 2). These pollen-based doubling times compare well with published doubling times estimated from population increases in present-day forests (Bennett 1986) with doubling times ranging from 8–350 years. These palaeo-based and modern estimates were confirmed by back-cast dynamic vegetation modelling (e.g. Lotter and Kienast 1992, Heiri et al. 2006, Wick and Möhl 2006, Henne et al. 2011, Schwörer et al. 2015) and suggest that tree populations generally double on timescales of tens to thousands of years, mostly hundreds of years (Bennett 1986, MacDonald 1993).

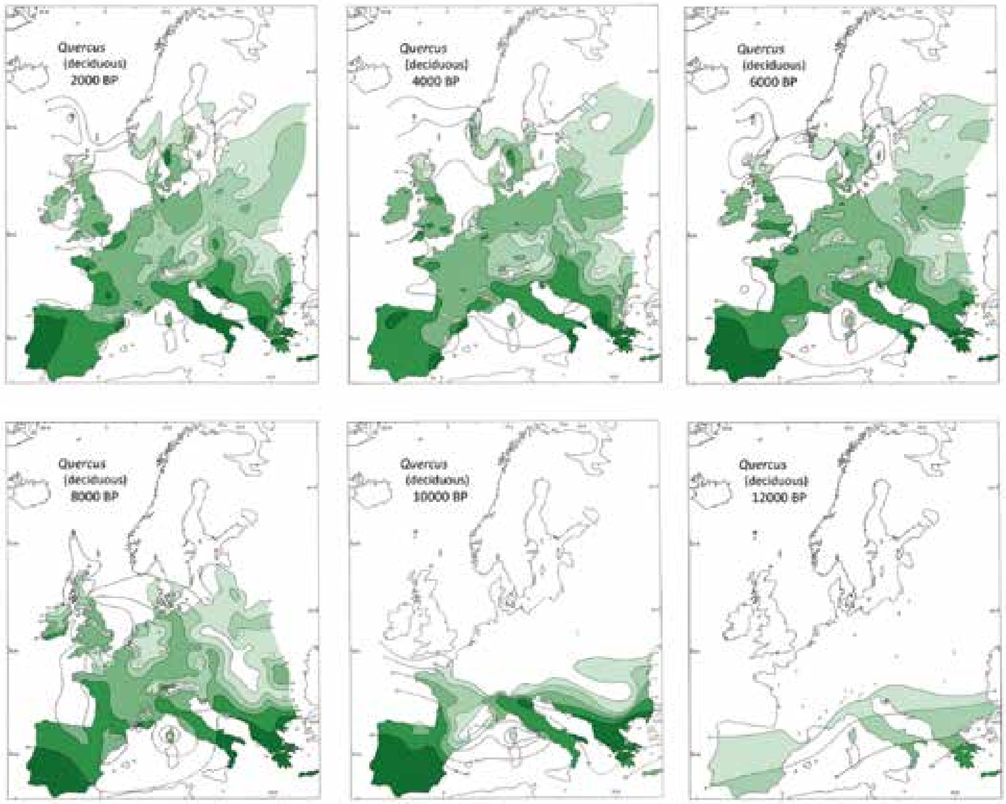

Figure 7. Isopollen maps of *Quercus* oak pollen percentages across Europe for 12 000, 10 000, 8 000, 6 000, 4 000, and 2 000 radiocarbon years before present (BP). Such maps summarise the spatial dynamics of *Quercus* population history in the last 12 000 years and its changing abundance patterns in space and time. Modified from Huntley and Birks (1983) and from Birks and Tinner (2016).

Interpretation of pollen-stratigraphical data in a qualitative manner such as past vegetation, flora, and landscape structure is relatively straightforward (Birks and Birks 1980). More quantitative interpretation of such data in terms of quantitative estimates of past population sizes and taxon abundances is much less straightforward because of differential production and dispersal, and hence differential representation of different pollen types. Approaches for the quantitative reconstruction of plant abundances (population sizes) and of past environment (e.g. regional climate) are currently areas of active research within Europe and elsewhere (e.g. Sugita 2007, Gaillard et al. 2008, Hellman et al. 2008, Birks et al. 2010, Theuerkauf et al. 2012, Salonen et al. 2013).

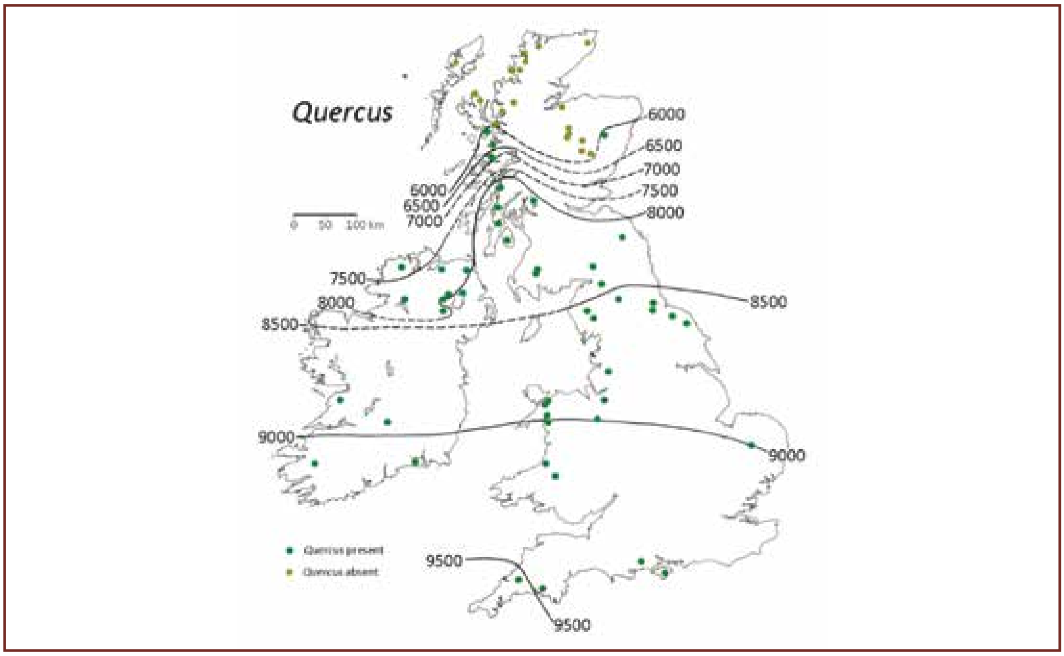

Figure 8. Isochrone map for deciduous *Quercus* (oak) in Britain and Ireland. It shows the progressive rate of spread and/or population expansion from the south-west at 9 500 radiocarbon years before present (BP) through England and southern and central Ireland to 8 500 BP and its declining rate of spread and/or expansions when it spreads north into Scotland from 8 000 to 6 000 BP. Such maps summarise the changing rates, patterns of spread, spatial dynamics, and the occurrence of *Quercus*. Modified from Birks (1986)and from Birks and Tinner (2016)

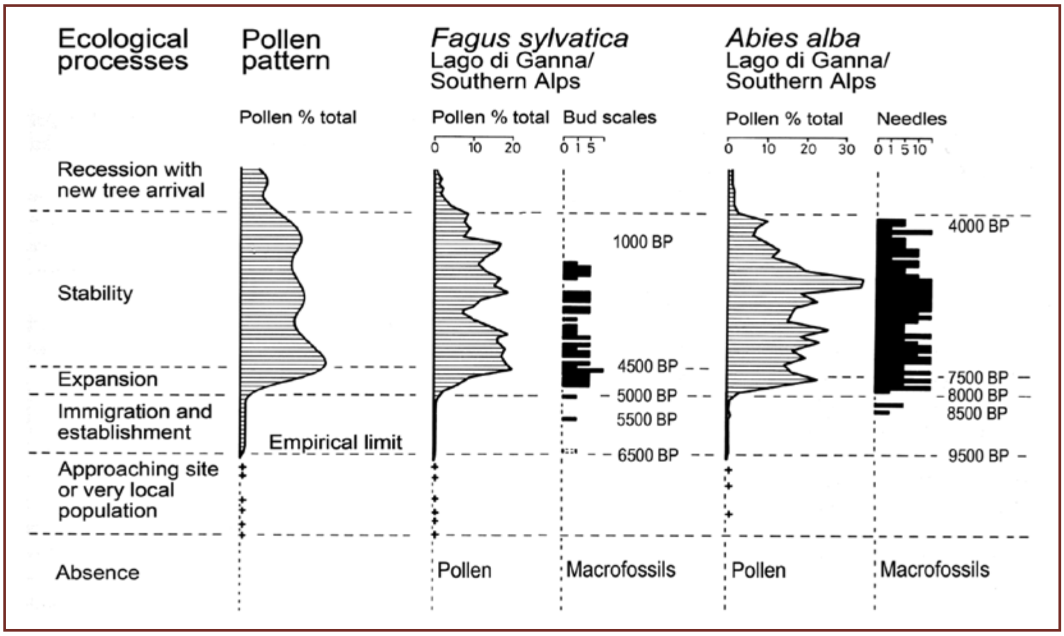

Figure 9. Biostratigraphical patterns in pollen and macrofossil records and inferred ecological processes. The phases, processes, and schematic pollen sequence follow Watts (1973) and Birks (1986), and the curves of *Fagus sylvatica* and *Abies alba* follow Schneider and Tobolski (1985). BP = uncalibrated radiocarbon ages before present. Modified from Lang (1994).

Table 2. Rates of increase of tree populations estimated from pollen-stratigraphical data expressed as doubling times based on several sites in south-east England (from Bennett 1986).

Taxon	Doubling time in radiocarbon years
Betula spp. (birches)	60
Pinus sylvestris L. (Scots pine)	75
Corylus avellana L. (hazel)	45
Ulmus spp. (elm)	30–70
Quercus spp. (oaks)	80–140
Tilia cordata Mill. (lime)	100
Alnus glutinosa (L.) Gaertn. (alder)	175–270

What were European forests like prior to the Quaternary period with its multiple glacial stages, often with ice-sheets, and intervening temperate interglacial stages beginning about 2.6 million years ago?

Palaeogene and Neogene forests

Knowledge of the flora and forest vegetation of the Palaeogene (66–23 million years ago) and Neogene (23–2.6 million years ago) is very fragmentary due to a shortage of fossiliferous sedimentary sequences in much of Europe (Mai 1995). Following the sub-tropical Palaeocene, Eocene, Oligocene, and Miocene epochs (66–5.3 million years ago) when plants found today in the tropical lowlands of the Indo-Malaya region initially co-occurred with temperate elements in north-west Europe (Willis and McElwain 2014), the European tree flora of the Pliocene epoch (5.3–2.6 million years ago) contained genera characteristic of modern European forests (e.g. *Quercus* oak, *Carpinus* hornbeam, *Fagus* beech, *Pinus* pine, *Picea* spruce, *Abies* fir) and genera growing today only in eastern Asia and/or eastern North American (e.g. *Pterocarya* wing-nut, *Liriodendron* tulip-tree, *Tsuga* hemlock, *Liquidambar* sweetgum, *Nyssa* blackgum, *Sequoia* redwood, *Taxodium* cypress, *Magnolia* magnolia, *Carya* hickory, *Clethra* pepper-bush, *Aesculus* horse chestnut) (van der Hammen et al. 1971, Willis and McElwain 2014). These trees belong to the so-called Arcto-Tertiary geoflora that in the Neogene occurred widely across North America, Europe, and Asia.

Late Pliocene and Quaternary forest shifts and tree extinctions

The Quaternary period (last 2.6 million years) witnessed very marked and widespread climatic and environmental changes (Birks and Willis 2008, Birks and Tinner 2016).

Temperatures were higher than today during the Palaeocene, Eocene, and Miocene epochs (Zachos et al. 2001) but they markedly declined during the Pliocene and early Pleistocene to reach today's or cooler levels. Large terrestrial ice-sheets started to form in the Northern Hemisphere about 2.75 million years ago, resulting in multiple (at least 50) glacial–interglacial cycles driven by secular variations in insolation as a result of periodic fluctuations in Earth's orbit around the sun. Glacial-stage conditions account for 80 % of the Quaternary (Pleistocene 2 600 000–11 700 years ago, Holocene and 'Anthropocene', past 11 700 years), whereas the remaining 20 % consist of shorter interglacial stages during which conditions were similar to, or slightly warmer than, the present day (Birks and Willis 2008). During the glacial stages, environmental conditions were very different from the present interglacial (Holocene epoch plus the recent 'Anthropocene') in which we live today. Much of the region north of 40°N was covered by large terrestrial ice-sheets and widespread permafrost with temperatures possibly 10–25°C lower than present. High aridity and temperatures 2–5°C lower than today were features of low-latitude areas. Global atmospheric CO_2 concentrations were as low as 180 ppm during glacial stages, rising to pre-industrial level of 280 ppm in interglacial stages. These high variations in environment were accompanied by the loss of the Arcto-Tertiary geoflora from Europe during the late Pliocene and the Quaternary.

The restriction today of these taxa to two almost opposite areas of the globe (eastern Asia and eastern North America) is explained by the hypothesis presented by Asa Gray (1810–88). Cool phases within the late Pliocene epoch and the subsequent Quaternary continental glaciations, combined with the west-east chains of mountains (e.g. Pyrenees, Alps, Carpathians, Caucasus mountains) and the Mediterranean Sea provided barriers to the southward retreat of much of the Arcto-Tertiary geoflora resulting in their progressive extinction in Europe. In contrast, the mountain chains and valleys of south-eastern Asia (e.g. Yunnan) and North America (e.g. Appalachians, Rocky Mountains) run north-west to south-east, north-east to south west or north to south reaching low latitudes without sea barriers, thereby permitting temperate and warm temperate trees to spread southward along unglaciated areas or valley corridors in cold stages and to spread northward during temperate intervals. As a result of the west–east barriers and the many relatively cold stages in the late Pliocene and Quaternary, Europe lost many trees or their close relatives that today are only found native in the warm-temperate-subtropical 'evergreen forests' of south-eastern China or eastern North America (Combourieu-Nebout et al. 2015). These were largely replaced in Europe by trees of the temperate 'mixed mesophytic forest'. Many taxa had already disappeared at the beginning of the Quaternary (e.g. *Liquidambar, Meliosma, Pseudolarix* false larch, *Stewartia*), while others survived longer (e.g. *Liriodendron, Magnolia, Taxodium, Sequoia, Phellodendron* cork tree, *Tsuga, Carya*) to vanish finally from Europe during the course of the early- or mid-Quaternary (Willis and McElwain 2014, Combourieu-Nebout et al. 2015, Birks and Tinner 2016).

Svenning (2003) presents a detailed analysis showing that these late-Pliocene and Quaternary tree extinctions were largely driven by ecological factors. Taxa that are still widespread in Europe are more tolerant of a cold growing season and low winter temperature than the taxa that became extinct in Europe or have relictual distributions today. These relictual taxa appear to be more drought tolerant than the taxa that became extinct in Europe in the late Pliocene or early to mid-Quaternary. Interestingly, some of these European extinct or relictual taxa are spreading today after re-introductions into parts of Europe (e.g. *Morus* mulberry, *Tsuga, Cedrus* cedar, *Aesculus, Rhododendron ponticum*), perhaps re-occupying 'empty niches' vacated earlier in the Quaternary.

Given the extreme conditions in the glacial stages, an obvious question (Birks and Willis 2008, Birks and Tinner 2016) is how did European forest trees survive these repeated long glacial-stage conditions and where did they grow in the glacial stages?

The evidence we currently have (Birks and Tinner 2016) suggests that many European trees survived the last glacial maximum (LGM) in relatively narrow refugial elevational belts (ca. 500–800 m) in the mountains of southern Europe (including the Caucasus) and possibly in parts of western Asia (van der Hammen et al. 1971, Bennett et al. 1991). These macrorefugial belts lay between lowland xeric steppe-like vegetation too dry for tree growth and high-elevation tundra-like vegetation, or permanent snow or ice, too cold for tree growth (Birks 2015). Such mid-elevation belts of trees can be seen today in the Andes, American Rockies, the Californian Sierra Nevada, the Pamir, parts of the Sino-Himalayan region, and the Tien Shan in Kazakhstan (Birks and Willis 2008). Trees may also have occurred scattered in locally moist sites (water seepages, ravines), so-called 'cryptic' or 'microrefugia' in Europe during the LGM as they do today on the Tibetan Plateau in Sichuan and Qinghai, in the Zagros mountains of Iran, parts of south-east Turkey, Tajikistan, Uzbekistan, and Kazakhstan (Birks and Willis 2008). There is increasing evidence from macrofossils and macroscopic charcoal remains in central, eastern, and north-eastern Europe that conifer trees such as *Pinus, Picea*, *and Larix* larch may have grown locally in such microrefugia during the LGM, along with *Betula* birch*, Salix* willow*, and possibly Alnus* alder*, Populus* aspen*, and Ulmus* elm, as far north as the north-eastern edge of the great Fennoscandian ice-sheet in Russia at 60°N (Birks and Willis 2008, Birks 2015, but see Tzedakis et al. 2013 for a contrasting view). Recent records of macroscopic charcoal of *Quercus, Fagus, and Pinus* from the late-glacial in the Harz Mountains (51°N) (Robin et al. 2016) suggest that microrefugia may have been commoner than originally thought or that tree spreading and expansion rates from southern European refugia were faster than originally thought. Much remains to be discovered about tree distributions in Europe during the LGM (Birks 2015).

The glacial–interglacial cycle

▶ *Are there any similarities in vegetation development in different interglacials?*

Pollen analysis and macrofossil studies show that in north-western and central Europe (Lang 1994) there is a strikingly similar vegetation development from the end of a glacial stage through the ensuing interglacial (about 10 000–15 000 years duration) and into the next glacial stage. Although the species and their relative abundances vary from one interglacial to another, there are such strong ecological similarities between interglacials that the Danish pollen analyst Johannes Iversen (1904–1971) recognised in 1958 (Iversen 1958) an interglacial cycle consisting of four or five ecological phases (Box 3) (Birks 1986, Birks and Birks 2004, Birks and Tinner 2016).

The cryocratic phase represents the cold and dry, often glacial, stage with sparse assemblages of pioneer, arctic-alpine, steppe, and ruderal herbs growing on skeletal mineral soils, frequently disturbed by ground-ice activities. Trees are absent, except in specialised refugia (see above). At the onset of an interglacial (Birks and Tinner 2016), temperature and moisture rise and the protocratic phase begins (Box 3). Base-demanding shade-intolerant herbs, shrubs, and trees (e.g. *Betula, Salix, Populus, Pinus, Juniperus* juniper*, Sorbus aucuparia* rowan) spread into formerly glaciated areas and expand to form a mosaic of grassland, scrub, and open woodland growing on unleached, fertile soils rich in nitrogen and phosphorus and with a low humus content. The mesocratic phase (Box 3) is characterised by the development of temperate deciduous forests of *Quercus, Ulmus, Tilia* lime*, Corylus* hazel*, Fraxinus* ash*, and Alnus* on fertile brown earth soils. Shade-intolerant herbs and shrubs are rare as a result of competition and habitat loss, except in openings caused by fire, wind throw, and, possibly, grazing mega-fauna (Mitchell 2005). The next phase, the oligocratic phase, comprises open conifer-dominated woods (*Pinus, Picea, Abies*), ericaceous heaths, and bog vegetation growing on infertile (low available phosphorus, Birks and Birks 2004) humus-rich podsols and peats. Climatic deterioration (temperature decreases, reduced moisture, etc.) occur in the final telocratic phase and, most especially, at the onset of the next glacial cryocratic phase (Box 3) as forests decline, frost action and cryoturbation destroy the leached infertile acid soils, and herbs expand on the newly exposed mineral soils. These ecological phases within an interglacial are not synchronous between sites because the onset of a phase such as the oligocratic phase may depend on local site features such as bedrock geology, topography, climate, and, for the Holocene, land-use (Birks and Tinner 2016).

The characteristic trees of the main interglacial phases differ in their reproductive and population biology and ecological and competitive tolerances (Iversen 1960, 1973, Birks 1986, Birks and Tinner 2016). Protocratic trees have high reproduction rates, low competitive tolerances, high rates of population increase, and display ‘pioneer’ and ‘exploitation’ traits (Birks 1986). Mesocratic trees have low reproductive rates, high competitive tolerances, medium–low rates of population increase, arbuscular phosphorus-scavenging mycorrhiza (Kuneš et al. 2011), and ‘late-successional’, ‘competitive’, and ‘saturation’ traits (Birks 1986). Oligocratic plus telocratic trees have medium reproductive rates, high competitive tolerances, medium–low rates of population increase, ectomycorrhiza with a phosphorus-mining strategy (Kuneš et al. 2011), and ‘cold-stress tolerant’ and ‘adversity’ traits (Birks 1986).

Within these three broad groups of protocratic, mesocratic, and oligocratic and telocratic plants, the actual floristic and forest composition varies from interglacial to interglacial in north-western and central Europe (Birks 1986). Factors such as location of refugia in the cryocratic phase, rates of spreading, distances over which spread occurred, competition, predation, genotypic variation, and chance as it affects survival, dispersal, establishment, and expansion, may all have contributed to the observed differences in interglacial forest patterns (Birks 1986, Birks and Tinner 2016).

Box 3. Phases in a glacial–interglacial cycle in north-western Europe (modified from Birks and Tinner 2016)

Cryocratic	Glacial stage Sparse assemblages of pioneer, arctic-alpine, steppe, and ruderal plants Skeletal mineral soils
Protocratic	Early-interglacial stage Rich assemblages of herbs, shrubs, and trees (birch, pine, willow) Unleached fertile soils
Mesocratic	Mid-interglacial stage Temperate deciduous forests Fertile brown-earth soils

Oligocratic	Late-interglacial stage Open conifer (spruce, pine), ericaceous heaths, bogs Infertile, humus-rich podsols and peats
Telocratic	Final interglacial stage Like the oligocratic but with deteriorating climate
Homo sapiens (unique to the Holocene and the 'Anthropocene')	Mid-late Holocene (6,000 years ago–present) Forest clearance, agriculture Range of soil types, often fertilised

Similar cycles occurred in southern Europe, yet with substantial differences in comparison to central and north-western Europe (van der Hammen et al. 1971, Combourieu-Nebout et al. 2015, Birks and Tinner 2016). Due to warmer conditions, European tree species persisted locally, although strongly reduced, in the steppe-like environments of the glacial stages (Birks and Willis 2008, Birks 2015). This corresponds to the cryocratic phase in central and northern Europe. At the onset of an interglacial, corresponding to the protocratic phase in central and north-western Europe, temperate taxa (e.g. deciduous *Quercus, Ulmus, Ostrya* hop-hornbeam*, Carpinus*) form open forests together with evergreen broadleaved trees (e.g. *Quercus ilex* holm oak, *Olea europaea* olive) and Mediterranean shrubs (e.g. *Pistacia pistachio*), while boreal and steppe vegetation decline (e.g. *Betula, Juniperus, Artemisia* wormwood*, Chenopodiaceae* goosefoot) (Tzedakis 2007, Tinner et al. 2009, Combourieu-Nebout et al. 2015). In the following phase during the mid-interglacial, corresponding to the mesocratic phase in central and north-western Europe, warm-temperate and Mediterranean conifers (e.g. *Abies, Pinus*) expand into the broad-leaved deciduous and broad-leaved evergreen forests and arboreal cover increases, probably in response to rising moisture availability. Towards the end of an interglacial, corresponding to the oligocratic phase in north-western and central Europe, moisture-loving taxa such as *Fagus, Alnus, and Abies* gradually replace Mediterranean evergreen broad-leaved trees, while broad-leaved deciduous trees remain important (Tzedakis 2007, Allen and Huntley 2009, Combourieu-Nebout et al. 2015). Finally, forest cover declines and steppe-like environments expand during the climatic deterioration at the transition from the interglacial stage to the next glacial stage (temperature decrease, reduced moisture), corresponding to the telocratic phase (Birks and Tinner 2016).

There is an apparent consistency within interglacial forest patterns when viewed at the broad-scale of an entire interglacial cycle of 10 000–15 000 years, whereas within each phase of an interglacial (ca. 5000 years) there is often great variation between interglacials, hence the ability of pollen stratigraphy to differentiate between many (but not all) of the different interglacials (Birks 1986).

The relative order of arrival and expansion of tree taxa in the protocratic phase of an interglacial are broadly consistent from one interglacial to another. In contrast, the order of arrival and expansion of tree taxa in the mesocratic phase is more variable and less predictable (Tzedakis, personal communication). The reasons for this contrast between arrival and expansion patterns in the protocratic and mesocratic phases in different interglacials are unclear. Locations of preceding glacial-stage refugia, propagule dispersal mechanisms, competition from established vegetation, and availability of 'empty niches' may all have been important. The current spread and invasion behaviour by certain 'exotic' taxa (e.g. *Tsuga, Morus, Aesculus, Rhododendron ponticum, Pinus* spp.) highlight the complexity of understanding why some taxa have high invasion abilities whereas other taxa do not. This complexity must have existed in the mesocratic phases of the Holocene and earlier interglacials for taxa such as F*agus, Carpinus betulus, Corylus, Picea, and Abies* that all have very different histories in different interglacials (West 1980, Lang 1994).

The mesocratic phase in the Holocene epoch was greatly modified in Europe about 5 000–6 000 years ago by the onset of forest clearance and cultivation and livestock farming, creating the 'Homo sapiens phase' (Birks 1986, Birks and Tinner 2016).

Human impact in the Holocene

In north-west Europe, there was a steep fall in *Ulmus* pollen values, probably a result of an interaction between prehistoric human activities and a tree pathogen, with elm pollen values halving within 5 years (population halving times are the opposite of population doubling times) at a site in southern England (Peglar and Birks 1993). Similarly, 5 000–6 000 years ago *Abies* disappeared from the Mediterranean and sub-Mediterranean lowlands of the Italian Peninsula, probably in response to excessive Neolithic disturbance by fire and browsing (Tinner et al. 2013, di Pasquale et al. 2014, Birks and Tinner 2016). As for *Ulmus* in England, *Abies* collapses were rapid, with pollen values of *Abies* halving within 13 and 22 years at sites in Italy (Colombaroli et al. 2007) and Italian Switzerland (Tinner et al. 1999), respectively.

In some areas of central and north-west Europe, forest clearance and subsequent dereliction of clearings may have facilitated local colonisation and expansion of new immigrants such as uropean beech, Norway spruce, and possibly European hornbeam (Huntley and Birks 1983, Birks and Tinner 2016). While the establishment of *Fagus sylvatica* during Mesolithic times followed climate change (cooling and a moisture increase) in southern and southern-central Europe (Tinner and Lotter 2001), it is possible that the rapid spread of Fagus across central Europe in the last 4 000–5 000 years (Huntley and Birks 1983) may have only been facilitated by the creation of abundant, large clearings within *Tilia*- or *Quercus*-dominated forests on well-drained soils. In some areas, depending on soil conditions, mixed beech – holly – oak forests developed whereas in other areas there was a rapid change from *Tilia*- or *Quercus*-dominance to *Fagus*-dominance (Birks 1986). These changes commonly occurred after an extensive phase of human activity involving clearance and grazing followed by the abandonment of cleared and cultivated areas (Birks and Tinner 2016). This abandonment may have occurred as a result of local population collapse following, for example, climate change, emigration, or over-exploitation of environmental resources (Bradshaw and Lindbladh 2005).

Other types of secondary woodland (Birks and Tinner 2016) developed in areas beyond the natural geographical range of beech, for example woods of pure European ash, oak spp., English yew, birch spp. or common holly became established on particular soil types following abandonment of cleared or cultivated areas, relaxation in grazing pressure, or reduction in fire frequency (Birks 1986).

The westward, northward, and southward spread and expansion of *Picea abies* through the Baltic countries, Finland, Sweden, and Norway over the last 6 000–7 000 years (Huntley and Birks 1983, Giesecke and Bennett 2004) may have been a contemporaneous response to subtle step-wise climate change, a delayed migration unrelated to simple climate change, a response to forest disturbance creating gaps for colonisation, or a combination of these factors (Giesecke 2004). Whatever its causes, the invasion of *Picea* into northern and central Fennoscandia over the last 6 000–7 000 years resulted in major changes in forest composition and structure and in soil conditions, with widespread accumulation of mor humus, soil leaching, and podsolisation and changes in the natural fire regime within the boreal forest (Lang 1994, Seppä et al. 2009, Ohlson et al. 2011).

In general, disturbance-sensitive taxa such as lime, elm, ash, maple, fir and ivy declined while disturbance-resistant taxa such as oak, hop-hornbeam, hazel, elder, willow, fagus (resprouters) and pine (non-palatable) (re-sprouters), and Picea (non-palatable) expanded (Tinner and Ammann 2005). *Quercus, Fagus, and Picea* were also favoured by humans for their valuable acorns or timber, ultimately forming monospecific forests (Tinner et al. 2013, Schwörer et al. 2015). Continued forest clearances and agriculture, interspersed by periods of abandonment and secondary regeneration, occurred as the result of the development and expansion of more permanent land use practices (e.g. animal husbandry, ploughing, crop cultivation, woodland management) during the late Neolithic, Bronze Age, Iron Age, Roman, Viking, Medieval, and recent times. Forests initially became more open, and wood- and scrub-pasture and hazel coppice expanded. However, increased human interference including regular burning (Tinner et al. 2005) led ultimately to the widespread deforestation of much of Europe and the development of extensive pastures of 'commons', fields, heaths, maquis, and settlements. This process was particularly intense in the lowlands of Mediterranean Europe, where practically no unplanted forest environments survive (e.g. Colombaroli et al. 2007, Tinner et al. 2009). Almost all extensive and naturally forested areas surviving today in Europe have been extensively managed by selective silviculture over many centuries (Figure 7) (Birks 1993, Bradshaw et al. 2015, Birks and Tinner 2016).

Tree spreading and invasions

Isopollen (Figure 5) and isochrones (Figure 6) maps can provide rough estimates of rates of tree spreading or, more likely, of tree population expansion (Huntley and Birks 1983, Birks 1989, MacDonald 1993). These estimates generally lie in the range of 50–100 m yr–1 but they do not take account of the likely existence of microrefugia north and east of the main macrorefugia in Iberia, the Italian Peninsula, and the Balkans (Birks and Willis 2008, Birks 2015). We know very little about the distribution or density of such microrefugia. Preliminary analyses that try to take account of microrefugia (e.g. Feurdean et al. 2013, Cheddadi et al. 2014) suggest that rates of spread may be significantly less than estimates originally proposed for European trees by Huntley and Birks (1983). On the other hand, pollen records may seriously underestimate the point in time when trees actually arrived near a site (Welten 1944, Tinner and Lotter 2006), given that arrival times and hence spreading rates are usually estimated from particular critical thresholds (e.g. so-called empirical limit; the beginning of the third phase on Figure 9). These thresholds may fail to detect the signal of individual trees or even small localised populations within the pollen or macrofossil catchment of a site (the problem of 'false absences' in palaeoecology) (Birks 2014, Birks and Birks 2016). Estimates of tree-spreading rates are critically important in predicting if modern tree populations can track climate change in the future (Clark 1998).

Given the existing uncertainties related to, for example, the 'false absence' problem, reliable estimates of past spreading rates are very difficult to obtain.

Pollen-stratigraphical sequences from temperate interglacial stages including the Holocene show a series of tree population establishments and expansions, and compositional equilibria or 'stability' phases (Figure 10). However, the ecological mechanisms by which new taxa establish and expand, i.e. invade, into existing forest vegetation are poorly understood.

Isochrone maps (Figure 8) give the impression that trees spread and advance as a continuously spreading front across the landscape and invade all possible sites (Figure 11.1). This hypothesis seems unlikely for many, if not all, mesocratic trees (Watts 1973, Giesecke 2005). An alternative hypothesis (Figure 11.3) (Rudolph 1930, Firbas 1949, Watts 1973, Walker 1982, Birks 1986) proposes that taxa spread by long-distance chance dispersal of propagules (Figure 9.2) from cryocratic or protocratic scattered microrefugial populations into locally favourable openings caused by windthrow, death, fire, or disease beyond the main range of the taxon to form small outliers. These mature and in turn act as seed parents for local expansion of these outliers and further establishment in new gaps. In contrast to the initial, slow phase of seedling establishment with low population densities, the expansion phase may occur rapidly because local propagule deposition within the forest increases, the probability of establishment rises, and population densities grow. Intraspecific competition may remain low at this stage. Over several generations, these populations may expand and coalesce with the main population.

Population growth may then flatten off or even decrease owing to interspecific competition, density-dependent self-thinning, and intraspecific competition, and the inability of some forest trees (e.g. *Quercus*) to regenerate under their own canopies. Eventually a relative balance between seedling establishment of resident and invading taxa may occur, thereby enabling co-existence in a quasi-equilibrium until the next invasion. Invasion and expansion of taxa may be triggered by climate change (extrinsic forcing sensu Williams et al. 2011) or by internal biotic and abiotic factors such as competition, storms, and pathogens (intrinsic forcing sensu Williams et al. 2011). Distinguishing between the role of extrinsic and intrinsic drivers in interglacial vegetation dynamics is a major challenge, which may be met by combining multiproxy palaeoecological evidence with dynamic landscape and vegetation modelling (Henne et al. 2011). Seddon et al. (2014) have developed new quantitative tools to identify intrinsic and extrinsic drivers of change in diatom assemblages in a Galápagos coastal lagoon. Their approach could usefully be extended to forest ecosystems and pollen stratigraphies.

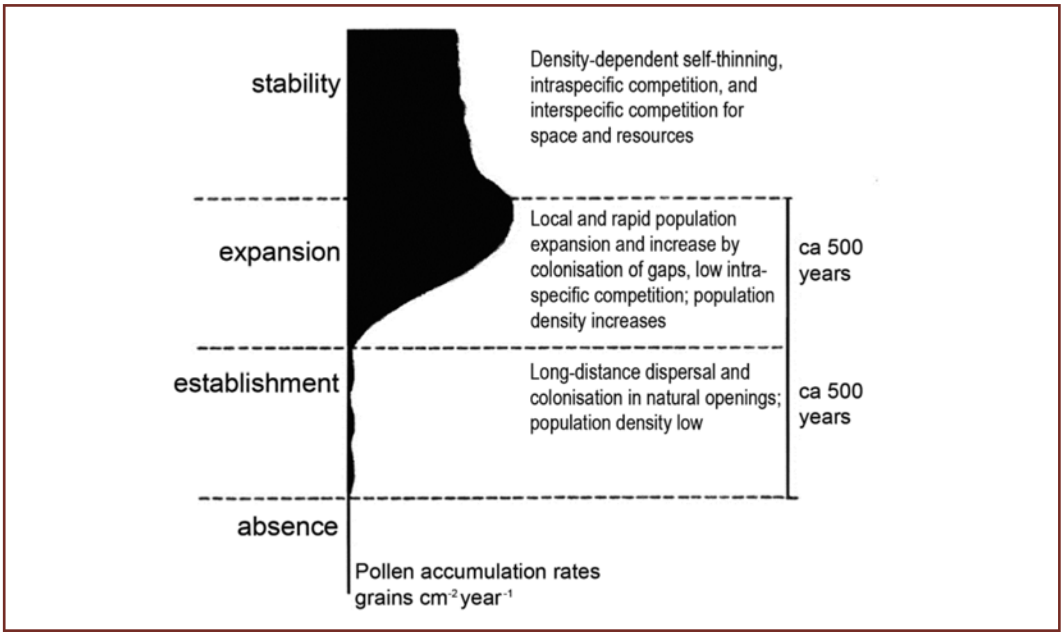

Figure 10. Observed generalised pollen-stratigraphical patterns and inferred population processes suggested by Watts (1973) in the establishment and expansion of a tree in the mesocratic phase within an interglacial stage. The approximate durations of the establishment and expansion intervals are also shown. Modified from Birks (1986).

There are interesting parallels between the landscape and stand scale processes involved in tree invasions in the Holocene and in modern invasions by introduced species (Gillson et al. 2008). Although from North America, two detailed studies of palaeo-invasions in the Holocene (Davis et al. 1998, Lyford et al. 2003) demonstrate the amazing complexity of the processes involved. Davis et al. (1998) studied the Holocene invasion of *Tsuga canadensis eastern hemlock* into mesic mixed deciduous-coniferous forests of northern Michigan. Four stands of *Tsuga* today were formed by an 800-year long invasion into patches of white pine about 3 000 years ago. There is no evidence for disturbance during these invasions. *Tsuga* co-existed with *P. strobus* for several thousand years but eventually became dominant at different times at three of the stands. The underlying extrinsic drivers of these changes may have been climatic changes over the last 4 000 years. The history of four nearby sugar maple stands is more variable. Three maple patches were originally dominated by *Quercus*. Two were not invaded by Tsuga and the third was invaded for a few centuries by low numbers of Tsuga trees only. Clearly invasion by Tsuga depended on the composition of the resident forest. Sugar maple and basswood increased and by 2 000 years ago they formed mixed mesic maple forest. The fourth *Acer* patch was invaded later by *Tsuga* but changed to an *Acer* stand 500–1 000 years ago. A wood layer in the forest-pond sediments indicates a catastrophic windstorm about 500–1 000 years ago that may have played a part in these complex forest dynamics. For further details see Davis et al. (1994), Davis (1987), and Parshall (2002).

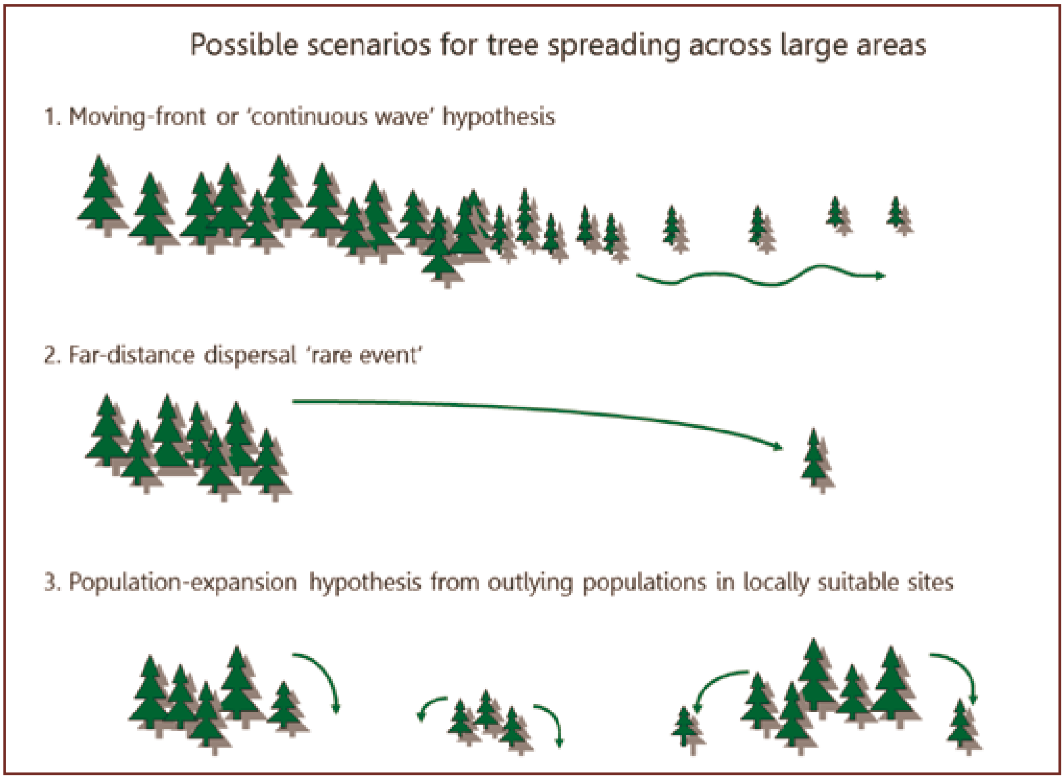

Figure 11. Possible scenarios for tree spreading in an interglacial stage. 1. The moving-front or 'continuous wave' hypothesis where trees 'march' across the landscape. 2. Rare far-distance dispersal events. In reality, scenarios 2 and 3 are likely to be most important. 3. Populations expand from outlying populations into locally favourable sites or 'enclaves'. Based in part on Giesecke (2013) and Davis (1987).

The other detailed example of the complexity of invasion processes (Lyford et al. 2003) is from the xeric areas of Wyoming, Utah, and Montana and concerns the invasion of *Juniperus osteosperma Utah juniper*. Its spread into Wyoming and southern Montana occurred as a series of long-distance dispersal events over 30–135 km (Figure 11.3) which were facilitated to some extent by climate variability between 7 500 and 5 400 years ago and the geographical distribution and connectivity of suitable habitats within the landscape. Further expansion of these initial outlying populations and the colonisation of suitable sites to the south of the outliers did not occur during a wet period from 5 400–2 800 years ago. The onset of dry conditions 2 800 years ago resulted in the rapid colonisation of *Juniperus osteosperma* into sites throughout its current range (Figures 11.2 and 11.3). In this case, climate change was an important extrinsic driver interacting with intrinsic landscape structure in determining the pattern and rate of invasion of *Juniperus osteosperma*.

Both studies show how difficult it is to generalise about the underlying processes and identify the critical drivers of tree invasion in the past.

Lessons from past tree dynamics and invasions

We see that European forests have being changing since the Palaeogene with progressive extinction from Europe of trees of the Arcto-Tertiary geoflora in the Pliocene and early to mid-Quaternary (van der Hammen et al. 1971, Willis and McElwain 2014, Birks and Tinner 2016). The repeated glacial–interglacial cycles (Birks 1986, Lang 1994) that are so characteristic of the Quaternary (Pleistocene, Holocene) have resulted in a continuous dynamic of tree survival in refugia during glacial stages and rapid spread and population expansion and unique tree combinations in the different interglacial stages (Iversen 1958, Birks 1986). Human impact with forest clearance and agriculture are unique to the Holocene, the so-called *Homo sapiens* phase (Birks 1986). What emerges from the many palaeoecological studies (mainly based on pollen analysis but increasingly strengthened by macrofossil studies) is continual change at time scales of millions, thousands, and hundreds of years (Birks and Tinner 2016). Forests develop when certain plant species become abundant and dominant at specific areas under particular environmental conditions (Jackson 2006). These forests may change gradually or abruptly when the dominant trees are replaced by other trees, usually in response to extrinsic environmental change (Williams et al. 2011) or major disturbances (e.g. forest pathogens, fire, human activity) (Birks 1986, Tinner et al. 1999). Few major terrestrial forest systems in Europe have existed for more than 10 000 years and most are considerably younger, some developing only within the last few centuries (Birks 1993 Bradshaw et al. 2015). Future forest systems are thus inevitably uncertain and historically contingent (Jackson 2006). Given the richness of forest-tree responses during the Quaternary with all its climatic shifts (van der Hammen et al. 1971, Birks 1986, Bennett et al. 1991, Lang 1994), many novel future responses, outcomes, and ecological surprises are possible or even inevitable (Jackson and Williams 2004, Veloz et al. 2012, Jackson 2013, Williams et al. 2013, Reu et al. 2014).

What 'lessons from the past' can be learnt from the ever-changing populations, composition, structure, and extent of forests in Europe? How can past tree dynamics inform modern ecologists and forest scientists about present and future forests and their dynamics and about invasion processes?

Assessing whether current forest systems are sustainable in the face of future global change can be aided by considering the range of environmental variation that these systems have experienced in the past and by reconstructing the environmental conditions under which these systems were initiated and developed (Jackson 2006). A narrow time window (e.g. 200–300 years) may underestimate the range of variation within which a forest system is sustainable, and this underestimates the risk of major disruption of the system by environmental change (Jackson 2006). Longer time periods (e.g. 1 000–2 000 years) inevitably increase the inherent range of natural variation in the Earth system (Jackson 2006). Most systems disappear, as shown by the palaeoecological record, when the time window extends to 10 000–15 000 years due to major changes in the Earth's climate system resulting from orbital forcing (Willis and McElwain 2014). Importantly the palaeoecological record can pinpoint the origination time of particular forest systems (e.g. Birks 1993, Bradshaw and Lindbladh 2005) and can, by inference in some cases, indicate the specific extrinsic or intrinsic changes that led to the development of the system and the range of environmental variation under which the system maintained itself in the past (Jackson 2006). Such information, only obtainable from the palaeoecological record, can thus help to identify critical environmental thresholds beyond which specific modern forest systems can no longer be sustained (Willis and Birks 2006, Birks 2012, Birks and Tinner 2016).

The palaeoecological record for European forests provides several additional insights and important lessons from the past (Jackson 2006, Birks and Tinner 2016). First, all existing forest systems have a finite time limit to growing in the places where they occur and all have been preceded by ecosystems (not necessarily forest systems) that differ in composition, structure, plant-functional traits, and ecosystem properties (Jackson 2006). Second, similar forest ecosystems, as defined by their dominant species have developed in different places and at different times (Birks 1986, Jackson 2006). Third, similar systems had different antecedents in different places. Thus apparently similar systems may have different properties owing to different histories and to legacy effects of different antecedents (Jackson 2006). Fourth, several different systems arose at approximately the same time in different places, presumably in response to regional- or global-scale shifts in atmospheric circulation, leading to major reconfigurations of climatic variables and widespread synchronous transformation of systems (Jackson 2006, Giesecke et al. 2011, Seddon et al. 2015). This pattern is not, however, universal but rapid regime-shifts in the Earth system may be accompanied by widespread ecosystem changes in diverse regions (Jackson 2006, Williams et al. 2011). Fifth, forest ecosystems of today have no long history even in the time span of the Holocene and forest systems existed in the past that have no modern counterparts ('analogues') (Jackson and Williams 2004, Jackson 2013). Examples (Birks and Tinner 2016) include the former abundance of Corylus avellana in the early Holocene of much of north-west Europe (Huntley and Birks 1983, Birks 1986) and the importance of *Abies alba* in southern Europe in the mid-Holocene (Tinner 2013, di Pasquale et al. 2014).

Palaeoecologists look to the past whereas global change ecologists look to the future, but both rely solely on their understanding of modern ecosystems and ecological processes as a basis for past reconstructions or future predictions. Palaeoecologists apply the concept that "the present is the key to the past" whereas global change ecologists project this forward and use "the present is the key to the future". But the present is only one time-slice in the last 11 700 years since the last glacial stage (Birks and Tinner 2016). A critical question is thus are today's populations, ecosystems, and climate representative of tree and ecosystem–climate relationships under past or future climate change? Are they robust to climate conditions beyond modern states? Are species ranges in equilibrium with environmental factors such as climate (Svenning and Sandel 2013) or have their realised environmental niches been significantly altered by climate-change or millennial-long land-use activities (Jackson and Overpeck 2000)? These palaeoecological questions suggest that it is inadequate to project future ecosystem conditions solely on the basis of present-day observations (Willis and Birks 2006). A promising novel approach is to combine dynamic eco-physiological models with palaeoecological evidence to produce palaeo-validated scenarios of future vegetation dynamics under global-change conditions (Henne et al. 2015, Birks and Tinner 2016, Ruosch et al. 2016).

The dynamic nature and the often non-analogue character of European forests in the time-span of the Holocene or even the last 5 000 years raises critical questions about appropriate targets ('baselines') for restoration efforts (Birks and Tinner 2016). Palaeoecological studies have revealed major human imprints on many, if not all, systems in Europe (Birks 1986, Tinner and Ammann 2005) and have shown that secular climate change has kept many targets moving at centennial to millennial time scales (Birks 1986, Jackson and Hobbs 2009, Willis and McElwain 2014). Ongoing rapid environmental changes may almost certainly ensure that many historical restoration targets will be unsustainable in the coming decades (Henne et al. 2015). Restoration efforts should aim to conserve or restore historical systems if possible, but more importantly, to design, create, and manage emerging novel ecosystems to ensure high biodiversity and a supply of ecosystem goods and services in the future (Jackson and Hobbs 2009, Birks and Tinner 2016).

The palaeoecological record of European tree populations and forest history is a rich and largely untapped record of ecological and population dynamics and tree invasions over a wide range of time-scales (Birks and Tinner 2016). As Karl Flessa and Steve Jackson (2005) discuss, this record is a long-term ecological observatory where ecological responses to past climate change and the ecological legacies of societal activities can be deciphered, quantified, and used as a key to "understanding the biotic effects of future environmental change" (Flessa and Jackson 2005). There is very much still to be learnt about past European forests and tree population dynamics and invasions using the vast amount of high quality palaeoecological data available in Europe (Huntley and Birks 1983, Birks 1986, Lang 1994, Tinner and Lotter 2001, Tinner et al. 2005, 2013, Giesecke et al. 2014, Birks and Tinner 2016). Palaeoecology and modern ecology need to work more closely together to enhance our understanding of European tree populations in the past, at present, and in the future. Much remains to be learnt from palaeoecology's 'lessons from the past'.

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1.2 The history of introduced tree species in Europe in a nutshell

Bart Nyssen, Uwe Eduard Schmidt, Bart Muys,
Pieter Bas van der Lei and Patrick Pyttel

The roots of the current European tree species diversity and composition lie in the distant past. During the late Neogene–Quaternary period, in the last 2.6 Million years (see Chapter 1.1.), extreme climate changes (i.e. ice ages) have caused dramatic range shifts of the European tree flora. It is generally accepted that, during these glacial periods, tree species distributions were much smaller when compared to the current inter-glacial period. The Mediterranean Sea in the southern part of Europe and the rather unsuitable environment for tree growth in the North restricted temperate European tree species during the glacial periods to the Iberian, Italian and Balkan peninsulas (Petit et al. 2003). Multiple processes and factors have led to the current distribution ranges and abundances of tree species occurring in Europe. This distribution does not necessarily coincide with the potential range that is based on their ecological requirements and competitive status. However, it often reflects the patterns of past human interventions (Keitt et al. 2001). The dynamics of (re-)colonisation, or invasion, are very much species specific.

The deliberate introduction of plant species from one geographical area into another is a process that started millennia ago, in the Mesolithic era, and has continued ever since.

It is known from pollen studies that hazel (*Corylus avellana* L.) was the first tree or shrub species of the temperate zone that reached central Europe after the late glacial periods. A surprising element is that it probably happened with the aid of Mesolithic hunter-gatherers who used the tree as a food source. There is evidence of the role humans had in this early migration of hazel, as hazelnut shells have been found in archaeological excavations of fire places, while hazel pollen was not reported to be present yet at the same period (Zagwijn 1994).

Food for humans and feed for their livestock was the first dominant driver for anthropogenic tree introduction (Zagwijn 1994) with the need for wood becoming more predominant at later stages. Although these drivers represent basic human needs, we should not underestimate the role of less materialistic drivers such as human curiosity and the sense for aesthetics or spiritualism in the process of introductions of new tree species. The continuous expansion of agriculture, the frequent migrations of people from one geographical area to the next, the extension of trade, the colonisation of new territories, the movement of troops in wars, etc. are all important vectors of the shifts in the tree species distributions (Culiță 2007).

The process of postglacial re-colonisation was still ongoing when the establishment of Phoenician, Greek and mainly Roman trade networks rapidly broadened the distribution range of archeophytic tree species, such as the sycamore maple (Acer *pseudoplatanus* L.), sweet chestnut (*Castanea sativa* Mill.) and common walnut (*Juglans regia* L.). Subsequently, the inter-continental transfer of valuable tree species was already ongoing during the expansion of the Roman Empire. The quince (*Cydonia oblonga* Mill.), for example, was brought from central Asia, via south-western Asia to south-eastern Europe, whereas the common medlar (*Mespilus germanica* L.) was transplanted by the Assyrians from the Caucasus to Turkey. The apple tree (*Malus pumila* Mill.) was introduced to Europe via the Silk Road (Goudzwaard 2013).


© look and learn

Figure 12. David Douglas went searching in Canada for nature's secrets; during one of his expeditions he was surprised by native inhabitants while selecting and picking seedlings of Douglas fir trees.

Another famous example of an archeophytic tree species is sweet chestnut that is a species that has played a distinctive role in providing food for humans and livestock, as well as being a source of timber. Prehistoric people used its fruits for food, and its wood for building palafittes (Neolithic dwellings built on piles on lakes in Switzerland and northern Italy), canoes and cabins. Man began to cultivate sweet chestnut between the Caspian and the Black Sea around 900–700 BC (Adua 1998). From there, chestnut cultivation spread quickly to Greece from where it reached the Balkan region. Because of its wide range of uses, the Greeks increased its cultivation and bred new varieties. Likewise, the Romans recognised its large potential (i.e. use of tan bark, high growth potential, easy grafting) and they selected new varieties and propagated chestnut cultivation in Italy, France, Spain, Portugal, Switzerland and Britain (Adua 1998).

The reasons behind the introduction of new tree species to Europe beyond medieval times, i.e. in 16^{th} and 17^{th} century, were rather unrelated to nutrition or timber; the main drivers of tree introductions during these times were mostly curiosity and scientific interest.

With the exploration and subsequent colonisation of the world, humans became increasingly mobile, which, in 17th century, also led to the world opening to the natural sciences with diverse forest ecosystems of other temperate regions capturing the imagination. Botanists tried to get a complete overview of existing species, collected them and presented them in herbaria, and established live collections in arboreta. Many arboreta and botanical gardens were already established in 16th century. In their colonies, Europeans grew familiar plants and trees from their home countries and, at home they enriched their gardens with new species from the colonies. The oldest known introduction of a North American tree species to Europe dates from 1536: the white cedar (*Thuja occidentalis* L.) in France (Wein 1930). In 17th century, the introduced tree species became an integrated part of the new French garden and park culture, which spread from the mid-18th century all over Europe. In 1683, the horse chestnut (*Aesculus hippocastanum* L.), originating from south-eastern Europe, was already present in parks in Finland (Ruotsalainen 2006). This interest in the world of plants culminated in the publication of the *Species Plantarum* in 1753 by Linnaeus.

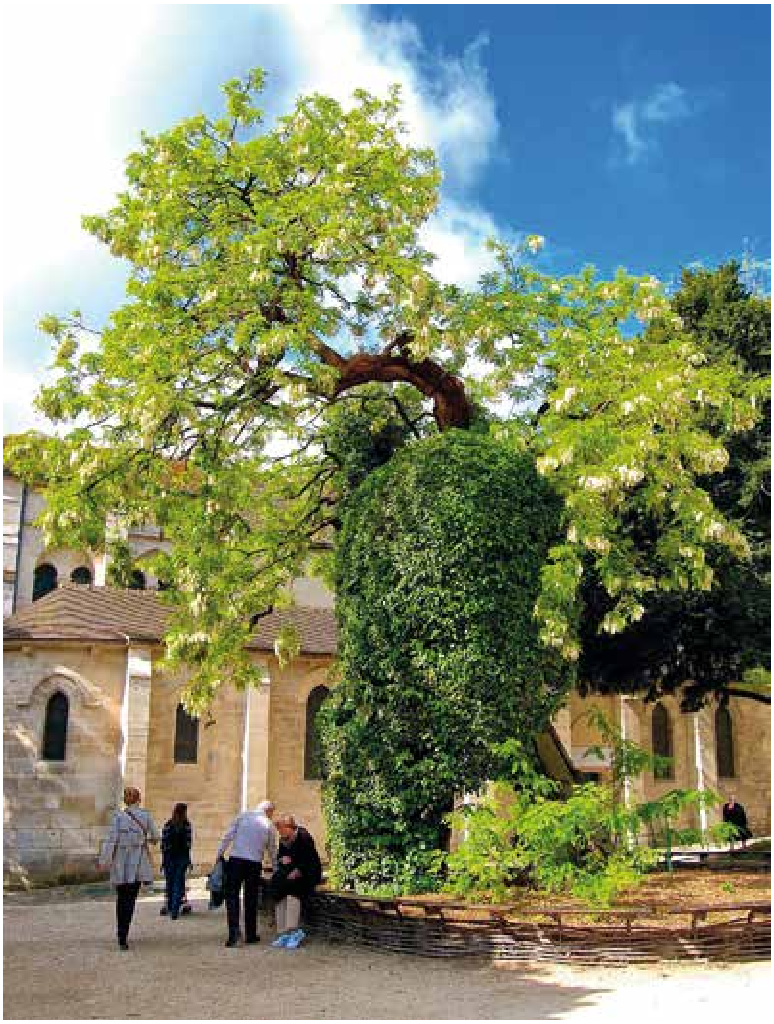

Figure 13. The first European black locust, planted by Jean Robin in 1601, is still alive on the Square René Viviani in Paris (photo: B. Berman).

Black locust (*Robinia pseudoacacia* L.) became the second North American tree species that was introduced from North America to Europe (Keresztesi 1988). The first black locust, planted by the botanist Jean Robin in 1601, is still alive on the bank of the River Seine in the centre of Paris. It was planted in other places in France in 1635 (Vor et al. 2015), in the Netherlands in 1646 (Buis 1985), in Germany in 1672 (Vor et al. 2015) and introduced into Hungary between 1710 and 1720 (Keresztesi 1983). Since its early introductions, black locust has been widely dispersed across Europe as well as across and in other temperate and Mediterranean zones of the world.

The introduction into Europe of another North American species, black cherry (*Prunus serotina* Erhr.), occurred two decades after the introduction of black locust. Jean Robin describes the species under the name Cerasus americana latifolia in the Enchiridion isagogicum from 1623 (Buis 1985). Half a century later, red oak (*Quercus rubra* L.) was introduced in Switzerland in 1691 (Badoux 1932) and in Germany in 1740, mainly planted as a park tree (Göhre and Wagenknecht 1955).

Figure 14. Trading of red oak and chestnut oak (*Quercus prinus* L.) acorns in North America at the end the 18th century (Burgsdorf von 1787). The German text “Europen zur Bereicherung” means: “For the enrichment of Europe”.

In 1705, Lord Weymouth brought eastern white pine seedlings (*Pinus strobus* L.; also called Weymouth pine) to England (Maloy 1997) from the eastern part of North America with Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) being the first tree species from the western part of North America to be introduced to Europe, specifically in 1827 to Great Britain (Troup 1932) and in about 1830 to Germany, mostly for aesthetic reasons (Vor et al. 2015). Introductions of noble fir (*Abies procera* Rehd.) in 1830, Sitka spruce (*Picea sitchensis* (Bong.) Carrière) in 1832 and grand fir (*Abies grandis* (Douglas ex D.Don) Lindl.) in 1833 followed soon after. The Lawson cypress (*Chamaecyparis lawsoniana* (A. Murray) Parl.) and the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) were introduced some decades later in 1854 and 1851, respectively (Troup 1932). The Australian silver wattle (*Acacia dealbata* Link), also called mimosa, was introduced to Europe around 1800, and was widely planted in the 19th century on the French Mediterranean coast, mainly for its winter flowering.

Figure 14. Mimosa or silver wattle that is also referred to as the 'King of Winter' for its yellow winter flowering in the Mediterranean region of Provence (photo: G. Pavaut)

Other plants from Oceania were first introduced to Europe about 1804 in the form of the Tasmanian blue gum (*Eucalyptus globulus* Labill.) (Penfold and Willis 1961). With regard to species of forestry interest, the Japanese larch (*Larix kaempferi* (Lamb.) Carrière) was late introduction to Europe, being introduced only in 1893 (Troup 1932). This larch species was, however, not the first tree species from Asia to be introduced; in 1740, a Jesuit priest introduced the tree of heaven (*Ailanthus altissima* (Mill.) Swingle) from China for the high quality silk that was produced when ailanthus silkmoth (*Samia cynthia* Drury) was grown on its leaves (Fotiadis et al. 2011) with the aim of producing silk in Europe.

The beginning of the industrialisation, the second half of 18th century, marked the advent of modern forestry.

The enormous expansion of the European population led already in the Middle Ages to regional wood shortages, which was the result of deforestation and consequent degradation of the remaining forests. Besides deforestation for agricultural purposes and cattle and sheep pasture, forest litter raking and excessive harvests of fuel wood for the early industrial production had caused forest devastation. Especially the early industrial production of salt, saltpetre, beer, bricks, lime, charcoal, glass, iron and steel needed large amounts of wood (Radkau and Schäfer 1987). This overexploitation of European forests persisted until the society realised the need for forest restoration and reforestation at the end of 19th century (Schütz 1990).

Box 4: **European forestry science and reforestation – The essentials in brief**

The enormous expansion of the European population in the Middle Ages led to a regional wood shortage and subsequently into the deforestation and the degradation of vast forest landscapes. Besides deforestation for agricultural purposes and pasture, litter raking and excessive fuel wood demands of early industries caused considerable forest devastation. Especially the production of salt, saltpetre, beer, bricks, lime, charcoal, glass, iron and steel needed huge amounts of fuel wood (Radkau and Schäfer 1987, Schütz 1990). This overexploitation of European forests persisted until the end of the 19th century and reforestation at end of the 19th century (Schütz 1990).

During the times of over-exploitation, the scientific knowledge of forest restoration on a large scale was absent; forestry basically did not exist as a scientific discipline. Driven by the wood shortage for ship building and mining, the foundations for the European forestry were laid by Evelyns book ‘Sylva’ that was written in 1664 for navy commissioners in England. Decades later, the mining administrator, at the court of Kursachsen in Freiberg, Von Carlowitz wrote the ‘Sylvicultura oeconomica´ in 1713 (Radkau and Schäfer 1987). Both Evelyn and Von Carlowitz called for forest restoration and for limiting the wood extraction to the level of the increment; i.e. at a sustainable level.

However, it would be incorrect to place these early science-based foresters in complete disconnection from the past. There are indications that they were inspired by traditions in France and Belgium, where the know-how of managing oak forests as coppice with standards or high forest (tire et aire) goes back centuries (Vandekerkhove et al. 2016). The earliest written concepts of ‘sustained yield‘ and ‘normal forest’ date back to the Middle Ages. The *Ordinance of Brunoy* by the French king Philips VI (1346) states that ‘forest masters will survey and visit all the existing forests and woodlands and realise any appropriate cuttings, with reference to what the forests and woodlands can hold sustainably in good condition in the long term’ (Lionnet and Peyron 2008).

In the first generation of modern forestry handbooks including *de l’Exploitation des Bois* (Forest Management) by Duhamel du Monceau, published in French in 1764 and in German in 1766, and books by Knoop (1790) in the Netherlands, Hartig (1791) in Germany, or de Poederlé (1792) in Belgium were published. However, it took until the end of 18th century and the beginning of 19th century before the academic education in forestry started in Europe. This education started first in Germany with the foundation by Cotta of the forest academy in Tharandt (1813) and attracted many foreign students. In France, the École National des Eaux et Forêts of Nancy was founded in 1824. The 19th century forestry concept was mainly formed by Georg Ludwig Hartig (1764–1833) in northern Germany and by Heinrich Cotta (1763–1844) in southern Germany. Both Hartig and Cotta based their forest restoration models on agricultural concepts that were widely accepted in this period (Schütz 1990). Forestry entered an era that was characterised by monoculture plantations of highly productive coniferous trees harvested by clearcutting. This industrial German forestry model that was characterised by monoculture and clearcutting was to dominate the forest development across Europe and beyond.

The industrial development fostered the conversion of broadleaved forests into presumably more productive coniferous plantations in order to meet the demands for standardised commodities. Due to such demands, the local wood shortages were taken as the major political reason to set the scene for the desired changes to come in the forest management (Grewe 2004). The big breakthrough in forest restoration was enabled by the rise of coal and fuel. This drastically diminished the need for firewood and the local resistance against the forest conversion of coppice and coppice with standards into industrial monocultures was suppressed (Schütz 1999).

In the course of the development of modern forestry and the application of robust reforestation measures after a long period of overexploitation, conifers and broadleaved tree species were planted on a larger scale. The role of introduced tree species slowly turned from a dendrological curiosity into an issue of great economic importance. From the mid-18th century, black locust was increasingly planted across Europe, initially, in most cases as coppice for firewood, viticulture and beekeeping, but later mainly for silvicultural purposes (Vor et al. 2015). It is also important to note that the species was mostly planted in monocultures in eastern Europe. Along with the expansion of black locust, the first forestry use of red oak in central Europe arises at this time (Göhre and Wagenknecht 1955). As for the southern Europe, the first Tasmanian blue gum plantations were established in Portugal in 1863 (Cortés y Morales 1883) and in Spain in 1874 (Penfold and Willis 1961)

The large-scale plantations comprising of introduced tree species were initiated by innovative land owners and curious scientists. The experiences with new tree species that were gained in parks were transferred to forests. Germany took the lead in these developments thanks to the well-developed forestry knowledge. Well-known early plantings of North American tree species can be found on the Harbke Estate in Saxony-Anhalt, Germany (Du Roi 1771) on the basis of which Von Burgsdorff realised the importance of his first plantations of North American tree species and published his experiences (Burgsdorf von 1787). In addition, the German dendrologist von Wangenheim described the introduced tree species relevant for planting in Germany in 1781 (Wangenheim von 1781).

Since the end of 19th century, the systematic forest restoration and the large scale plantations of introduced tree species were organised by the state forest services in many European countries. The introduction of tree species boosted the European research on forest ecology and management. For example, in 1871 the German administrative organisation of experimental forest stations was established. One of the main goals of research was to test the introduction of North American and Japanese tree species on a large scale. In Prussia, in 1880, Bismarck formulated the question “whether and to what extent it would be possible to enrich our forest flora by naturalisation of alien tree species” (Schwappach 1907). The Prussian state forest organisation started with introduced tree species cultivation trials in 1881. Other countries followed this example. The Belgian agriculture minister decided in 1897 that research on the suitability of introduced tree species with rapid growth and high productivity was necessary in wooded areas in order to increase the profitability of forests (Rouffignon 1899). In response, a network of 23 forestry arboreta (with stands of trees in contrast to botanical arboreta with individual trees) was established throughout the country between 1890 and 1914, comparing the growth and response to silvicultural treatments of introduced tree species over a long site gradient (Delevoy and Galoux 1949). In France, the ‘Société Nationale d’Acclimatation’ encouraged the planting of introduced tree species for timber production (Naudin et al. 1887).

However, the scale of these plantings in 19th century remained limited. The inventory of the royal Prussian forester Weise in 1882 shows that the plantings where introduced tree species were used in the Prussian Rhenan provinces were still very limited. It consisted of ten eastern white pine plantations while Douglas fir was only planted in one forest (in addition to several city gardens). The largest plantings of red oak in the Prussian kingdom were established in the Saar province, covering an area of 100 ha (Weise 1882). In accordance to that governmental agencies, the focus was concentrated mainly on the cultivation of experiments using the most promising introduced tree species such as Douglas fir, Japanese larch, red oak, black cherry, Sitka spruce, eastern white pine, black walnut (*Juglans nigra* L.), shagbark hickory (*Carya ovata* Mill.) and grand fir (Schwappach 1918).

Some of the introduced tree species were never planted in forests or they proved to be unsuitable for wood production. This is for example the case for ash-leaved maple (*Acer negundo* L.), tree of heaven, green ash (*Fraxinus pennsylvanica* Marshall; also known as red ash), honey locust (*Gleditsia triacanthos* L.) and staghorn sumac (*Rhus typhina* L.) (Vor et al. 2015).

> ▶ *The non-European tree species that are currently present in European forests on a substantial scale are those that were used for reforestation in Europe in 20th century.*

In southern Europe, the introduced tree species used for reforestation purposes in 20th century were mainly silver wattle (*Acacia dealbata* Link), Australian blackwood (*Acacia melanoxylon* R. Br.), Long-leaved wattle (*Acacia longifolia* (Andr.) Willd.), Tasmanian blue gum and red gum (*Eucalyptus camaldulensis* Dehnh.). The tree of heaven was also used for reforesting and afforestation purposes in Hungary, the Czech Republic, and the south-eastern Europe (Kowarik and Säumel 2007). In central and northern Europe, Douglas fir is the most planted introduced tree species used for forestry purposes. In Germany for example, it is currently growing on ca. 217 600 ha representing 2.0 % of the total forest area (Vor et al. 2015). The second and the third most commonly occurring introduced tree species in German forests are Japanese larch covering 0.67 % and red oak representing 0.4 %, respectively of the forest area (Vor et al. 2015). Red oak is widespread all over western, central, southern and south-eastern Europe with the largest concentrations in Germany, France, Belgium and the Netherlands (Vor et al. 2015). Black locust is also present in large parts of Europe, especially in southern and eastern European countries. In Hungary, 23 % of the forest area consists of black locust, which equates to 415 000 ha (Rédei et al. 2012).

The most planted tree of the *Abies* genus is silver fir (*Abies alba* Mill.), but also grand fir, and to a lesser extent, noble fir and balsam fir (*Abies balsamea* (L.) Mill.) have also been planted (Vor et al. 2015). The only non-European species of pine planted in large amounts is eastern white pine. However, its area has been decreasing due to the needle rust affecting it (Vor et al. 2015). Jack pine (*Pinus banksiana* Lamb.) and lodgepole pine (*Pinus contorta* Douglas ex Loudon) have been planted to some extent in Europe. In Great Britain and Ireland, the main introduced plantation tree species has been Sitka spruce (Quine and Humphrey 2010). Japanese larch was also considered as 'a useful species for establishing a first crop on the better types of heatherland' in the British Isles (Troup 1932).

During the 20th century reforestation, black cherry was planted together with silver birch (*Betula pendula* Roth) and speckled alder (*Alnus incana* (L.) Moench) on sandy soils in north-western Europe. Black cherry was, in fact, the most planted broadleaf tree species after 1920s on these poor sites. The first use of black cherry in forestry was as an admixture species in the Netherlands in 1898 planted by Van Schermbeek (Bakker 1963). In Belgium, black cherry was used in the first half of 20th century as a soil improver when reforesting drift sands and heathlands (Masson 1920). In Germany, reforestation peaked after the Second World War. Between 1950 and 1980, hundreds of thousands of hectares were reforested in Germany, on the sandy soils in northern Germany where mostly Scots pine and Japanese larch were used. Black cherry was a part of the classic planting plan (Starfinger et al. 2003). It is not surprising that black cherry is nowadays extensively present on the sand belt from Belgium and the Netherlands over the North German plains and into Poland and Hungary (Sitzia et al. 2016).

Figure 15. 125-year-old Black cherry near Aachen (Germany), planted by Adam Schwappach (photo: B. Nyssen).

Following are four the key messages based on the short historical overview of the introduction process of tree species in to Europe

1. The active introduction of new tree species has always been driven by human needs and dates, at least, back to the Mesolithic (about 10 000 to 5 000 BC). Tree species introductions, in combination with increasing human land use, have strongly shaped the composition of European forests.

2. The motivations for the earliest introductions were mostly driven by the establishment of reliable food sources. Hazel is the earliest example, but oak, sweet chestnut and European beech have also been spread northward for this reason. The introductions of new tree species from the New World were driven by human curiosity, mainly that of botanists, but also by ornamental and aesthetic reasons.

3. Due to the growing wood demands that rose during the industrialisation of Europe, a significant part of the European forest cover was restored in 19th and 20th century. This restoration of overexploited forests and the reforestation of wastelands catalysed the use of the introduced tree species. Since 19th century, introduced tree species became part of the modern plantation forestry, which was, from a social-ecological viewpoint, closely linked to the development of the capitalistic economy of growth.

4. The current need for adaptation of forest ecosystems to a relatively rapidly changing environment urges finding a proper role and place of introduced tree species in forest ecosystems. In this reality, natural forest references are in large parts of Europe a hypothetical situation of little practical use (Chapter 3.6). The already naturalised introduced tree species could best be integrated in forest management (Sitzia et al. 2016).

The question, whether the restoration of degraded forests and the reforestation of Europe would have been possible without the use of introduced tree species, is hypothetical. More important is the analysis of the role of these tree species in today's adaptive and integrative close-to-nature forest management.

Box 5: The dominance of monocultures, coniferous tree species and clearcutting was from the beginning criticised by the proponents of 'close-to-nature' forestry, which, by now has become a widely accepted forestry concept.

Wilhelm Pfeil (1783–1859) was the first forestry scientist who tried liberating forestry from these dogmatic principles by opposing every generalisation of forestry measurements. However, the big change in conceptualising forest management came around 1880 when Karl Gayer, the forestry professor at Munich, based his close-to-nature forestry on the concepts of mixed uneven-aged forests and natural regeneration. The extending research and publications on the close-to-nature forestry concept remained rather marginal and most of 20th century reforestations were still carried out following the 'rational' plantations principles.

It is only since the 1970s, that this situation changed and more ecological and multifunctional types of forest management have become dominant creating diverse, mixed and well-structured forests strongly resilient to the dominance of introduced tree species with the application of the close-to-nature forestry concept enabling the integration of introduced tree species in forest ecosystems.

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Black locust stands protected in the urban nature reserve 'Natur-Park Südgelände', Berlin, to allow the development of novel urban woodlands. (photo: Ingo Kowarik)

2 From introduced to invasive – the characteristics of invasiveness

The second section includes chapters focusing on aspects that are important to be considered when dealing with introduced as well as invasive tree species. The question of how culture shapes attitudes towards introduced species is addressed in chapter 2.1 'Strangers in paradise'. Changing perceptions towards introduced tree species are discussed and the question of whether we can predict if a species becomes invasive is examined. Determinants of invasiveness of tree species in Europe are presented since introduced tree species are not often introduced on their own but co-invasion of invasive trees and their associated belowground mutualists are crucial. Finally, the experience from South Africa, a country with a long history of dealing with the effects of introductions of tree species, is presented.

2.1 Strangers in paradise – how culture shapes attitudes towards introduced specie
Uta Eser

2.2 What determines the invasiveness of tree species in central Europe?
Petr Pyšek

2.3 Can we predict whether a species will become invasive?
Tina Heger

2.4 Praise and damnation – perceptions towards introduced tree species vary and change with time
Uwe Starfinger and Ingo Kowarik

2.5 Co-invasion of invasive trees and their associated belowground mutualists
Martin A. Nuñez, Nahuel Policelli and Romina D. Dimarco

2.6 Maximising benefits and minimising harm associated with invasive introduced trees – lessons from South Africa
Brian W. van Wilgen

2.1

Strangers in paradise

How culture shapes attitudes towards introduced species

Uta Eser

Disquieting parallels between social and natural phenomena are reasons for critical reflection.

Migration is currently a ubiquitous and controversial issue. We hear and see news daily of refugees fleeing their home countries and seeking shelter in Europe. Challenges and opportunities of immigration are highly contested within and between European societies. While some welcome refugees and support their integration and naturalisation, others react with misgivings and some with outright xenophobia. Sceptics are concerned that the newcomers might impair the quality of life of the domestic population.

Against this background, this chapter looks at parallels between the socio-cultural discourse on immigration and the conservation discourse on introduced species. The introduction of tree species raises questions that are quite similar to questions raised by immigration:

- Can introduced species enrich the native flora?
- Will the new arrivals assimilate into existing communities or will they change or even dominate them?
- How much immigration can a community take without losing its valued identity?

Many invasion biologists deplore the emotional quality of the debate about introduced species and advocate a fact-based approach. Some have rightly urged caution in the use of terms such as ‘native’, ‘invasion’ and ‘alien’ in an effort to avoid triggering xenophobic reflexes (Binggeli 1994, Larsons 2005, for definitions also see *Introduction*). To understand the reasons for the passionate discourse regarding this controversial topic, this chapter explicitly focuses on the emotive aspects of the topic in relation to introduced and invasive tree species. Conservation decisions do not solely depend on facts but inevitably involve values and norms that are deeply rooted in individual, social and cultural identity. They, therefore, can arouse strong emotions.

To understand how scientific facts, social values and ethical norms intermingle in the discourse on introduced species, in 1998 I reviewed the ecological literature on biological invasions as well as the historic and cultural backgrounds of nature conservation (Eser 1998a,b). These studies showed that the discussion about species introductions reflects socially constructed images of humans and nature sketching ways in which introduced species either irritate or reaffirm these sociocultural images.

Assuming that the assessment of introduced species involves judgements about human action, the negative notion of humanity prevailing in conservation literature is first discussed. There are three different images of nature that are relevant for understanding the discourse on introduced species: (1) nature as ‘our home’; (2) nature as ‘pristine beauty’; and (3) nature ‘red in tooth and claw’ (brute nature). I will demonstrate how these images contribute in different ways to a negative assessment of invasive introduced species. Concluding, I plead the case for broadening the scope of the debate. The controversy about species introductions is not simply a matter of xenophobia. Rather, it is a reflection of modernity’s struggle to cope with difference and change.

▶ *The negative connotations associated with introduced species reflect a misanthropic tendency of nature conservation.*

Introduced species are defined as species in a given area whose presence is [...] a result of human activity” (see table 3). The assessment of introduced species, thus, inevitably involves judgements about human activities. Between the lines of ecological texts about introduced species, one can find hints on the author’s attitude towards humans and human actions. In invasion ecology, this attitude is generally rather pessimistic, if not plainly misanthropic. Charles Elton, the founder of invasion ecology, already revealed a negative image of humanity in his landmark book *The Ecology of Invasions by Animals and Plants*:

> “The reason behind this, the worm in the rose, is quite simply the human population problem. The human race has been increasing like voles or giant snails and we have been introducing too many of ourselves into the wrong places” (Elton 1958:144).

In a similar vein, Warren Wagner stated in the anthology *Biological Pollution*:

> “The species *Homo sapiens* itself is without question the super invader of all time” (Wagner 1993).

Such a generic argumentation is very common in the environmental discourse. Without acknowledging different individual, social or cultural ways of living, many friends of the Earth regard humanity as a problem for nature. They tend to idealise nature (‘nature knows best’) and accordingly regard any human intervention into natural processes *per se* as wrongful.

From an ethical perspective, however, such a view is questionable. Unlike voles or snails, humans do not simply follow their instincts. Though they do not always act reasonably, they are capable of reason, they can recognise and evaluate consequences of their actions, and they can (and ought to) take responsibility for them. A merely biological perspective misses this specifically human dimension of action. People have reasons for what they are doing. If these reasons are good reasons or bad reasons, if the consequences are desirable or undesirable is a matter of judgement, and reasonable judgement follows from reflection, not from instinct.

Hence, the mere fact that the presence of a species in a given area is a result of human activity is not a sufficient criterion for its assessment as ‘bad’. ‘Natural’ does not equal 'good' and 'anthropogenic' does not equal 'bad'. Consequently, case-based assessments of species introductions do not apply to species as such, but to reasons and consequences (e.g. Palmer and Larsen 2014). Alternative approaches may evaluate reasons for and consequences of an introduction and consider all possible benefits and costs (e.g. Aubin *et al.* 2011).

> *The discourse on introduced species refers to and reaffirms three images of nature: cultivated nature as home to humans, pristine nature as the epitome of the morally good, and brute nature as the arena of the struggle for existence.*

There is a certain tendency among environmentalists to idealise nature. Since the rise of the environmental movement in the 1970s, environmentally concerned citizens and scientists have sought to re-orient our modern life-styles towards more sustainable ways of living. Many regard nature's complexity and vulnerability as limiting human dominion over nature, not only factually, but also morally. Representatives of ecological ethics seek to overcome anthropocentrism and claim that nature itself should become an object of ethical reflection and theory. They expect nature to provide moral orientation.

However, the environmentalist directive to follow nature faces two problems. Firstly, 'natural' does not equate to 'good'. To infer a moral 'Ought' from an empirical 'Is', counts as naturalistic fallacy. Secondly, nature functions as a projection screen for all kinds of human preferences and fears. We can see cooperation in nature as well as competition, we find aggression as well as care, and we observe fight as well as flight. In seeking to orient our lives according to nature, we are in danger of interpreting nature according to our culturally shaped sets of norms and values and, then, justifying these values and norms by declaring them natural. Such circular reasoning risks reaffirmation of values that are socially constructed and deserve critical reflection.

Many conservationists deem introduced species as a problem; in order to understand what exactly nature means to conservationists a literature review of biological invasions was conducted resulting in realisation of three contrasting images of nature (see table 3):

1. Cultivated nature as home to humans;
2. Pristine nature as the epitome of the morally good;
3. Brute nature as the arena of the struggle for existence.

Table 3: Three images of nature

Image of nature	Cultivated nature	Pristine nature	Brute nature
Represented by	Gardens, Cultural landscapes	Primeval forests	Jungle
Leading idea	Harmony between humans and nature	Nature is good, human interventions are bad	Eat or be eaten, no room for morals

Perspectives on introduced species that behave invasively relate to these images in different ways: for those who value cultivated nature as home to humans, introduced species may be considered as too natural (i.e. the brutal side of nature) to be an object of conservation; for those admiring pristine nature, introduced species are not natural enough to be thought of as valuable and may actually threaten the pristine characteristic; for those adhering to nature as the arena of the struggle for existence, the spread of introduced species is just natural and therefore does not pose a problem.

The anti-modern origins of nature conservation regard cultivated nature as home to humans ("Heimat"). Introduced species impair the uniqueness of this homely nature.

One early example of the projection of a particular ideology onto nature is from the founding father of German nature conservation Ernst Rudorff. In 1897, the conservative traditionalist lamented the "uglification" of landscapes through land re-parcelling:

> "What has become of our beautiful, glorious 'Heimat' with its picturesque mountains, rivers, castles and friendly towns. [...] [The re-parcelling] transfers the barren principle of straight lines and squares so blindly into reality that an area that underwent the tempest of such regulation looks like an incarnate example of economic arithmetic" (Rudorff 1926: 22, my translation).

Rudorff was not only concerned about nature, but about a particular culture that brought forth this beloved landscape. He criticised the annihilation of traditional culture by a modernity whose sole valid standard is instrumental rationality. This 'barren principle' endangers the uniqueness of landscapes and cultures brought forth by tradition. To Rudorff, the term 'Heimat' was key for nature conservation.

In this tradition, the opposite of 'Heimat' was internationalism. While the conservative view values regional and national differences, it regards the modern ideal of equality and justice as morally objectionable egalitarianism ('Gleichmacherei'):

> "With our equalisation we play into the hands of the ideals of uprooted internationalism. [...] Which patriotic goods are there to protect, that merit to risk one's life, when every uniqueness of 'Heimat', its historically developed landscapes and character, every peculiarity in essence, custom and appearance, has been eliminated?" (Rudorff 1926: 76, my translation)

According to such a conservative worldview, landscapes and habits that have historically developed are good, while the substitution of uniqueness by global uniformity is bad. In this spirit, the 1993 Congressional Office of Technology Assessment (OTA) report on invasive species presented as a worst-case scenario

> "One place looks like the next and no one cares" (US Congress 1993).

In this view, in order to be a home for humans, nature needs to be familiar, traditional, unique and rooted to the ground. Introduced species are clearly not this kind of nature. They are unfamiliar, modern, common and detached. They leave the cultivated land and become feral. In contrast to harmonious cultural landscapes, they epitomise the hostile aspects of nature. Table 4 shows the mutually exclusive qualities of nature as a home and the nature of introduced species.

Table 4: Mutually exclusive qualities of nature as home and of introduced species.

Qualities of nature as home	Qualities of introduced species
familiar	unfamiliar
traditional	modern
cultivated	feral
unique	common
rooted to the soil	detached
harmonious	hostile

▶ *Romanticism regards nature as a treasure of morality – introduced species contradict this ideal by showing ruthless behaviour.*

While nature as a home represents the ideal of a suitable cooperation of humans and nature, romantic nature is considered to be untouched by humans. This image of nature is exceedingly morally charged. In Romanticism, nature appears as a treasure of virtue and a source of morality. Nature's virginity is constitutive for its moral appeal. In his famous tale "Der Hochwald" (The High Forest), the German poet Adalbert Stifter wrote:

> "For there is decency, I want to say an expression of virtue in the countenance of nature that has not been touched by human hands, to which the soul must bow as to something chaste and numinous" (Stifter 1841, my translation).

The attributes that Stifter uses – 'untouched', 'chaste' 'numinous' – refer to the second important image of nature: nature as a virgin. The loss of virginity is also a central theme in Rudorff's idea of 'Heimat'. He laments the 'shameless prostitution of nature' and the 'powerful advertising of scenic attractions' by modern mass tourism as they ruin the moral effects of pristine nature by mentioning 'But to be moral, that is to purify and uplift, nature must, above all, remain unsullied, and unadulterated" (Rudorff 1926: 74, my translation).

The metaphor of virginity is not restricted to the romantic tradition of nature conservation. It also appears in a concept that invasion ecologists use to portray healthy natural communities, the concept of integrity. Integrity describes the capability of natural plant communities to resist invasion by intruding species. According to Elton, natural communities are highly complex due to their long co-evolution. The complex interactions (competition, predation, parasitism) between individuals prevent newcomers (individuals from an introduced species) from thriving as the niches are occupied. The system is therefore stable and can resist intruders. A precondition for successful invasions is a disruption that forcibly destabilises this evolutionarily protective mechanism.

Introduced species hence represent the deflowering of nature by man. They destroy the illusion of virginity and are the proof of the fact that the respective piece of nature is no longer pristine, but has been desecrated and disgraced by human actions. While virgin nature is pure and modest, invasive species are libidinous and animalistic. Table 5 demonstrates the opposition of virgin nature and the nature of introduced species.

Table 5: Mutually exclusive qualities of pristine nature and introduced species

Qualities of Pristine Nature	Qualities of Introduced Species
virgin	penetrant
untouched	destructive
chaste	libidinous
virtuous	animalistic
numinous	profane
threatened	threatening
in need of protection	dangerous

So far, I have presented two reasons why conservationists have their difficulties in accepting introduced species: they do not fit in with the ideas of homely nature nor virgin nature. So what kind of nature are they? They are that kind of nature that romantic idealisation tends to deny: they are a brute nature.

Evolutionary biology regards nature as the arena of the struggle for existence. As representatives of brute nature, introduced species are subjected to control measures.

The image of nature as the arena of a remorseless struggle for existence is diametrically opposed to the romantic idea of nature as a symbol of a harmoniously ordered divine cosmos. In 1798, Thomas Malthus had published his landmark essay ‘On the principle of population’, where he depicted life as a ‘perpetual struggle for room and food’, which became an influential paper. While Adalbert Stifter enthused about nature’s virtuousness, the English poet Alfred Tennyson decried the cruelty of nature. In his poem *In Memoriam A.H.H.* he contrasts it with the capability of love, given to humans by their creator God:

> “Who trusted God was love indeed /
> And love Creation’s final law /
> Tho’ Nature, red in tooth and claw /
> With ravine, shriek’d against his creed” (Tennyson 1994 [1851]).

Charles Darwin’s theory of evolution by natural selection and Richard Dawkins’s Selfish gene trace back to this image of brute nature.

While romantics idealise nature as harmonious and stable, adherents of brute nature accept nature as cruel and reckless. From an evolutionary perspective, nothing in nature is constant but rather ever changing. Therefore, the spread and establishment of new species can be regarded as natural phenomena. “The current state, or the one presented shortly before, is by no means better or the best of all possible states of nature. On the contrary: nature is dynamic, not static, and the species that live in a given area are not fixed elements of the ecosystem, as the niches of a house, a metaphor that is often used” writes zoologist Josef Reichholf (Reichholf 1996: 87, my translation).

From a conservationist perspective, however, introduced species with invasive character are undesirable. They are neither homely nature nor virgin nature, but represent a brute nature that cannot give moral guidance. When scrutinising biological texts about successful invaders, one finds many characteristics that resemble the rejected brute nature: they are highly competitive, they tend to dominate the vegetation, they are aggressive and ruthless, they occur in masses, and they are hard to control. In contrast, cultivated humans strain for cooperation, they expect integration, courtesy and consideration from each other, and individuality and self-control are valued highly.

Table 6: Mutually exclusive qualities of culture and of brute nature

Qualities of Culture	Qualities of (brute) Nature
Cooperation	Competition
Integration	Domination
Courtesy	Aggressiveness
Considerate	Ruthless
Individual	Mass
Self-controlled	Impulsive

Table 6 shows that introduced species considered as invasive behave in ways cultivated people despise; they are not suitable moral models. Rather, they symbolise the kind of nature that must be dominated. One could almost say they are not humane enough to be valuable nature.

This psychologic dimension of the problem occurred during a symposium on introduced plant species in Offenburg (Germany) in 1995, where control of invasive species was a key topic. One of the participants portrayed an effective control of Japanese knotweed (*Fallopia japonica* Houtt. Ronse Decr., Chapter 3.8) as impossible. In a desperate exclamation, he noted following: 'This plant simply is eerily potent!' Such uneasiness with regard to the impressive vigour of Japanese knotweed is a key to the understanding of negative emotions towards introduced and invasive species.

The construction of 'otherness' is the downside of the construction of the modern 'self'. Qualities that do not comply with this ideal are projected onto others.

For the benefit of the community, human individuals learn to suppress certain aspects of human nature: egoisms, instinctive behaviour, aggression etc. In his seminal book 'Civilisation and its discontents', Sigmund Freud described how the civilisational process of self-control gives rise to feelings of discontent. The process of self-control is quite painful for the individual. Max Horkheimer and Theodor Adorno expressed this pain in dramatic terms:

> 'Humanity had to inflict terrible injuries on itself before the self – the identical, purpose-directed, masculine character of human beings – was created, and something of this process is repeated in every childhood' (Horkheimer and Adorno 2002 [1944]: 26).

Socio-psychological studies explain racism and sexism in modern societies by interpreting 'the others' as a projection screen for our own, tediously suppressed instinctive nature. What the (male) subject cannot accept or cannot integrate into itself is projected onto others. Historically, such 'others' have been nature, women and people of different cultures. Uta von Winterfeld has called this phenomenon 'modernity's inability to cope with otherness'. Modernity can only eliminate, or subject, or assimilate the other (Winterfeld 2006).

Invasive introduced species are therefore not simply aliens. They are a symbol of the other *par excellence.* In this regard, biologist James Brown is quite right in saying:

> "There is a kind of irrational xenophobia about invading plants and animals that resembles the inherent fear and intolerance of foreign races, cultures, and religions" (Brown 1989: 105).

I hope to have shown that such xenophobia is not a natural given but a product of culture.

Invasive species of non-native origin provide a projection screen for all characteristics that humans do not like in themselves.

Therefore, let's summarise what makes introduced species problematic for nature conservation:

Firstly, the ideal of nature conservation is rooted in the movement for the conservation of natural and cultural heritage ('Heimatschutz'). With regard to this historical background, introduced species are (perceived as) strangers that do not belong to the landscape. Being strangers, they simply do not fit into the image of nature as home.

Secondly, introduced species are, by definition, proof of human activity. Therefore, they spoil the illusion of purity and perfection that is decisive for the appreciation of virgin nature. If only virgin nature is a valuable nature, invasive introduced species are not only worthless, but they endanger the value of the natural state of the environment.

Thirdly, invasive introduced species represent qualities of nature that are not valued in the ideal of nature conservation. Their vitality, their vigour, their massive spread and their mass occurrence represent the image of brute nature. Usually, this kind of nature is subject to control by cultural means. Invasive introduced species, however, have managed to escape from culture; they have escaped from gardens and invaded the (valuable) virgin nature surrounding the (valuable) cultivated land. Such reasons foster the most vehement emotions.

Hence, the analogy to societal processes with regard to introduced species is not simple xenophobia. Conservationists do not reject introduced species just because they are foreign: one major cultural reason for rejecting invasive alien species is that they provide a projection screen for all the characteristics that we do not like in ourselves, and therefore vicariously fight in the outside world.

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2.2 What determines the invasiveness of tree species in central Europe?

Petr Pyšek

The aim of this chapter is to explore what factors determine the likelihood that a species introduced for forestry purposes (hereafter termed a 'forestry tree') becomes invasive, by passing through the stages of the invasion process (Blackburn et al. 2011). How is the likelihood of the species becoming invasive influenced by species traits, time since the species was introduced into cultivation, and area over which it has been planted is also addressed. These topics are central to the current research in invasion biology (Catford et al. 2009) and, depending on the studied system and analytical attitude, their exploration may lead to varying results (Kueffer et al. 2013). These issues are illustrated using a comprehensive data set on invasion by forestry trees in the Czech Republic. The data can be considered representative for the wider area of central Europe. These data were previously analysed in a series of papers (Křivánek et al. 2006, Křivánek and Pyšek 2006, Pyšek et al. 2009) where the reader can find more details.

▶ *Invasive woody species have serious ecological and economic impacts and are hard to eradicate.*

Woody species have generally not been widely considered as important non-native invaders until recently because only a small proportion of plants with this life form (0.5 % of the world's tree species and 0.7 % of the world's shrub species) are currently invasive outside their native range. This represents altogether 622 species, of which 357 are trees, and 265 shrubs, and belong to 78 families and 286 genera. The highest numbers of introductions of invasive woody species is accounted for by horticulture (62 % of the total number of invasive woody species), with forestry being the second most important pathway (79 species, i.e. 13 % of the total). Species used for forestry are often selected for fast growth, and are typically grown in large-scale plantations (Richardson and Rejmánek 2011). This creates a massive propagule pressure, which is one of the major concepts in invasion biology (Lockwood et al. 2009). Although only 38 species are reported to be very widespread globally (i.e. invasive in six or more regions of the world), the impact of tree and shrub invasions on local ecosystems and biota is often detrimental. Some of the most invasive groups of plants worldwide are trees, such as acacias (*Acacia* spp.), eucalypts (*Eucalyptus* spp.), or pines (*Pinus* spp.), and have invaded a wide range of habitats and have had a variety of impacts in invaded ecosystems (Richardson 1998, Richardson et al. 2011). Once woody species have become established over a large scale, they are extremely difficult to eradicate (Richardson and Rejmánek 2011).

In the Czech Republic, the number of introduced tree and shrub species recorded in the wild is 71 and 139, respectively, of which 15 tree and 33 shrub species are naturalised, and nine tree and three shrub species have become invasive, according to the most recent review (Pyšek et al. 2012). Nevertheless, tree species used for forestry purposes represent a special case because they have been planted over a large area, and also over a period of many decades to centuries.

More than a third of introduced tree species planted in the Czech Republic have become naturalised.

Křivánek et al. (2006) found that of the 28 tree species that are commonly used in forestry in the Czech Republic, there is a great variation in how likely they are to become invasive. Fourteen species are not recorded as having escaped from cultivation, four do so occasionally but never reach a stage beyond casual (they do not reproduce in the wild and hence do not form sustainable populations). Ten species have become naturalized in the wild (unlike casuals, they do form sustainable populations without, or despite intervention from humans; Blackburn et al. 2011). Of those 10, as many as seven are known to be invasive in the Czech Republic (Table 7); they are capable of spreading at considerable distance from mother trees and founding populations. The fact that 25 % of introduced tree species used in forestry have become invasive is an alarming message making forestry as one of the major invasion pathways. The key questions are then, what determines this variation and why do some species become invasive while others do not? Is it due to the differences in species traits? Is it a consequence of where they come from? Or are there other factors of similar, or even greater, importance? These questions can be addressed using data on forestry trees in the Czech Republic (Křivánek et al. 2006, Pyšek et al. 2009).

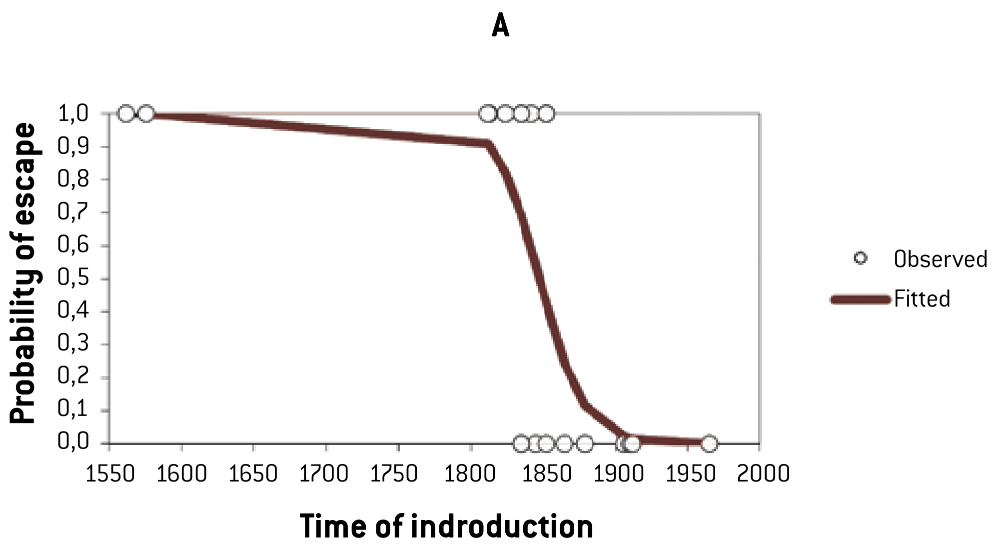
Time since introduction, and how extensively a species was planted, are major factors determining whether tree species escapes from cultivation, becomes naturalized in local plant communities, and eventually becomes invasive.

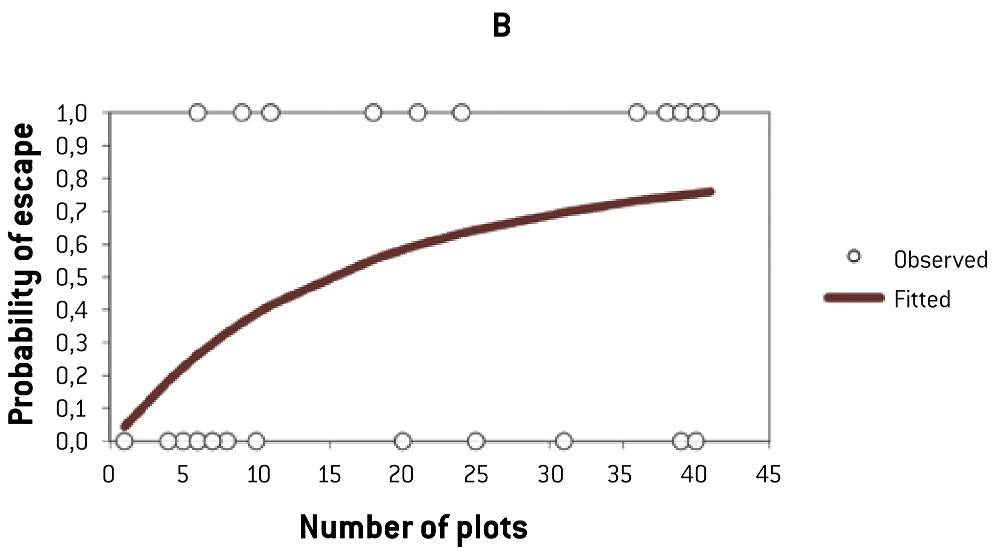
The effect of the two most important factors affecting invasion success, residence time and propagule pressure, may differ at different phases of the invasion process (Blackburn et al. 2011). Křivánek et al. (2006) used propagule pressure and time of introduction into cultivation as explanatory variables in regression models to estimate how likely it is that a species used in forest plantations would escape from cultivation, and subsequently become naturalized. In plant invasion biology it is often difficult to obtain reasonable estimates of propagule pressure. However, this is not the case in forestry where the data on planting history are often available. The number of administrative units that are related to the number of plots where a species is planted in the country and the total planted area were used as proxies for propagule pressure associated with each species (Table 7; Křivánek et al. 2006).

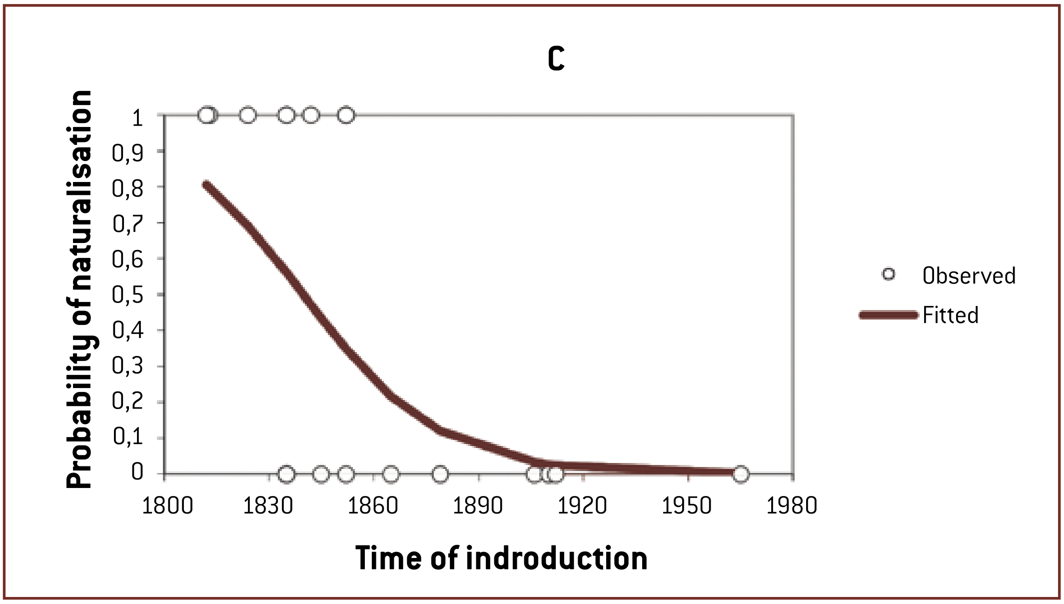
Table 7. Overview of species planted as forestry trees in the Czech Republic with information on their area of native range (Origin), invasion status (inv = invasive, nat = naturalised, cas = casual; see introduction, table 1 for definitions), planting area in the Czech Republic, number of planting plots (these correspond to so-called natural forest areas, which are 41 administrative units defined on the basis of geography, geomorphology, and climate) and the number of localities in the wild, outside cultivation, from which the species is reported (data from Křivánek et al. 2006).

Species	Origin	Invasion status	Year	Planting area (ha)	Number of planting plots	Number of locations
Robinia pseudoacacia	NAm	inv	1835	14190	36	615
Quercus rubra	NAm	inv	1852	4380	40	194
Acer negundo	NAm	inv	1835	337	21	133
Pinus strobus	NAm	inv	1812	3090	41	114
Populus cultivars	hybrid	inv	1852	1934	24	58
Prunus serotina	NAm	inv	1852	12	18	22
Ailanthus altissima	As	inv	1813	13	6	17
Pinus nigra	Eu	nat	1824	3689	39	175
Pseudotsuga menziesii	NAm	nat	1842	4370	41	96
Juglans regia	As	nat	1852	84	18	48
Aesculus hippocastanum	Eu As	cas	1576	552	38	181
Castanea sativa	Eu Af As	cas	1562	25	11	21
Juglans nigra	NAm	cas	1835	679	9	20
Platanus x hispanica	hybrid	cas	1835	4	11	1

For the first stage, escape from planting, 39 % of the variance was explained by the number of planting units and the time since introduction with the latter factor being the most important variable. If a species was introduced early, it had a higher probability of escape than those introduced later. The probability of naturalisation is also largely driven by these two predictors; although the probability of naturalisation increases with longer and more extensive planting rather gradually, it does not follow the pattern of an abrupt change after a certain threshold, as is the case with the probability of escape (Figure 16). On a more general note, such results highlight the fact that forestry represents a threat in terms of generating future invaders; if a species has been planted long enough and over a large enough area, there is a high probability of it becoming invasive. This threat is further emphasized by a very close relationship between the area where an introduced tree species was planted and how widely it became distributed in the landscape after it had escaped, which is generally accepted as a measure of invasiveness (Figure 16).







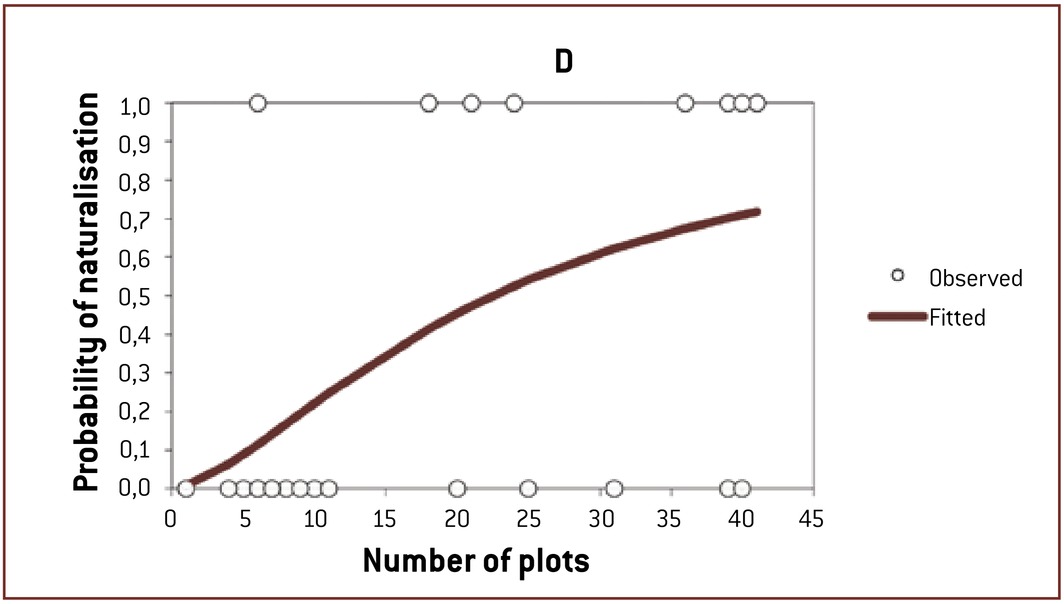


Figure 16. The probability that an introduced tree species will escape from cultivation in the Czech Republic based on (A) the time of introduction to cultivation and (B) and number of units at which it is planted, and that it will become naturalised in the wild, depending on the same two factors (C and D, respectively). The figures are based on simple logistic regressions. Interestingly, while the probabilities of both escape and naturalisation (panels B and D, respectively) increase with the number of planting units (these correspond to so-called 'natural forest areas', which are 41 administrative units defined on the basis of geography, geomorphology, and climate), hence with increasing propagule pressure, gradually and in the same manner, the effects of time since introduction strikingly differ. For escape from cultivation, there is an abrupt change of probability over the 19th century introductions (with >95 % probability of escape for trees introduced in 1801 and <5 % probability for those after 1892). The probability that the species would naturalize, after it has escaped from cultivation, gradually decreases for species introduced later and becomes extremely low if a species was introduced later than ff200 years ago. Taken from Křivánek et al. (2006). Printed with permission.

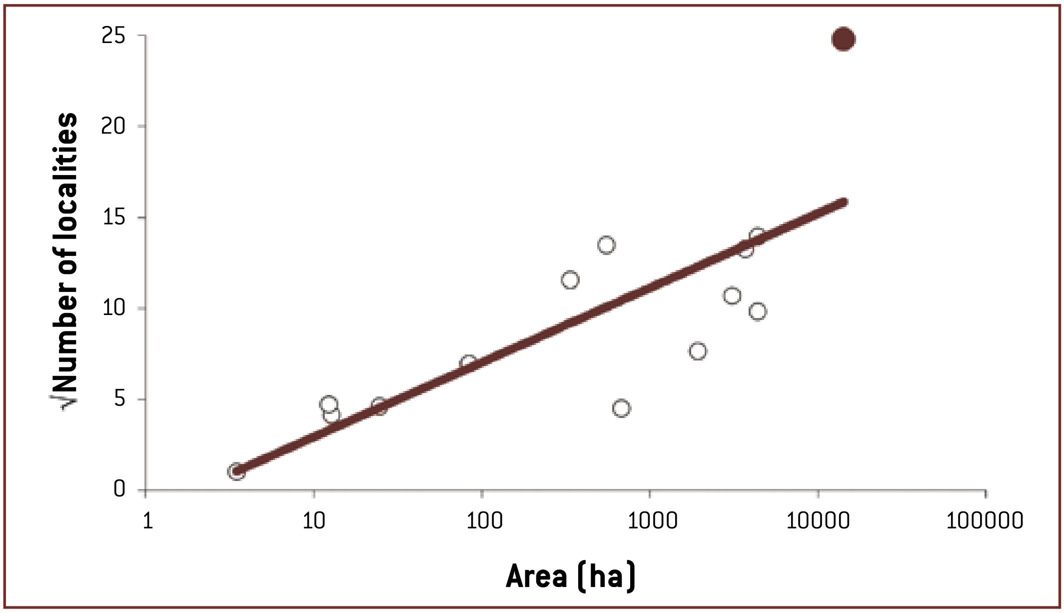


Figure 17. The positive relationship between the number of localities outside cultivation in which the species was recorded and the total estimated area of planting, plotted for 28 forestry tree species in the Czech Republic (√ number of localities=—1.169 + 4.096 log(planting area), df = 1, 12, F = 19.68, p = 0.00081, r^2 = 0.62.), illustrates the role of propagule pressure in invasion. The more it is planted the more widespread outside cultivation, therefore more invasive. The most widespread species, Robinia pseudoacacia, is indicated with a black spot. Taken from Křivánek et al. (2006). Printed with permission.

▶ *Invasion by woody plants can be explained using a relatively simple suite of factors.*

Propagule pressure and the time since introduction can be considered as the material upon which the differences in biological traits act in determining the invasive potential of a species (Catford et al. 2009, Pyšek et al. 2015). This is because the different species have different characteristics, and even within a concise and well-defined life history group such as trees, some traits may play an important role in favouring invasion. However, we need to keep in mind that invasions are context-dependent (Box 6); hence, rather than analysing species traits on their own, it is more appropriate to consider their effects in models that account for confounding factors such as propagule pressure and time since introduction. To eliminate the possibility that potential differences in species traits are, rather than representing drivers of invasion success, phylogenetically based and hence inherited from common ancestors without any relation to invasion, Pyšek et al. (2009) compared escaped versus not-escaped from cultivation, naturalised versus not-naturalised, and invasive versus non-invasive pairs of species within the same genus. The analysis also revealed another facet of the well-known effects of the time since introduction; the probability of escape increased with time since introduction in the Czech Republic, whereas the probability of naturalization increased with the time elapsed since the introduction of the species to Europe. This indicates that some species were already adapted to local conditions when introduced to the Czech Republic. The main message of Pyšek et al. (2009) was that in addition to propagule pressure and residence time, some traits or species-related attributes co-determined the probabilities of the trees becoming invasive, but did not affect the probability of escape from cultivation. In other words, whether a species occasionally escapes from cultivation had nothing to do with its biological and ecological traits, only with high levels of propagule pressure from large-scale plantations. However, the biological traits play a role in later stages of invasion; species originating from Asia and those with small fruits were at disadvantage for naturalisation, and the ability to tolerate low temperatures was a necessary precondition for reaching the stage of invasion.

Overall, these results indicate that a relatively restricted number of factors determine, with a high probability, the invasion success of alien trees, and that the relative role of biological traits and other factors is stage-dependent (Pyšek et al. 2009).

Knowing what makes a species invasive allows for the prediction of which woody species can be safely introduced and which are potential invaders.

Over the last 30 years, our ability to predict which species will become invasive has improved. We can provide managers with scientifically based criteria to decide which species can be safely used commercially and which species should not be planted because of the risk of it becoming invasive. Various schemes to assess the risk of invasion associated with introductions of particular species are in use, and to which extent they are transferable from one part of the world to another has also been tested for central European invasive woody species.

Křivánek and Pyšek (2006) compared three schemes for predicting the risk of invasion by woody species in the Czech Republic. Of 180 introduced woody species in central Europe, 17 species were invasive, nine species were naturalised but non-invasive, 31 species were casual aliens, and 123 species were not reported to have escaped from cultivation. The risk assessment scheme that performed best was based on a scheme by Pheloung et al. (1999), in spite of the fact that it was originally developed for Australia. The probability that an accepted species (i.e. considered as “safe” by the risk assessment procedure) will become invasive was zero for this model and the probability that a rejected species (i.e. considered as likely invasive) would become invasive was 77 %. This is a fairly promising result, and proved that some weed risk assessment schemes provide robust templates for building a widely applicable system for screening introductions of plants (Křivánek and Pyšek 2006).

Each coin has two sides: trees native to central Europe have become invasive elsewhere.

Box 6. Context-dependence of biological invasions.

The context-dependence of invasion outcomes is important for risk assessment and screening of species for potential introduction because we cannot make inferences about the role of species traits in determining invasion potential without considering confounding factors such as propagule pressure (the amount of seed or other reproductive parts that enter the system), time since introduction (so-called residence time), or climate and habitat match between the source and target regions. From a practical point of view, this complexity may have serious implications. For example, when considering whether a species should be approved for introduction and planting, it is important to consider time since introduction and propagule pressure in the region of interest. These factors, which must be included in any proper assessment of the role of species' biological traits, themselves play important roles in affecting the outcome of invasion. Only by addressing these factors in concert, can we understand how they interact and what is their relative importance in determining the outcome of invasion. As a consequence of the context dependence in invasions, studies that do not include effects of habitat niche in the native range, intensity of planting in both the native and invaded range, or that of time since introduction on species invasion may seriously overestimate the role of biological traits, and arrive at spurious predictions. The application of models that analyse several factors at the same time is therefore crucial to properly address the role of traits affecting the invasiveness of species (Pyšek et al. 2014, 2015).

Because of the long history of trade and movement of people, there has been an extensive exchange of plants among world regions (van Kleunen et al. 2015); each region has not only received alien species but also acts as a source of plant invaders to elsewhere, with central Europe being no exception (Pyšek et al. 2015). A convenient approach to investigate these multidirectional patterns is the source area approach that makes it possible to eliminate some of the biases otherwise limiting assessment of factors determining invasion success (Box 7). Pyšek et al. (2014) carried out an analysis for woody plants where they evaluated the global invasion success of temperate trees and shrubs with native ranges in central Europe and explored the role of their native distribution and biological traits in determining whether they have become invasive in other parts of the world. Out of the 94 species included in this study that represented the source-area species pool, 27 % are known to be invasive in at least one region of the world. Tall woody plants flowering early in the season, and widely distributed in the native range were more likely to become invasive than species not possessing these traits. However, even species not having these traits may become invasive because there are other traits that can result in a potential to become invasive – species that do not depend for reproduction on another individual, those pollinated by wind and dispersed by animals are also likely to become invasive even if they do not have extensive native distributions (Pyšek et al. 2014).

The studies reported in this chapter collectively demonstrate how data from ecological research in plant invasions, generating knowledge of regional distribution patterns and species invasion status, if combined with the wealth of information from forestry archives, on introduction and planting history, can generate novel insights for invasion biology. On the more applied side, they illustrate that we can make reasonably reliable predictions of potential threat resulting from introduction of some tree species.

Box 7. Source-area approach.

Use of the source-area approach is one way to eliminate bias that usually limits the applicability of macroecological studies of plant invasion (Pyšek *et al.* 2014, 2015); the approach is based on defining a source pool of species native to a certain region and following their post-introduction performance in another region. This allows confounding variation that arises when considering multiple source areas of introduction to be minimised, both in terms of evolutionary predispositions acquired in disparate regions of origin, as well as various historical contingencies that shape introduction dynamics. Specifically, the source-area approach is based on the assumption that, all else being equal, members of the flora of a single biogeographic region have comparable chances of being transported by humans from their native range into other parts of the world because they are exposed to the same historical, socioeconomic, and biogeographic factors. The differences in the success as aliens can be thus more reliably attributed to their biological and ecological traits if the source-area approach is applied. Moreover, for European species as invaders in other parts of the world, this approach is likely to be highly informative also for historical reasons, assuming that Europe has been a major donor of introduced plants into other parts of the world (van Kleunen et al. 2015).

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2.3 Can we predict whether a species will become invasive?

Tina Heger

Life is complex, and so are invasion processes. Since the beginning of research on invasions the aims were to identify a set of traits which characterize invasive species, or a set of factors characterising areas that are invaded (Crawley 1987, Rejmánek 1995). Unfortunately, the more research that has been done, the more evident it has become that these aims cannot be achieved (Williamson 2001, Rejmánek et al. 2005). Common characteristics of invasive species in one region can differ significantly from the characteristics identified as being common in invasive species of a different region. As an example, invasive plants in the British Isles have been found to produce significantly larger seeds than native species (Crawley et al. 1997), whereas in Ontario invasive plant species produced smaller fruits than native species (Cadotte and Lovett-Doust 2001). Efforts to create lists of traits indicating invasiveness have so far only been successful for relatively small groups of similar species. Invasibility of an area, i.e. its vulnerability to invasion, at the beginning of research into invasions has been thought to strongly depend on disturbance, and it was thought that undisturbed ecosystems are stable and resistant to invaders. This notion has also proven untrue. To give an example, in protected near-natural forests in New Jersey introduced tree species are common, with Norway maple (*Acer platanoides* L.) (native in central Europe, but introduced and invasive in North America) reaching high abundances especially in the innermost, remote and undisturbed parts (Webb et al. 2000).

What is the reason for these observations? Are the given examples only minor exceptions of a rule, or do they indicate some inherent mechanism complicating explanations and predictions? In this chapter, I will argue that the latter seems to be the case.

It is an obvious fact that every organism and every species is unique, and the same is the case for every ecosystem, and every near-natural or human-altered area. With this in mind it is easier to think about what makes a species invasive if a specific, potentially invasive species is considered, along with a specific area that might be invaded. Certain characteristics of this species will significantly increase its potential to be invasive in one specific ecosystem (e.g. an open grassland), but these same characteristics may not increase its potential to be invasive in a different situation (e.g. a dense forest). Vice versa, the abiotic characteristics (e.g. soil and climate) and the biotic community in this specific area may make it a perfect spot for one invading species, but not for a different one. Species traits and abiotic as well as biotic characteristics of a site are, therefore, linked to each other like a key and a lock (Heger and Trepl 2003).

► *Invasiveness and invasibility cannot be used as absolute categories. No species is invasive everywhere, and no area is invasible for every species.*

Which species characteristics are favourable to become a successful invader depends on which ‘problems’ the potential invader has to solve during its specific invasion process (see Box 8). For a potentially invasive tree, a seed with a thick coat may be very helpful in the case where at the site to be invaded, seed predators exist which can be repelled by this feature. If the seed has been transported to a site without seed predators, this feature is not necessary. Depending on the situations that occur during the invasion, a species may thus pass through the whole process even if it does not have any of the traits that are considered favourable for an invasive species. Nevertheless, having many such favourable traits will increase the probability to become a successful invader. Similarly, favourable conditions at a site can increase the probability that an introduced species will be able to establish. But the crucial mechanism to keep in mind is: favourable species traits or favourable environmental conditions are necessary conditions for invasion success only if the corresponding ‘problems’ actually do occur (see Box 8; Heger and Trepl 2003). This circumstance has been termed context-dependence and it increases the above mentioned complexity, which we have to understand and handle when trying to explain, and – even more difficult – predict invasion processes.

Box 8: The model of invasion steps and stages (INVASS model)

From the viewpoint of an invading species, the invasion process can be dissected into different steps and stages, each connected to a certain set of problems that need to be overcome. This is the basic idea of the model of invasion steps and stages (INVASS model; Heger and Trepl 2003, Heger 2004). In Figure 18, each invasion stage describes a status that a species can reach during its invasion process. To get from one invasion stage to the next, an invasion step needs to be taken, which means that a specific set of problems needs to be solved (Figure 19).

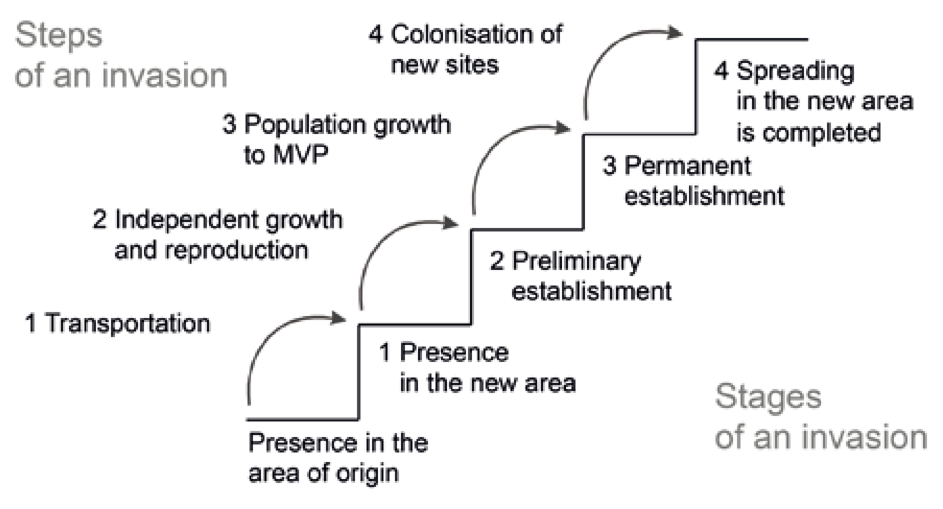

Figure 18: Chronological dissection of an idealised invasion process into steps and stages. Different stages are reached by overcoming a sequence of steps in the course of an invasion. MVP: Minimum viable population. From Heger and Trepl (2003), with permission of Springer.

To give an example, seeds of a cultivated tree may have been transported to a nearby site outside the plantation, e.g. by a bird. During invasion step 2, this seed will now have to grow without being cultivated, and the mature plant needs to reproduce. A first problem that could potentially occur is a seed predator. A favourable condition at the site, from the viewpoint of the invader, would be the presence of fewer predators than could be expected, e.g. as a consequence of enemy release (Keane and Crawley 2002). A favourable trait would be to have a general defence mechanism, e.g. a thick seed coat. With this approach of "taking the viewpoint of the invader", potential problems that may hinder the invasion process can be named for every invasion step, and conditions as well as species traits favourable to overcome every one of these problems can be identified. Respective lists can be found in Heger (2004) and Heger and Böhmer (2005).

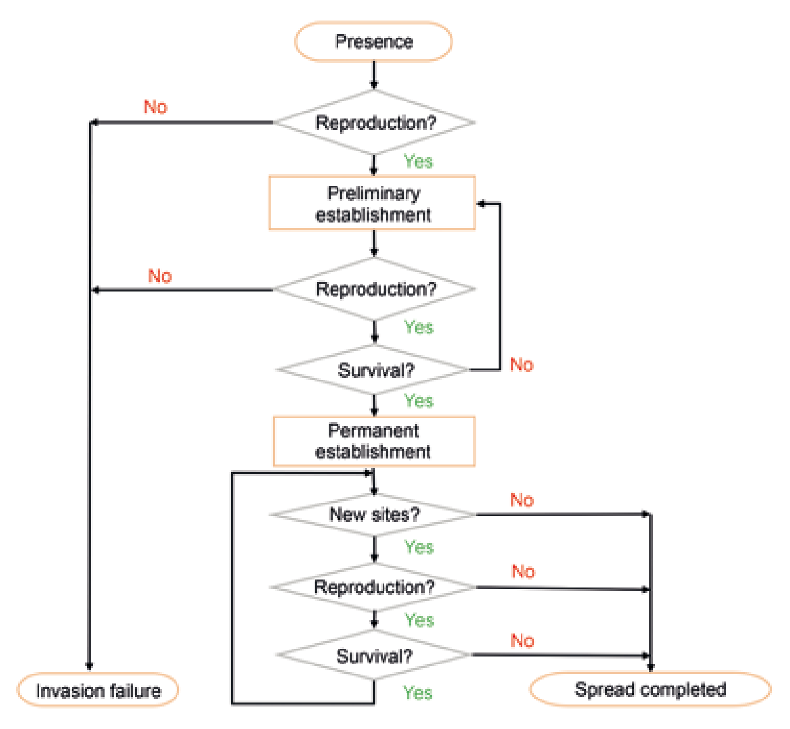

Figure 19: Flow chart of an idealised invasion process according to the INVASS model. Invasion stages are shown as orange rectangles; the major problems species have to overcome during each invasion step are shown as grey diamonds. "Reproduction?" means "Is the species able to reproduce without being cultivated?", "New sites?" means "Are other suitable sites available, and can they be reached by the species?" (from Heger 2004).

In addition to species traits, abiotic characteristics of a site and the composition of the resident species community, there are more factors influencing whether a species will be able to invade. The most important of these factors seems to be the so called 'propagule pressure', i.e. the number of times a species is introduced into an area, and the number of organisms (seeds, root fragments, adult organisms or other) that are present. It has been shown several times that propagule pressure is a very good predictor of invasion success: the more often a species is transported into a certain area, the more likely it is that this species will be able to establish.

Propagule pressure adds a new dimension to the set of factors influencing invasion processes. How often a species is transported into an area is determined by socio-cultural processes, such as occurrence of trading routes, planting frequencies, or number of visitors to a national park. The high importance of this factor in determining the fate of an invasion shows how strongly biological invasions are driven by non-ecological factors. Socio-cultural factors are the main reason why invasions occur, and they can influence invasions during every phase of the process. This is why it is not possible to explain and predict the course of an invasion taking into account only biological features of the species or its environment. Socio-cultural factors make predictions about invasions challenging: invasion science has to leave the realm of natural sciences to improve abilities to explain and predict (Küffer 2010).

Not only ecological, but also socio-cultural factors, e.g. trends and trading routes, determine the course and the outcome of invasion processes.

An additional aspect complicating explanation and prediction of biological invasion results from the fact that during an invasion, species get transported into areas where they did not evolve. In the new area, these species in many cases are confronted with abiotic conditions they have not experienced before (e.g. different soils, different humidity) and biotic conditions (presence or absence of competing and predatory organisms). As a positive effect from the viewpoint of the invaders, many predators within the native range are left behind, and in exchange, they encounter species they did not have any experience with in their native range. In almost every invasion case, the invading species meet novel predators and novel competitors. They may also not find the mutualists they have co-evolved with in the novel range. Much of the 'eco-evolutionary experience' they gathered in their native range is no longer applicable. Vice versa, the resident species are confronted with a species they did not encounter before (Saul et al. 2013). The outcome of an interaction which has never occurred before (e.g. of an invading tree and the resident insect herbivores) is difficult to predict.

Furthermore, no species is a stable, unchanging object, but instead, species are evolving constantly. Evolution has been perceived as a process taking place very slowly, and evolutionary change as something that happened long time ago. Meanwhile it has become clear that evolutionary change can happen quite fast, i.e. in just a few generations, and that species are constantly confronted with selective pressures eventually causing changes in species traits (e.g. Erfmeier 2013). It has been shown that many invasive species did change genetically in the new range (Maron et al. 2004), and also that resident species sometimes change in response to an invader (Leger 2008, Lau 2012). Also, hybridisation of introduced and native species can lead to the formation of novel species which are sometimes even more vigorous than their parents (Ellstrand and Schierenbeck 2000). It may be possible to predict such general patterns (e.g. that closely related species are likely to hybridise), but concerning the probability of establishment and spread of introduced species, the possibility for evolutionary change is another factor challenging precise predictions.

Novel interactions and evolutionary changes are some of the processes challenging predictions of the outcome of invasions.

Despite these inherent difficulties which make precise predictions difficult or even impossible, there is an urgent need to assess the risk from potentially invasive species. Prevention of biological invasions has been named as a prime aim in the Convention on Biological Diversity (CBD 1992) and the EU regulation No 1143/2014 on the prevention and management of the introduction and spread of invasive introduced species (EC 2014). In order to apply efficient measures for preventing the introduction of potentially invasive species into a region, it is necessary to distinguish high risk species from those that are very unlikely to become invasive in that area. Several risk assessment schemes have been developed and applied to reach this aim. Many of these tools achieve good results, and it can be expected that further improvement of the procedures will lead to even better results in the future.

Nevertheless, due to the factors named above, i.e. complexity, context-dependence, the influence of socio-cultural factors, novel interactions and evolution of invaders and resident species, risk assessment schemes will never be able to correctly classify the analysed invasion cases all the time. Risk assessment procedures will become better and better in predicting the probable invasion cases, but the less likely an event is, the more difficult it is to predict. This so called ‘base rate effect’ has been identified as a problem also for weather forecasts and the prediction of earthquakes (Matthews 1996, 1997). As an example, during times when the weather forecast has not been as accurate as it is today, someone going for a walk for an hour in England was better off taking an umbrella for the walk instead of looking at the forecast – because the event of ‘no rain for one hour’ is so unlikely that the forecast in most cases did not make a correct prediction. For invasions this means that we may get better and better in predicting very likely invasion cases, but there will always be a base rate of unlikely events which are unpredictable (Lonsdale 2011).

Risk assessments for obvious reasons are based on data reflecting current states. Data on current distributions of species oftentimes can be a good basis for predictions: whether a species is invasive elsewhere has proven to be a very good predictor of future invasion risk (Reichard and Hamilton 1997, Herron et al. 2007). Most risk assessment schemes require judgment on how establishment and spread may be influenced by predicted climate change. In many cases, this is done by assessing whether the species in question may benefit from a warmer climate or not. Sometimes ecological models are used to improve these predictions. In any case, what cannot be taken into account by current expert judgment or modelling techniques is the fact that species may change genetically in response to a changed climate. Also, the long-term effects of invasions are far from understood: the abundance and impact of invasive species in their new environment may change drastically over time, due to many interacting ecological and evolutionary processes (Strayer et al. 2006).

Predictions of the risk of establishment of introduced species have already reached acceptable accuracies. Much harder to predict is the future development of the established populations, especially under the influence of changing climate and novel interactions.

In conclusion, there are many reasons why precise predictions of biological invasions will always be difficult or even impossible. Nevertheless, the prediction of 'common cases' is possible. Future research should try to push the limits of predictability, and to improve existing risk assessment methods and predictive models as much as possible. The aim should be to improve predictability also of the less likely cases, and to put more research effort into long-term effects of invaders in the face of likely ecological and evolutionary changes. Concerning management approaches and also the evaluation of invasive species, we will have to stay flexible. The future will show how many species will decrease in abundance again after some generations, even without management, and how well resident species will be able to respond to their novel neighbours in the long run.

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2.4 Praise and damnation – perceptions towards introduced tree species vary and change with time

Uwe Starfinger and Ingo Kowarik

▶ *In addition to facts, with regards to introduced trees, perception matters.*

There is a long tradition and ongoing practice of using introduced tree species for many different purposes, including trees planted as ornamentals in parks, gardens and as street trees as well as for timber production or other forestry purposes. Yet, such plantings can induce biological invasions that are often considered as a major driving force in decreasing biological diversity (Richardson and Rejmánek 2011). Invasive alien species also cause substantial economic loss; the total cost of these species in Europe was recently estimated to be at least €12.5 billion per year (Kettunen et al. 2009). They consequently rank very high in international policies for nature conservation; e.g. the Convention on Biological Diversity or the recent Regulation of the EU on the prevention and management of the introduction and spread of invasive alien species (EU 2014).

The co-existence of risks and benefits associated with introduced tree species obviously generates different and often conflicting perspectives and perceptions about using such species (Dickie et al. 2014). Such conflicts are particularly noticeable in the case of introduced tree species in forestry and landscaping. Many of these species are valued for their timber production and superior growth rates and are preferred over native tree species in forest plantations. As a consequence, an estimated 25 % of the global forest plantations consist of introduced tree species (FAO 2010). In some parts of Europe, foresters rely strongly on introduced tree species, which are seen as better suited for plantation forestry than native ones (Brundu and Richardson 2016).

In the face of existing, or assumed, invasion risks, many stakeholders argue for preferring native species over introduced ones since the former do not invade and are better integrated into native ecosystems (Kendle and Rose 2000, Sjöman et al. 2016). Consequently, policies have been developed that generally prefer the use of native species (Brundu and Richardson 2016). Such policies on introduced species are largely related to invasion risks, but assessing such risks is also a matter of perception and underlying values. In this chapter, we will use the case studies on two prominent introduced tree species in order to illustrate how attitudes towards (formerly) frequently cultivated invasive species may differ in specific situations and how they may change over time.

▶ *Perceptions vary among stakeholders.*

Perception on invasive tree species varies widely between parts of the public and between different professional fields. Laypersons have been reported as being not aware of the negative impacts that invasive plants may have (Lindemann-Matthies 2016) and judge plants as attractive, exotic or familiar on the basis of their appearance. The same people in this study mostly agreed with the eradication of plants when they were informed about the high cost or health problems these plants cause. Even the perception of professionals is not necessarily based on impacts. In Spain, Andreu et al. (2009) found a high awareness of invasive species among environmental managers. The decision to control such species, however, was based on local perceptions of abundance, distribution, and perceived impact rather than on the status of a species in the national classification system. Similarly, the perception of invasion risks broadly varied among stakeholders in northern Germany, and an important proportion of decisions on control were not backed by reported impacts (Kowarik and Schepker 1998). A South African study demonstrates the significance of local factors (e.g. land tenure or proximity to invasions) in modulating perception patterns (Shackleton et al. 2015). Yet, a recent study on beliefs and attitudes towards introduced species suggests that "ways of reasoning about invasive species employed by professionals and the public might be more compatible with each other than commonly thought" (Fischer et al. 2014). Transparency in processes regarding assessment of the impacts of introduced tree species and whether they should be planted or controlled would thus increase the acceptance of related decisions.

It took time to understand the multiple effects of introduced trees.

Exploration of unknown regions has always resulted in the discovery of new plant species and where possible bringing them home. These exotics were highly valued and sought after and gave rise to a whole industry, that of the plant hunters (e.g. Fry 2013). When forestry became a popular subject in Germany between 1770 and 1850, the possible introduction of exotic tree species was a topic of much interest as their use was proposed to help increasing the production of timber after centuries of deforestation in Europe. In the second half of the 19th century, systematic testing of introduced tree species began with the aim to improve timber production. After long periods of clear-cutting without regenerating the forests, a shortage of wood led to the search for the best species to produce valuable timber fast and on a wide array of soils. In several European countries, experimental forest research stations were set up with the task of finding suitable tree species, among the first of which were black cherry (*Prunus serotina* Ehrh.) and black locust (*Robinia pseudoacacia* L.) (Booth 1896; see Chapter 1.2.).

Biological invasions as an ecological and biogeographic phenomenon received a growing interest after the publication of Charles Elton's (1958) book '*The ecology of invasions by animals and plants*'. Trees and shrubs, however, were for a long time not recognised as an important group of invasive introduced plants and only between 0.5 and 0.7 % of tree and shrub species are known to be invasive (Richardson and Rejmánek 2011). Through the wide use of these species in forestry and other for other purposes, the importance of woody plant invasions has been increasing.

Not so easy: is a forest pest a forest pest or is it not?

The North American black cherry (*Prunus serotina* Ehrh.) can be used to show how perception of different people varied throughout the time (Starfinger et al. 2003). In the years following its first introduction to Europe in the early 17th century, this tree species was valued as an exotic rarity like many other newly imported plants of that time. With its stunning flowers, edible fruits, shiny foliage and bright autumn colours, it was also a welcome addition to parks and large gardens as an ornamental. Further positive perceptions of the species came from the forestry sector as this species was hoped to be able to produce valuable timber even on poor soils. Later, it was claimed that it would improve soil and site conditions in conifer plantations (von Wendorff 1952) and it was perceived as an 'assisting tree species' – a species valuable not for its quality timber, but for its benefits to the forest as a whole; e.g. due to positive effects on soil processes. A programme of widespread planting led to the existence of forests with dense shrub layers of black cherry in a large proportion of the north central European alluvial soils from Poland to France. These stands mostly originate from initial plantings and subsequently increased due to the spontaneous regeneration and spread of black cherry.

This development led to the next change in perception. Starting in the 1960s in the Netherlands, foresters began to call the species a 'bospest' (forest pest; further detail in Chapter 5.6). The perception of black cherry as a forest pest was closely tied to the idea that it could, and should, be controlled; however, even the perception of it as a controllable plant was outstripped by reality. In many forests, the idea of getting rid of black cherry is no longer prevalent now. Many foresters rather feel that, not only do we have to live with the species, but living with it is also not such a frightening bad option. Recent work in several German forests hints at chances to develop Scots pine (*Pinus sylvestris* L.) forests, where dense stands of black cherry occur, into more species rich mixed forests by scheduling measures in accordance with the changing light availability during the development of the black cherry population (Hamm et al. 2015a). As the cherry population ages, the available light on the forest floor is minimised, which increases the chances for establishment of other (shade-tolerant) tree species. In a glasshouse experiment, Hamm et al. (2015b) even found evidence of a positive influence of cherry litter on growth of other trees.

The black cherry story illustrates how the perception of a plant by the public and by professionals varied in the course of the centuries (Figure 20). It is striking how perceptions and attitudes towards the species that have persisted, and were often based on assumptions rather than evidence, and how studies of the species come up with new ideas on management after decades of applying management practices. In addition to changing assumptions, even the ecological behaviour of a species may change over time: relatively few herbivorous insects were recorded feeding on black cherry in the past, but, a more diverse herbivore community has developed over the course of the last centuries (Schilthuizen et al. 2016).

In the case of black cherry, experts from the fields of nature conservation and forestry agreed that the species is undesirable; this decision was supported by the scheme for identifying invasive alien species (i.e. German-Austrian Black List Information System – GABLIS; Essl et al. 2011) that placed black cherry on the black list (Seitz and Nehring 2013a). In addition, black cherry was also evaluated by an alternative assessment scheme, based on foresters' perspective (Vor et al. 2015), that assessed black cherry as invasive and not recommended for cultivation in forests. In conclusion, the case of black cherry provides an example of changing attitudes towards a species and associated management practices. Only recently, the assessments of pest status have been made based on more clearly described protocols.

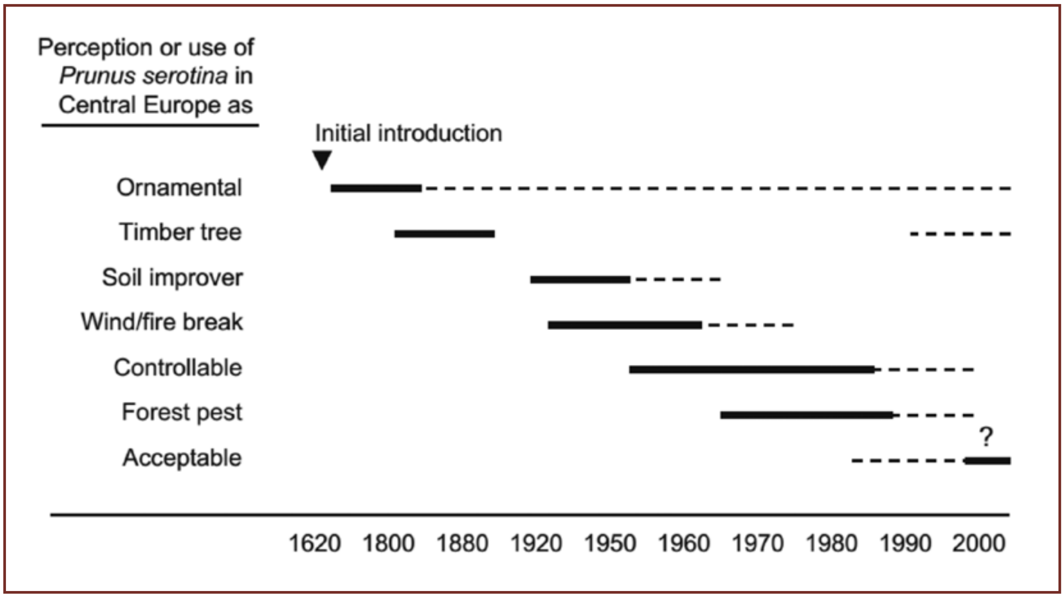

Figure 20: Perception and uses of black cherry in Europe at different time periods. The dotted line indicates that a perception exists at a time, the thick line indicates the time when this notion prevailed (reprinted from Starfinger et al. 2003 with permission of Springer).

A harmful species in a nature conservation area: not necessarily a problem.

Black locust (*Robinia pseudoacacia* L.) is another species native to North America that has a long tradition of uses as an ornamental, forest tree, street tree, and is also favoured by beekeepers (Cierjacks et al. 2013). The tree is naturalised in many parts of the world including Asia, Africa and several countries in Europe. Black locust is an early successional species readily colonising open grounds, but not regenerating in the shade usually out-competed by longer living hardwoods in the course of succession. Because of its nitrogen-fixing ability it can strongly influence nutrient cycles in invaded ecosystems. It is considered an invasive species because of its ability to invade and strongly alter open habitats, e.g. grassland, by shading out present vegetation and changing soil conditions. It is therefore classed as an invasive alien species, and has been placed on, for example, the German black list (Seitz and Nehring 2013b) as well as on lists of invasive species in other countries (further details in Chapter 5.1). In near-natural sites, it is often considered as a nuisance and a lot of effort is made to control it. In many countries, the control is predominantly done by chemical means, albeit with varying success (CABI 2016). However, where the use of chemicals is limited, alternatives like girdling are applied with mixed success (recent overview in Schmiedel et al. 2015). These negative impacts are contrasted by some positive uses in forestry and in short rotation coppice systems used for bioenergy production. Foresters (Vor et al. 2015) attest it limited invasiveness as it does not regenerate and spread under tree canopy and some degree of suitability for forestry use.

In its invaded range, black locust is often found in urban-industrial habitats with a high degree of disturbance, where it forms new communities and since it is nitrogen fixing, even completely ‘novel urban ecosystems’ (Kowarik 2011). In Berlin, the political situation after the Second World War led to the development of many such unusual ecosystems, which resulted in the development of urban ecology as a more developed branch of science (Sukopp 1990). Much of the built-up area was destroyed in the war and when the city was divided between East and West Germany some of these sites were not re-developed for a long time. One example is an inner city cargo railyard from the 19th century that was left abandoned for decades after the war, the so called Schöneberger Südgelände. Here, black locust formed a large part of the developing plant communities, while other parts were dominated by the native silver birch (*Betula pendula* Roth) or remained open for a long time. The almost completely undisturbed succession of the vegetation on strongly artificial soils was unique. After the fall of the Berlin Wall, many of these inner city wilderness areas were developed. The Schöneberger Südgelände was an exception, and it was set aside as one the first formally acknowledged nature conservation areas in Germany dedicated to urban-industrial nature (Kowarik and Langer 2005). Here, the role of black locust in a nature reserve is the absolute opposite to its role in other natural reserves, where it is perceived as a noxious species that needs to be exterminated. In Schöneberger Südgelände, a new chance arose for allowing the successional development of novel forest communities in an urban setting over a long period. The black locust example shows that even where judgement of a species is based on a clear protocol like the black listing, alternative attitudes may co-exist and result in e.g. control measures, local eradication, forestry use or conservation.

▶ *Listing the bad guys is good – but does not solve every problem.*

The above examples show that assessment of introduced species depends on context, which is not always openly acknowledged. Policies dealing with introduced species need to be based on transparent, reproducible and documented procedures. These should guarantee – and allow for discussion – the use of underlying data on impacts (e.g. impact sizes or affected resources) and normative assumptions that guide the assessment of damage or benefits. For this purpose, assessments for black lists of invasive alien species may be used such as the one developed for the German Federal Agency for Nature Conservation (Essl et al. 2011, Nehring et al. 2013, 2015). The above-mentioned example of black cherry demonstrates the need to make judgements about a species based on facts rather than vague notions and perceptions as happened in the past. Transparency is also necessary in order to take into account the different perspectives and perceptions (Pergl et al. 2016). Black lists may be a valuable tool in enhancing biosecurity of countries or regions. The black locust example, however, shows that a species is not inherently noxious or totally beneficial in all situations, but that its damage or value needs to be assessed on a case by case basis. It is the rule rather than the exception that black listed plant species can be harmless and favourable in certain situations. In the context of the EU regulation 1143/2014, work has been done on the development of a listing mechanism and on a first list of invasive species of EU concern, which will consequently be banned from sale, use, planting, etc. This list will be further developed. Though this list is not meant to contain very large numbers of introduced species, it may result in conflicts of interest.

A further question is how to handle tree species that (i) do not fall under the EU regulation 1143/2014 but, (ii), are black listed in one or more European countries, and (iii), result in detrimental and beneficial effects, depending on the context. For supporting decisions on using or managing such species, black list classification provides important but insufficient information. Black lists classify species on a typological level and are thus not expected to consider impacts that usually vary at a regional scale. Moreover, the question of which categories of ecosystem services are addressed matters (Dickie et al. 2014). Take again the black locust example: this tree broadly changes ecosystems due to its specific ecological features. Yet, not all of these changes conflict with the aim of biodiversity conservation. A comparison of plant and animal assemblages associated with black locust and silver birch stands in urban areas revealed the missing of clear negative impacts of the introduced tree species on biodiversity. Stands of the native tree species had some more plant species, but the dominance of the introduced tree species did not result in homogenization of associated plant species assemblages; native species assemblages were even more heterogeneous in black locust stands (Trentanovi et al. 2013). Assemblages of spider and carabid species associated with black locust were as diverse (alpha, beta diversity) as those in native forests on similar urban sites (Buchholz et al. 2015).

Planting even black listed trees may thus be considered for certain occasions, on the understanding that comprehensive and realistic risk assessments are available that consider variation among geographical and ecological contexts and exposure to susceptible ecosystems of conservation concern. In northern countries with a cooler climate, potential risks are considerably lower than in warmer parts of Europe such as in Austria or Hungary. In urban greening in particular, a complete rejection of introduced trees may compromise the variable goals of tree planting (Sjöman et al. 2016). With climate change, invasion risks will increase (Kleinbauer et al. 2010), but due to dispersal limitation, plantings of black locust at an adequate distance to susceptible ecosystems may be safe even in warmer regions.

Help from plant health: risk analysis can standardise verdicts.

Many invasive species meet the criteria for the definition of plant pests in the sense of the International Plant Protection Convention (IPPC), because they threaten other plants. The plant health realm protocols for pest risk analysis (PRA) have been in use for a long time. They follow internationally agreed standards (International Standard on Phytosanitary Measures (ISPM 11) and were developed as a basis for preventing the introduction of unwanted pests. Because they are acknowledged by the World Trade Organization as a reason to impose trade barriers, PRAs were strictly required to be transparent, detailed and impartial. They are thus less biased than statements based on perceptions. Because of the wide overlap between the concept of 'Invasive Alien Species' in the Convention on Biological Diversity and the 'Quarantine Pest' in the IPPC, the phytosanitary PRA can also be used to help assess the potential negative effects of tree species used for forestry purposes (Schrader and Starfinger 2009).

In a complex matter, some signposts help lead the way.

Finding solutions to the problems posed by invasive alien species is a task for the society as a whole, not for experts alone. Therefore, it is important to acknowledge that different groups have different perceptions. Legal regulations at national and European scales clearly define important signposts. They imply some fixed consequences in handling invasive tree species, but often also leave opportunities for developing approaches that may vary across regional and cultural contexts. Knowledge generated in the quickly developing discipline of invasion science may help to guide the discussion. Better understanding invasion impacts in relation to biodiversity conservation and other societal goals is in the scope of modern invasion science as is the development of approaches towards preventing or managing biological invasions (Kühn et al. 2011). Despite this broad scope, (invasion) scientists often have a different focus than other stakeholders (Bayliss et al. 2013). Stakeholder involvement is thus of vital importance for developing and implementing policies and decisions on using or managing introduced plant species.

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2.5 Co-invasion of invasive trees and their associated belowground mutualists

Martin A. Nuñez, Nahuel Policelli and Romina D. Dimarco

The majority of trees need mutualistic associations to thrive and survive. This can be a fundamental limitation for their ability to colonise new areas and consequently invade them. While many non-native tree species may form associations with local mutualists that substitute those present in their native range, others, probably with a higher degree of specialisation invade along with their native range mutualists (co-invade). An example of this is the case of some figs (*Ficus* spp.); in the USA, these trees which have a highly specialised pollination system depending on particular species of wasps, became invasive only after their native pollinator had arrived (Richardson et al. 2000). Other examples can be found in many invasive trees that need belowground mutualists, like nitrogen-fixing symbionts and mycorrhizal fungi, to thrive in their new geographical range (e.g. Nuñez et al. 2009, Dickie et al. 2010). These soil mutualists have been found to play a key role on the invasion of numerous introduced tree species (Nuñez and Dickie 2014).

> *New technologies allowed researchers to understand and further appreciate the role of belowground organisms and how they can influence plant populations and communities.*

Historically, researchers have had biases when studying mutualistic interactions since they were solely focused on the plant perspective with a strong emphasis on aboveground interactions (e.g. pollination). This has been, in part, due to our own view of the world from an aboveground perspective, and based on the paradigm that soil microorganisms are everywhere and are not dispersal limited (Peay et al. 2010). In the last few decades, new technologies have emerged, involving molecular tools, allowing researchers to understand and further appreciate the role of belowground organisms and how they can influence plant populations and communities. Given this historic absence of focus on the belowground aspect of the invasion process, we currently have many unanswered basic questions about plant invasion and their associated mutualisms. One example is the limited information we have on how mycorrhizal fungi are dispersed (Galante et al. 2011). In the last years there has been more research on this topic and hopefully soon, we will have a deeper understanding of the importance of invasive belowground biota for the success of tree invasions.

This chapter presents the current understanding of tree species invasions and their invasive belowground mutualists. The term invasive species (for both plants and their mutualists) will be used following an accepted classification (Blackburn et al. 2011), which does not include non-native species that were introduced to an area and never escaped from their introduced range – e.g. dwarf mountain pine (*Pinus mugo* Turra) or giant sequoia (*Sequoiadendron giganteum* (Lindl.) J.T. Bucholz) in Patagonia (Nuñez et al. 2011) and many commercial tree species. Mutualistic species only colonising tree species that have never escaped plantations will also not be included – e.g. eucalypts (*Eucalyptus* spp.) in Spain (Diez 2005). All possible scenarios of tree invasion and their belowground mutualists, particularly focusing on the co-invasion process are addressed in this chapter.

> *The majority of invasive trees require belowground mutualists to successfully invade.*

While most invasive tree species require belowground mutualists to successfully invade, other tree species do not need them. Invasions by species that are not dependent on mutualisms are not limited by absence of a mutualist (Figure 21). For example, invasive trees such as woody Proteaceae (Allsopp and Holmes 2001) do not associate with mycorrhizal fungi or nitrogen-fixing bacteria to colonise. Most of these plants have non-symbiotic nutrient uptake alternatives, such as cluster roots in the case of Proteaceae (Allsopp and Holmes 2001), and sometimes, they can successfully invade by disrupting existing mutualistic interactions of their competitors, therefore increasing their competitive ability (van der Putten et al. 2007, Meinhardt and Gehring 2012).

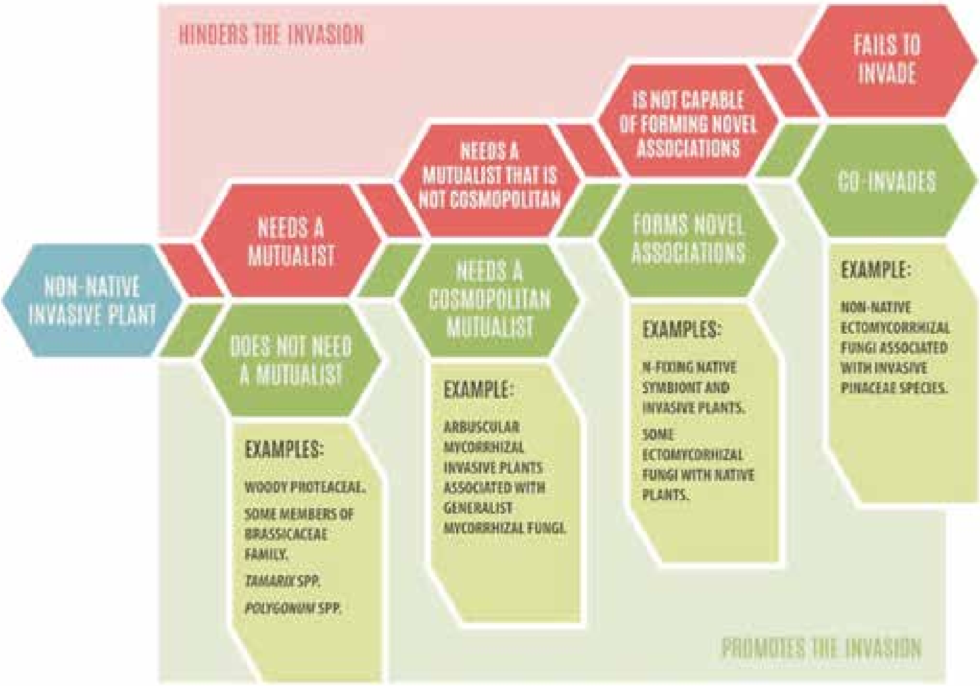

Figure 21. Four different strategies that allow plants to become invasive in relation to the presence or absence of soil biota. Some common examples are mentioned below each strategy.

> *Belowground mutualists can be cosmopolitan, establish a novel association or co-invade with tree species.*

Three main strategies can be recognised in tree species requiring belowground mutualists (Dickie et al. 2010) (Figure 22).

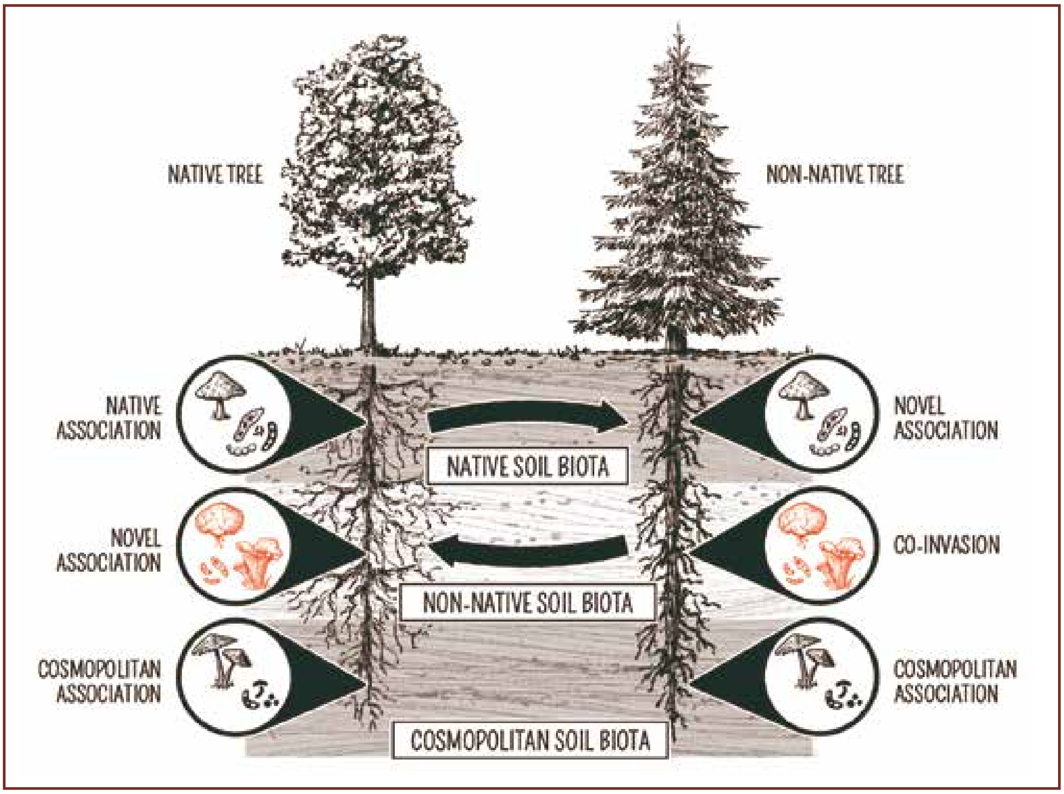

Figure 22. Diagram of the possible ways that native and non-native tree species havefor interacting with native, non-native and cosmopolitan soil mutualists. Co-invasion occurs when both, the plant and the mutualist, are non-native. Novel associations can occur with a native plant and a non-native symbiont, or with a non-native plant and a native symbiont. A special type of novel association is the "co-xenic" association where both plants and mutualists are non-native, but originate from distinct geographical ranges.

'**Cosmopolitan**' associations occur when there are introduced tree species and the mutualists are native to both the home range of the tree and the introduced range. These cosmopolitan associations are common between arbuscular mycorrhizal invasive plants that associate with generalist cosmopolitan mycorrhizal fungi – e.g. Chinese windmill palm (*Trachycarpus fortunei* (Hook.) H. Wendl) (Moora et al. 2011).

A second strategy involves the formation of '**novel**' associations and includes those introduced tree species that are capable of establishing novel associations with symbionts that are present in the introduced range but not in the native range (non-native tree, native symbiont). A reported example of this strategy is the case of native fungi from the Republic of Seychelles that form ectomycorrhizal symbioses with planted *Eucalyptus* spp. (Tedersoo et al. 2007). Another type of novel association occurs when an intoduced symbiont associates with native trees (native tree, non-native symbiont) as documented for the association between native southern beeches (*Nothofagus* spp.) trees and non-native *Amanita muscaria* (L.) Hook.) in New Zealand (Orlovich and Cairney 2004). A third type of novel association occurs when an introduced plant associates with a non-native symbiont but that do not share the same home range (co-xenic associations). An example is the ectomycorrhizal fungi *Suillus luteus* (L.) Roussel from Europe colonising North American trees, such as ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) and lodgepole pine (*P. contorta* Douglas ex Loudon), in South America (Hayward et al. 2015a).

The third strategy is '**co-invasion**' and seems to be at least as common as the occurrence of novel interactions (Figure 22). Co-invasion occurs when mutualists that are present in the native range of an introduced species are also introduced (intentionally or by accident) along with the introduced plant (Mikola 1990). Ectomycorrhizal Pinaceae species tend to co-invade more than other groups, although this tendency could be driven by the effort that has been made in introducing ectomycorrhizal symbionts due to the commercial importance of Pinaceae, and biases in research effort. After co-invasion, the mutualistic species can expand from their introduced host and form novel associations with native trees such as the economically important ectomycorrhizal fungi *Tuber indicum* Cooke & Massee, or the toxic *A. muscaria* and *A. phalloides* (Vaill. ex Fr.) Link (Dunk et al. 2012).

There are also exceptions to the above-mentioned strategies. Although many invasive nitrogen-fixing plants are able to generate novel interactions in their new range (Rodriguez-Echeverria et al. 2009), there is evidence that some may need to co-invade to successfully become invasive (Rodriguez-Echeverria et al. 2011). Something similar happens in the case of black locust (*Robinia pseudoacaccia* L.), a plant that associates with arbuscular mycorrhizal symbionts; black locust performs better with arbuscular mycorrhizal fungi from its native range (co-invade), despite being known to be promiscuous in associations as is general the case for arbuscular mycorrhizal plants species (Smith and Read 2008).

▶ *Not all soil mutualists have the capacity to invade.*

There are numerous factors that can affect the invasive capacity of non-native soil organisms. Some mutualistic mycorrhizal fungi, for example, that produce high numbers of spores, and have the ability to disperse the spores by wind, water or local dispersal agents such as animals are likely candidates as invaders (Nuñez et al. 2013). Moreover, invasion can be facilitated if soil organisms can associate with an abundant plant species and/or a variety of plant species. The production of high number of propagules has also been shown to be associated with invasion (Peay et al. 2012). Previous studies have found that mycorrhizal fungi species with high production of spores tend to invade (e.g. *Rhizopogon* spp., *Suillus* spp.), while many species that are found associated to roots of planted trees are rarely, or never, found outside plantations (e.g. *Cortinarius* spp., *Inocybe* spp.) (Hynson et al. 2013, Hayward et al. 2015a). In general, the soil organisms that tend to invade are species that are found colonising the native range after a disturbance (Hayward et al. 2015a).

The invasion capacity of mutualists is also determined by their host specificity. If a mutualist has a high level of host specificity, but associates with a highly invasive tree species, then specificity is not a limitation for its invasion. This seems to be the case for several species that co-invade with pines, such as *Suillus* spp., which are highly invasive in the southern hemisphere (Hayward et al. 2015b). If the soil mutualist species has a low level of host specificity, it could thrive by forming novel associations in the invasive range with different tree species. This seems to be the case of arbuscular mycorrhizal fungi, some nitrogen-fixing bacteria, and some ectomycorrhizal species (Dunk et al. 2012).

New ecosystem functions may be created with co-invasion of certain species.

There are multiple impacts of co-invasions. One main effect is that it allows non-native tree species to invade. This could notably change ecosystems, for example by converting grassland into a forest. The absence of co-invaders could limit the growth and spread of invasive trees and also result in the failure of forestry plantations because of the absence of adequate ectomycorrhizal inocula. Non-native soil mutualists can also present novel enzymatic pathways for the invaded ecosystem that could include, for example, atmospheric nitrogen fixation (see Vitousek et al. 1987) and nutrient uptake from previously unavailable sources, such as organic forms by ericoid mycorrhizal or ectomycorrhizal fungi. This could have important impacts especially if such a function is new to the system. For example, the invasion of ectomycorrhizal fungi and their co-invasive plants on some oceanic islands like Hawai'i would represent an entirely novel ecosystem function, since there are no native ectomycorrhizal trees on some of these islands (Hynson et al. 2013).

Invading soil mutualists may also have impacts on native mutualists as the displacement of native plant species is the most obvious effect when non-native plants invade. Therefore, non-native mutualists could be expected to have the same effect. However, to date there is no strong evidence of this occurring (Nuñez and Dickie 2014). Some co-invasive mutualists (e.g. *Bradyrhizobia* associated with invasive acacias) have been found on native nitrogen-fixing plants (Rodriguez-Echeverria 2010). Also, *A. phalloides* originally associated with introduced tree species is now invading native plants in North America. However, studies on this topic showed no loss of ectomycorrhizal diversity in soil samples where *A. phalloides* was present (Wolfe et al. 2010).

If there is an impact by soil mutualists, it can result in a significant long term effect influencing future ecosystem trajectories.

Soil legacies tend to persist after the removal of introduced species and modify future plant communities and their native ecosystem function (Malcolm et al. 2008). As mentioned above, many effects of co-invasive mutualist can result insignificant long-lasting effects; however, co-invasive mutualists can also directly affect local plants and animals. Non-native *Bradyrhizobium* spp. colonise native legumes in parts of Europe and have notably less beneficial effects (i.e. nitrogen fixation) than native *Bradyrhizobium* species (Rodriguez-Echeverria et al. 2011). It is also important to note that some mycorrhizal fruiting bodies can be harmful to humans and animals if consumed. The highly toxic *A. phalloides* poisoned people in Australia and North America even resulting in some deaths (Trim et al. 1999).

The current understanding suggests that co-invasion of trees and their co-evolved symbionts is not a rare phenomenon, especially for ectomycorrhizas and nitrogen fixing symbioses, which are common for trees (e.g. Pinaceae, Fabaceae, Betulaceae, Myrtaceae) (Nuñez and Dickie 2014). The absence of a co-invader can limit the invasion of the tree and the associated soil organism since both must co-invade and in many cases are dispersed independently (Nuñez et al. 2009). In other soil mutualistic groups, such as arbuscular mycorrhizal fungi, the most important mutualistic group for invasive plant species (Figure 22), there is a relatively high promiscuity in terms of potential associations and wide fungal distribution (Tedersoo et al. 2014). For this reason, novel and cosmopolitan associations are common for many invasive plant species.

> ▶ *Management of invasive soil biota could be determinant for plant species invasions.*

A more detailed understanding of symbiotic interactions and the co-invasion process can be important in order to better understand plant invasions. Lag times, very common in invasive trees (Richardson and Higgins 1998, Simberloff et al. 2010), can be explained by interactions with soil biota (e.g. late arrival of the co-invasive symbiont). Also, from a management perspective, once soil mutualists are widespread, their control or eradication can be challenging given the small propagule size, and the potential to persist in an inactive form for long periods (Bruns et al. 2009).

There are ways to minimise the potential impacts of co-invasive mutualists; for example, the introduction of highly invasive non-native soil biota into new areas should be avoided. Also there are some mutualists that mostly spread asexually and seldom produce spores and they could be considered ideal for introduction. As mentioned before, absence of a co-invader may result in limited growth or complete failure of an introduced species, and so in some cases deliberate introduction of a mutualist might be considered desirable. For some introduced tree species that rely mostly on co-invasive mutualists, it could be possible to use native soil symbionts (Moeller et al. 2015), or to minimise introductions of new, non-native symbionts without biosecurity measures (e.g. by restricting movement of soil or trees in pots). Where deliberate introduction of a mutualist is considered, the potential for invasion by the mutualist, and the possible negative effects of that invasion, must be considered. Management of invasive soil biota or the restoration of areas invaded by soil symbionts is a daunting task given their belowground habit, their microscopic size and their ability to persist for long periods (Dickie et al. 2016). Therefore, it is of fundamental importance to control the spread of soil symbionts to avoid the numerous detrimental effects co-invasion can have. Efforts to control the spread of invasive species might be wasted if managers are unaware of co-invasion as a determining factor in whether a plant species becomes invasive or not.

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2.6 Maximising benefits and minimising harm associated with invasive introduced trees: lessons from South Africa

Brian W. van Wilgen

Although introduced trees are generally regarded as valuable, there are many examples of such species becoming invasive and generating more harm than good. It is therefore necessary to carefully consider the potential risk of a species becoming invasive before a decision is made to introduce it, or to plant it widely.

People introduce trees into areas outside of their natural distribution ranges for a number of reasons. The most important of these are for use in plantation forestry (for timber and wood products), or as ornamental plants in towns and gardens, but they are also used to provide fodder for livestock, firewood, fruit, shade, windbreaks, to sequester carbon and to combat erosion. Introduced trees are widely perceived as environmentally beneficial (Dickie et al 2014, van Wilgen 2012), and many are, leading to their widespread promotion by governments and aid agencies. However, several species can and do become invasive, spreading away from the areas where they were originally planted into adjacent land, where they bring about negative impacts, which in many cases eventually exceed the value of any benefit they may have. This often leads to conflict (van Wilgen and Richardson 2014), and unless clear policies are developed to resolve these conflicts, disagreements will continue and impacts will grow.

In South Africa, these issues seem to have received more attention than elsewhere; there are a number of possible reasons for this. The South African situation is arguably unique in that it is a largely treeless environment with a long (>350 years) history of colonisation (accompanied by the aggressive introduction of trees) that has led to extensive and well-established populations of invasive introduced trees (van Wilgen and Richardson 2012). There have consequently been many case studies of the impacts of invasive trees of non-native origin in South Africa, and many attempts to deal with the problem of managing invasions. Many valuable lessons have arisen from this experience, and they can be useful for informing policy and management in other parts of the world.

Impacts of invasive introduced trees. Numerous studies have documented negative impacts associated with invasive introduced trees in South Africa. Invasive introduced trees can substantially reduce surface water runoff from important watershed areas (Le Maitre et al. 1996, 2000), and this is a serious issue in South Africa, where water resources are limiting. Invasive introduced plants (mainly trees) are currently reducing surface water runoff by an estimated 43 billion m^3 (about 7 % of the national total); the potential reductions would be more than eight times greater if these tree species were to occupy the full extent of their potential range (van Wilgen et al. 2008). In addition, in arid areas, invasive introduced tree species reduce water levels in underground aquifers, again with substantial negative impacts (Dzikiti et al. 2013). In rangelands, invasive mesquite trees (Prosopis spp.) reduced grazing capacity by one third when they reached a relatively modest level of 15 % cover (Ndhlovu et al. 2011); and relatively heavy invasions of grassland by black wattle trees (*Acacia mearnsii* (De Wild.) reduced grazing capacity by 75 % (Yapi 2014). Invasive trees of non-native origin also impact negatively on biodiversity, and this is made more significant by the fact that several biodiversity hotspots (unique to South Africa) are particularly prone to invasion by introduced tree species (van Wilgen et al. 2008). In fire-prone ecosystems, invasive introduced trees increase the amount of fuel available to burn, which increases the impact and difficulty of controlling periodic wildfires (van Wilgen and Scott 2002). A number of studies have also estimated the net value generated by introduced tree species that simultaneously deliver benefits and cause harm, and these studies have indicated that the monetary value of harmful impacts often exceeds the value of benefits, leading to negative net values (e.g. Wise et al. 2012). The situation is not static either, as the costs of the impacts grow as the trees invade larger areas over time (van Wilgen and Richardson 2014).

Table 23. Examples of introduced trees that have become invasive in South Africa

Trees	Useful attributes	Invasion status and impacts
Pines (*Pinus* spp.)	Timber and pulp products; shelterbelts (*for wind*)	Several species highly invasive in fynbos shrublands. Reduces biodiversity and water resources; increases the risks of wildfires.
Australian gums (*Eucalyptus* spp.)	Timber and pulp products; firewood; pollination services	One species (*E. camaldulensis*) is highly invasive along rivers. This species has large negative effects, including the reduction of river flow and biodiversity, and destabilisation of river banks.
Australian wattles (*Acacia* spp.)	Timber, bark products, and firewood; stabilization of coastal sand dunes	Several species are highly invasive, especially along rivers, streams and drainage lines. Reduces biodiversity and water resources; increases the risks of wildfires; destabilises river banks.
Mesquite (*Prosopis* spp.)	Fodder and shade for livestock; firewood.	Highly invasive in arid areas. Depletes groundwater aquifers, reduces grazing capacity of rangelands; reduces biodiversity.
Jacaranda (*Jacaranda mimosaefolia* D. Don)	Ornamental flowering tree; iconic symbol of South Africa's capital city Pretoria	Not documented, but invades savanna vegetation and assumed to reduce biodiversity and water resources.
Willows (*Salix babylonica* L.)	Ornamental tree	Not documented, but invades river courses in savanna and grassland regions and assumed to reduce biodiversity and water resources.

Introduced and invasive trees in South Africa. Trees make up a significant proportion of the invasive introduced plants in South Africa (Figure 23). For example, 75 of the 238 (38 %) invasive plant species of non-native origin listed by Henderson (2001) are trees (excluding species that are listed as 'shrubs or small trees'); 15 out of the 19 groups of plants (79 %) targeted for control at a national level were trees (van Wilgen et al. 2012); 27 out of 79 species (34 %) listed as either 'very widespread' or 'widespread', and 'abundant' or ‘common’ by Nel et al. (2004) were trees; 12 out of 17 species (71 %) identified by managers as most deserving of control efforts were trees (Forsyth et al. 2012); and 19 out of 70 (27 %) of the species that have been targeted for biological control were trees (Klein 2011). A few genera make a disproportionate contribution to the national list, including Australian wattles (*Acacia*, 12 species), pines (*Pinus*, 9 species), Australian gum trees (*Eucalyptus*, 7 species) and poplars (*Populus*, 4 species). Several of these species, although they have several uses, have become particularly problematic (Table 23).

Figure 23. A: Invasive introduced pine trees spreading across fynbos shrublands; B: Invasive Australian wattles along a river course. Photo: B. van Wilgen

Experience in managing invasive introduced trees. The management of introduced invasive tree species has evolved over the past 40 years in South Africa in response to emerging problems such as excessive water use by plantations, changing values and markets, and the realities of a new ecological order brought about by invasive introduced trees (van Wilgen and Richardson 2012). Introduced tree control programmes were initiated in the 1960s, and they grew in size and geographical extent over the next decades as an understanding of the consequences of these invasions grew (van Wilgen and Wannenburgh 2016). The South African approach has included taking courageous steps to address the problem of highly invasive species that are also important commercial crops or popular ornamental species. Several important principles arise from this experience, and are summarised briefly in the sections below.

> *The ratio between the benefits and impacts of introduced trees changes over time. Initially, trees can provide net benefits, but these changes as they become invasive and start to spread. The current generation may reap some benefits, but future generations will suffer a net impact, and this needs to be considered when decisions are made to introduce trees.*

Values change over time. Introduced trees generally tend to provide benefits following their introduction to new regions, but this can change when some of them later become invasive and spread. Usually, introduction and widespread planting is followed by a period in which the net value is positive, arising from harvested products or other benefits (Figure 24). However, in cases where the species become invasive, values are eroded as the impacts of invasions grow, and the benefits are outweighed by the negative effects. Attitudes also change over time as values and priorities change, and as unforeseen impacts begin to manifest themselves. For example, in South Africa, European settlers initially introduced species with which they were familiar, but over time there was a growing recognition of the value of indigenous trees, followed by drives to plant indigenous rather than introduced species, and by the rise of a conservation ethic that followed the inaugural Earth Environmental Summit in 1992. Attitudes can become polarised, especially between those with vested interests in growing trees or trading in their products, and conservationists; the balance of opinion between those holding opposing views is also constantly changing, adding to the complexity of the issue (for more information on the conflict between forestry and nature conservation, Chapter 3.3). Almost certainly, the South African experiences with changing attitudes and values will be mirrored elsewhere in the world, especially as awareness of environmental issues, including the need to protect native biodiversity, is growing. It is therefore likely that the widespread use of introduced trees will be increasingly challenged in the future, especially if the species are invasive.

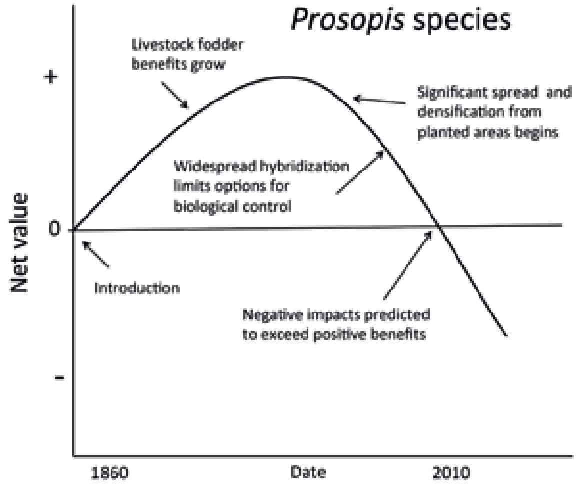

Figure 24. Changing net values (sum of benefits minus sum of impacts) over time associated with introduced mesquite trees (*Prosopis* species) in South Africa (after van Wilgen and Richardson 2014 and Wise et al. 2012).

> *Once invasive introduced trees have established in an area, gaining effective control will require a long-term commitment, and eventual success in reducing invasions to sustainably-manageable levels is not guaranteed. It is therefore much better to avoid introducing invasive trees than to try to control them later.*

Control requires long-term, focussed commitment. If a policy is adopted to control the spread of introduced trees in selected areas (for example in protected areas where there is an intention to maintain native biodiversity, or in agricultural areas where negative impacts need to be reduced), then it would be important to make a long-term commitment to the intervention. Unplanned, inadequately-funded, or short-term interventions will invariably fail. The existing evidence shows that poor understanding of the ecology of invasive species, as well as a lack of follow-through when clearing is done, can lead to much wasted effort and money. For example, Macdonald et al. (1989) reviewed 47 years of attempts to control invasive tree species on the Cape Peninsula, and concluded that they were 'almost totally ineffective for the first 35 years'. It was only after the introduction of long-term plans, with adequate funding, that progress was made in reducing invasions. In cases where control programmes are being considered, it is therefore vital to ensure good, long-term planning based on sound ecological understanding, and adequate funding. This principle would be universally applicable in all parts of the world.

Biological control is safe, and often essential. Biological control of introduced plants involves the identification and collection of selected 'biocontrol agents' (insects, mites or pathogens), in the country of origin, and the subsequent release of the agents in areas where the introduced plants have become problematic. This practice is cheap, safe and sustainable, and is regarded in South Africa (and several other countries, including the USA, Australia and New Zealand) as an indispensable component of any control operation (van Wilgen et al. 2013). For example, the deployment of biological control agents onto ten invasive alien tree species in South Africa's Cape Floristic Region has resulted in a substantial decline in the abundance and/or aggressiveness of most of the targeted host-plants (Moran et al. 2011). In other regions (including many countries in Europe) there is a reluctance to use biological control, despite the levels of success achieved, low costs, a track record of safety, the advantages of sustainability, and the absence in many cases of viable alternatives to biological control. The reasons for the reluctance of European countries to use biological control are complex, and they include the lack of previous experience, unclear responsibilities, poor funding and vague or even absent legislation (Bale 2011). The South African experience suggests that any programme to control invasive introduced plants should maximise the use of biological control to ensure that the overall control is effective and sustainable (Moran et al. 2011). Despite the outstanding track record of safety and effectiveness, the benefits of biological control remain poorly understood, allowing the risks to attain disproportionate attention (Sheppard et al. 2003). It is nonetheless also true that more biological control projects will be needed in the future to prevent impacts arising from an increasing number of invasive plants that are becoming established worldwide. There will thus undoubtedly be a growing need for biological control programs that will require the joint efforts of biological control practitioners, invasion biologists, ecologists, taxonomists, policy makers, and conservation specialists (van Driesche et al. 2010).

Biological control of invasive introduced plants is cheap and safe, and it often provides the only chance of achieving sustainable control. Despite an exceptional safety record, the biological control of plants is remarkably under-utilised. Every effort should be made to include biological control into integrated control plans, wherever possible, to improve the chances of gaining control.

Perceptions are as important as facts. Many people perceive trees as useful and beneficial organisms, and trees are often of substantial cultural importance in many societies (Dickie et al. 2014). Some aspects of the problem are open to multiple interpretations, depending on whose views are being considered. For example, in South Africa, some people believe that introduced trees have been in the country for long enough to be regarded as indigenous, or that landscapes invaded by trees are more beautiful than similar landscapes with indigenous (treeless) vegetation (van Wilgen 2012). There are no right or wrong answers to these questions. Consequently, and even in the face of strong evidence that some introduced and invasive trees can be very harmful, it can be difficult to implement control operations where they may be needed. Active engagement with affected parties is therefore necessary to address perceptions and to seek common ground, a principle that is almost certainly universally applicable.

Introductions have often been misguided. Governments and aid agencies often propose the introduction of trees into new environments (especially in developing countries) to supposedly improve conditions and to provide opportunities for use. However, experience has shown that in many cases these well-intended introductions were promoted in the absence of a full understanding of the long-term consequences should they become invasive. Examples from South Africa include mesquite trees (widely promoted as a solution to drought-ravaged areas, but subsequently depleting water resources, reducing biodiversity, and forming dense, impenetrable thickets that are inaccessible to livestock); pines (widely planted as forestry trees in areas where they now spread in an uncontrolled manner, impacting on water resources and biodiversity); and wattles (widely planted on un-vegetated coastal dunes, resulting in the cessation of sand movement, and the severe erosion of the coastal beaches). Any future projects of this kind need to be subjected to careful risk assessments before introductions are made. European and other countries that provide foreign aid to developing countries need to consider the potential long-term impacts of promoting the use of introduced trees to avoid such problems.

Look before you leap. Many valuable lessons regarding the risks of tree introductions have been learnt in certain parts of the world, and it would seem to be wise to consider these lessons before further introductions are considered. For example, aggressive afforestation programmes where introduced tree species are extensively used are being pursued in South America, apparently in the absence of any risk assessments that could identify possible negative outcomes (Richardson et al. 2008). Transferring experience from elsewhere could help to minimise the risks. Once these risks are understood, it would be useful to develop a sound regulatory environment in which any afforestation programme could be implemented in a way that would minimise risks. Participation in voluntary schemes, such as certification of forestry operations by the Forestry Stewardship Council could also help (Simberloff et al. 2010).

Develop an innovative regulatory environment. In order to manage the introduction, propagation and use of introduced tree species in a way that they will maximise benefits and minimise harm, a sound regulatory environment should be created. In South Africa, this has taken two forms.

First, the introduction of any new species (not yet found in the country) is subject to a risk assessment. If the risks are deemed to be acceptable, an import permit will be granted, and the importer will be liable for control costs in the event of the introduced species becoming invasive.

Second, invasive trees (and other species) that are already in the country are classified into three categories: (1) those of no value; (2) recognised invasive species that also have commercial value; and (3) recognised invasive species that have ornamental, but no commercial value. For invasive species in the first category, control is required, and trade is banned. Landowners require permits to grow species included in the second category, and are required to take steps to limit their spread; trade of these species and their products are permitted. The species in the third category (created to accommodate popular ornamental plants) are also subject to permits that require steps to limit their spread, but further plantings, and sale of plants and their products, is prohibited. While it is still too early to assess the true effectiveness of these regulations, it is already clear that they can only be effective if sufficient capacity is created to ensure compliance. Clearly, there is scope for similar approaches to be adopted elsewhere, but this should only be attempted if the capacity and political will are in place to ensure widespread compliance.

Provide support for research. The management of invasive introduced trees needs to be based on a sound understanding of the complex socio-ecological environment in which it has to operate. In 2004, South Africa established a Centre of Excellence for Invasion Biology (C•I•B), with the primary goal of providing the scientific understanding required to reduce the rate and impacts of biological invasions. During its first decade, the C•I•B generated over 800 publications in the primary peer-reviewed literature, and produced almost 200 graduates at honours, masters and doctoral levels (van Wilgen et al. 2013). This made a considerable contribution to capacity in the field of biological invasions. The knowledge generated by the C•I•B has been used to inform policy and improve management practices at national and local levels. The adoption of similar research initiatives elsewhere would be extremely useful for managing the problem of invasive species.

> *Attempts to control invasive trees are often met with resistance by the public who are, by-and-large, unaware of their potential impacts. It is therefore important to raise awareness of the problem, especially among key stakeholders such as garden centres, managers of public parks, and foresters.*

Raise awareness: Many people are simply not aware that invasive introduced species can become problematic, so it is necessary to take steps to address this. Individuals, organisations, and businesses in the private and public sectors all drive the introduction and spread of introduced species in the country, and it is vital to ensure that people are aware of: (1) of the risks associated with any activity involving biological invasions; and (2) of the legal requirements that regulate the ownership, cultivation, trade and transport of introduced species. In South Africa, advocacy has been a key element of the strategy for dealing with biological invasions since 2001. There has been a conscious effort to communicate directly with key stakeholders, including farmers with invasive species on their land; people who use invasive species for commercial gain; people who sell invasive species, or purchase them to plant in their gardens, or to keep as pets; and government officials who have to make decisions about the use of introduced species. In particular, there have been very successful partnership programmes with landscapers, garden centre owners, conservationists and passionate gardeners since 2001. Our experience, which would be relevant in most other countries, has been that a targeted approach should be used to inform stakeholders that have been identified as playing key roles in influencing the spread of introduced trees.

Figure 25. Mountainous protected area in the Genadendal Nature Reserve. The trees in the foreground are invasive Australian wattles (*Acacia mearnsii*). Trees in the background are invasive Monterey pines (*Pinus radiata*), showing scattered trees spreading from the source population (photo: B.W. van Wilgen).

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Non-native species in Ozark Mountains in central USA as a challenge for forest managers (photo: L. Vítková).

3 Management of introduced and invasive tree species – concepts and approaches

The third section includes theoretical as well as practical insights into the management of introduced and invasive tree species. The theoretical support for the management of introduced species is covered in three chapters: risk analysis of invasive trees; the European database on invasive alien species; and the assessment of invasive tree species in nature conservation and forestry. Management experiences with introduced and invasive tree species are demonstrated in the subsequent chapters, including the part of the management of introduced invasive tree species in protected areas.

3.1 From impact studies to management actions: practicing risk analysis of introduced trees
Etienne Branquart, Bram D'hondt, Sonia Vanderhoeven and Sabrina Kumschick

3.2 European databases on invasive alien species
Annemarie Bastrup-Birk and Andreas Schuck

3.3 Assessment of invasive tree species in nature conservation and forestry – contradictions and coherence
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3.4 Eradication as an option for managing invasive tree species in protected areas
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3.5 Introduced species in Polish National Parks: distribution, abundance and management approaches
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Fanny Dommanget, Paul Cavaillé, André Evette and François-Marie Martin

Text Boxes

I. The challenge of ash dieback – conceptual framework for practitioners based on forest management in Ortenaukreis, Germany
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II. Code of Conduct on planted forests: recommended management for introduced and invasive tree species
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III. Insights into certification in relation to introduced and invasive tree species
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3.1 From impact studies to management actions: practicing risk analysis of introduced trees

Etienne Branquart, Bram D’hondt, Sonia Vanderhoeven and Sabrina Kumschick

Plants that become introduced in an area for horticultural, agricultural or silvicultural purposes potentially exert impacts beyond their intended use, and some of them may behave as weeds or pests and become undesirable. The wide and multidisciplinary field of risk analysis thus also applies to species introductions, with the associated risks being treated in much the same way as, for instance, food safety or other health risks. In this chapter, we illustrate how risk analysis of potentially invasive species is put into practice with a focus on the assessment of environmental impact and environmental risk, and a short overview of quarantine and management measures that may be recommended to reduce the level of risk. Furthermore, we provide a specific example with black locust (*Robinia pseudoacacia* L.) in Europe that allows exploring further details and highlighting context dependency of impacts and invasiveness of introduced tree species.

Formal frameworks for invasion risk analysis have emerged only recently. As a case in point, the Society for Risk Analysis included invasive species in their operational programme only at the beginning of the century (Andersen et al. 2004), with the topic accounting for about 2 % of its journal (*Risk Analysis*) content since. The major driving forces that underlie the development of risk analysis schemes are international trade and environmental policies that adhere to scientific risk screening for protecting human, animal and plant health against pests and diseases, but also to the preclusion of unjustifiable barriers to trade. Such legally binding risk analysis standards have been set in various sectors by several authoritative organisations, namely the World Health Organization (WHO, for human health), the World Organisation for Animal Health (OiE, for animal health), and the Food and Agriculture Organization (FAO, for plant health).

More specifically, the potentially harmful effects of introduced species to cultivated and wild plants are accounted for by the International Standards for Phytosanitary Measures (ISPMs) issued under the International Plant Protection Convention (IPPC) since 2003. This convention is overseen by the FAO, and effectuated through the European and Mediterranean Plant Protection Organization (EPPO) for most European countries (Schrader et al. 2010).

The above standards share a common framework (Figure 26), with risk analysis encompassing: (i) risk assessment, evaluating the likelihood and consequence of undesired impacts; (ii) risk management, managing the risk to minimise negative effects; and (iii) risk communication as a transversal activity.

Risk analyses that aim to be relevant for guiding management decisions need to be scientifically rigorous while at the same time reflecting concerns of society and public policy. Invasion biologists accordingly have created risk analysis schemes that act as templates for collecting information on species’ risks in a coherent and relevant fashion. Many such schemes exist, accounting for, among other features, different taxa, areas and impacts (overviews by Leung et al. 2012, Kumschick and Richardson 2013, McGeoch et al. 2015). Some of these are also applicable to the risks posed by introduced tree species, as we will showcase below.

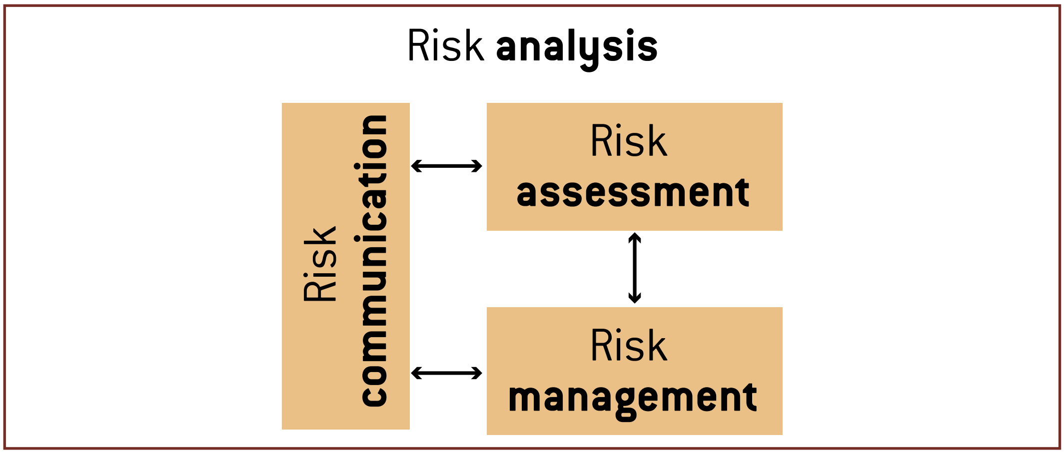


Figure 26. The risk analysis framework common to standards set by FAO, OiE and WHO (modified from EFSA Scientific Committee 2012).

Importantly, *risk assessment*, by definition, is concerned only with negative consequences. Whether these are offset against the perceived gains therefore, ultimately, remains out of its scope, though this is within the scope of the broader risk analysis (Figure 24).

How the native species and ecosystems are affected and how they react is crucial; impact magnitude matters.

Many introduced species change the environments where they are introduced, affecting native biodiversity, human health, as well as socio-economy. Some species affect invaded systems in such a severe manner that native species are driven out of their normal habitats, some may even go extinct in the process at a local or regional scale, and ecosystems can no longer persist in the invaded areas. Sometimes these effects lead to an irreversible shift in ecosystem functioning even when the introduced species is removed.

This process has been observed for many types of organisms including some trees. In central Europe, black locust is a good example of such a transformer species as it was shown to cause the local extinction of native plant species and to favour the establishment of other invasive plants (Essl et al. 2011). It may change open habitats into persistent dense groves and is capable of altering chemical and physical properties of soils, resulting in a totally different type of ecosystem (Rehounkova and Prach 2008, Cierjacks et al. 2013). Removal of individuals is a difficult operation as the species re-grows readily from root suckers. Additionally, seeds are known to persist in invaded soils (see chapter 3.6 and 5.1). Where black locust forms dense groves, it may prevent original native communities from recolonising invaded areas as the newly encountered conditions are not suitable anymore for their survival and reproduction. Identifying potentially problematic species is therefore important to prevent such detrimental consequences from occurring.

The impact of invasive plants on native ecosystems is often driven by their density or dominance.

Impact is usually found to be maximal where introduced trees become dominant and produce large, dense and persistent populations (Valery et al. 2008, Branquart et al. in press). For example, in riparian forests of central Europe, modification of soil properties (e.g. content of soil nitrogen) and presence of nitrophilous species like nettle (*Urtica dioica* L.) and elder (*Sambucus nigra* L.) typically increase along with black locust density (Staska et al. 2014) (Figure 27).

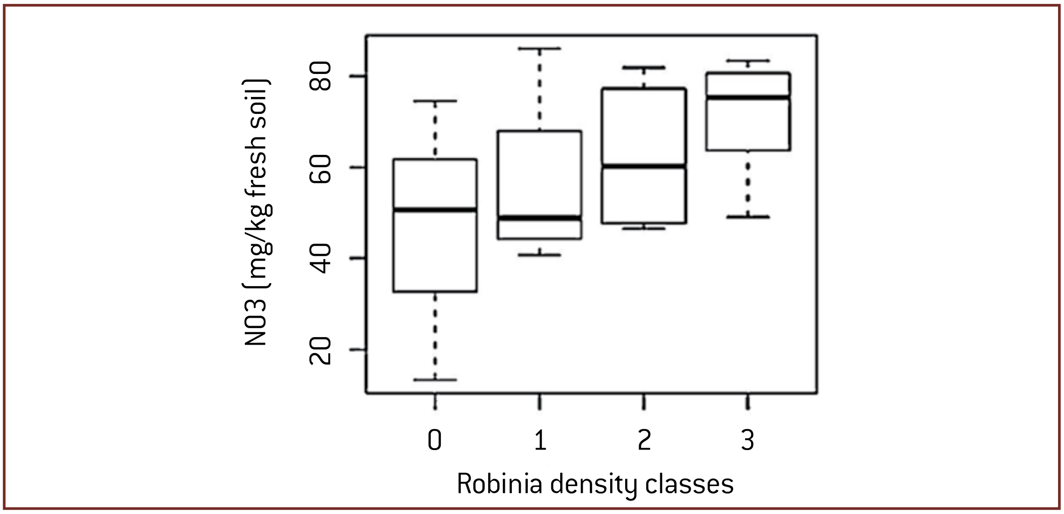


Figure 27. Effect of black locust density on soil nitrate contents. Adapted from Staska et al. 2014.

In the case of genetic hybridisation and pathogen pollution, detrimental impacts of introduced plants can already be observed at a low density. Impact can be studied in a number of ways, including observations in the field, laboratory experiments, or common garden experiments, to mention a few (see Kumschick et al. 2015a). Furthermore, variables measured related to impacts are highly diverse, and range from changes in the nutrient or microorganism composition in the soil to the number of native species in invaded versus uninvaded habitats.

Considering the high diversity in measures taken and experimental designs to study impacts, comparing such studies and the underlying impacts is not straightforward. However, in many specific cases such as prioritisation exercises for decision making, there is a need to compare impacts between species. Impact scoring systems like the Environmental Impact Classification for Alien Taxa (EICAT) and the Generic Impact Scoring System (GISS) (Box 9) have been developed to this end.

Impact scoring systems can help to pinpoint the species with the most severe effects on the environment and socio-economy in a specific habitat, or on a global scale.

They are, therefore, useful tools to assist the management of introduced species, and the prevention of potentially high impacting species becoming established.

Box 9: Environmental Impact Classification for Alien Taxa (EICAT)

A standardised tool for comparing magnitudes of impact between species has long been missing. In 2010, the Generic Impact Scoring System (GISS) was developed (Nentwig et al. 2009, Kumschick and Nentwig 2010), which enables the impacts of introduced species of various taxonomic groups to be scored and compared. So far, it has been used for a diverse range of taxa such as mammals, birds, fish, invertebrates and plants (Kumschick et al. 2015b). This system was improved and extended subsequently, which resulted in the EICAT scheme (Blackburn et al. 2014, Hawkins et al. 2015). The general structure of EICAT consists of twelve mechanisms through which introduced species can cause environmental impacts and are affecting native species. Each mechanism has verbal descriptions of the five impact categories possible: Minimal Concern (MC) – impact detected, but no effect on individual fitness of native species; Minor (MN) – affecting fitness of individuals of native species, but no effects on populations; Moderate (MO) – changes to populations are detected, but no changes in communities reported; Major (MR) – community changes found, but they are reversible if introduced species is removed; Massive (MV) – irreversible community changes and global extinctions (Figure 28).

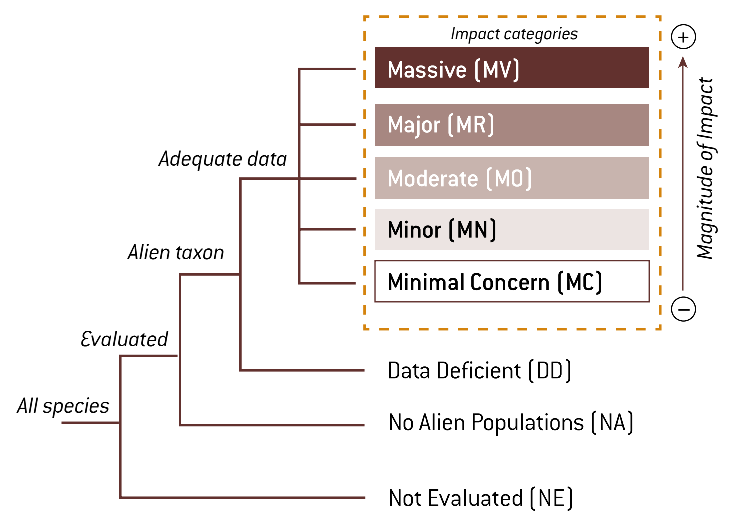


Figure 28. The different impact categories and the relationship between them (from Hawkins et al. 2015).

EICAT can be used at different scales, and impacts can be compared not only between species but also between continents or habitats.

Considering black locust as an example, we performed EICAT assessments separately for two habitat types found in central Europe – natural riparian forests and dry semi-natural grasslands – to assess if the impact caused is dependent on the habitat context. In riparian forests, black locust rarely forms monospecific stands due to shade conditions and soil waterlogging (Akatov et al. 2012, Staska et al. 2014); it only reaches a Moderate (MO) impact, i.e. it affected populations of native species, but did not change community compositions. However in dry grasslands, it irreversibly changes community compositions by excluding several native species and depleting their seed banks, and therefore gets classified as potentially having a Massive (MV) impact in this habitat type (Matus et al. 2003).

However, we do not have information on impacts for all species which have been introduced outside their native range, and many species have never been introduced outside of their native range. Suitable impact data is, therefore, not yet available for many species. Also, impacts can be highly context dependent as they are on the one hand dependent on the attributes of the introduced species, and on the other hand, they are usually caused in interaction with the recipient environment. Depending on the conditions in the recipient environment, the magnitude and nature of impact can differ. Consequently, impact scoring systems on their own only have limited use as predictive tools.

Going back to our example, black locust as a pioneer species is dependent on light for its establishment (Niinemets and Valladares 2006), and therefore impacts are higher in open habitats where light is abundant than in closed-canopy forests. Looking at impacts in semi-natural dry grasslands of central Europe, these were indeed classified as massive; in contrast, impacts were found to be lower in natural riparian forests (Box 9). A higher density and impact were, however, reported in other forest environments, where spread and dominance by black locust are favoured by woodland clearing, coppicing, forest decline, fire and other disturbances (see e.g. Benesperi et al. 2012, Maringer et al. 2012, Radtke et al. 2013).

Risk assessments are a holistic approach to invasion and harm potential.

In addition to impact evaluation as described above, risk assessments also include: (i) the likelihood of introduction of a species; (ii) establishment; and (iii) spread in a new region, i.e. the different stages of the invasion process (Figure 29, Blackburn et al. 2011). These three stages together define the exposure of an area to the species in question. Whether this factor is of interest to risk managers depends on their stakes; while highly relevant for preventive or rapid response measures, they are not so relevant to managers that are confronted with species that are already widely established. A high impact on biodiversity may potentially be observed once an introduced tree species has overcome those different barriers and is widely established at a landscape scale, but sometimes is independent of a species' density; therefore, impact is usually considered separately in risk assessments.

Figure 29. The three major stages in the process of biological invasions defining the exposure of an area to an introduced tree species.

High invasiveness of introduced trees is usually linked to a suite of life history attributes like fast growth rate, vigorous vegetative reproduction, and prolific seed production (Dodet and Collet 2012). The most efficient predictor of tree invasiveness is a high growth rate of seedlings (e.g. Lamarque et al. 2011). Black locust seedlings have higher growth rates than European oaks (*Quercus* spp.) seedlings, resulting in a competitive advantage over oaks when both species grow together (Figure 30) and consequently facilitating establishment capacity and dominance of the black locust.

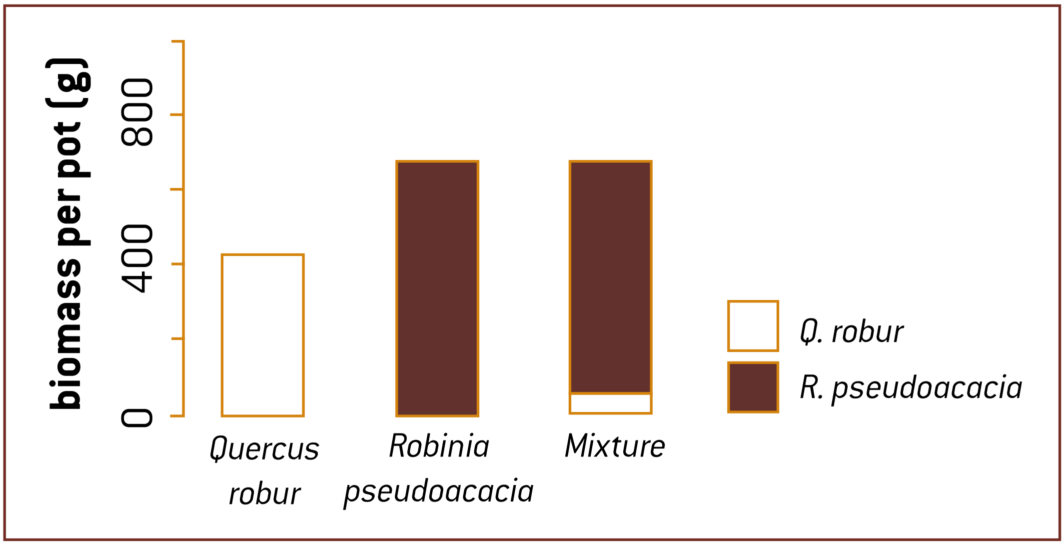


Figure 30. Measurement of biomass production by seedlings of pedunculate oak (*Quercus robur* L.) and black locust (*Robinia pseudoacacia* L.) cultivated in monoculture and in mixture in pot experiments. Adapted from Kawaletz et al. (2013).

An example of a risk assessment scheme that allows to separately evaluate the risk of the different stages presented in Figure 30, as well as impact, is provided by the *Harmonia+* protocol (D'hondt et al. 2015). The environmental risk of a species assessed with this protocol is derived from the product of exposure × environmental impact. It means that the most invasive species combine a high establishment ability, a high spread capacity, and a strong environmental impact. An overview of this scheme is given in Box 10, which also describes the results of a risk assessment for black locust in contrasting environments similar to the EICAT assessment in Box 9.

Because of long generation time of many tree species and the important lag phase between tree introduction and further spread, assessing the risks caused by introduced trees is more difficult than for other life forms such as annual plants. Detailed risk analyses have rarely been conducted on introduced trees in Europe (but see Křivánek and Pyšek 2006).

Lack of adequate data about the capacity of a tree species to establish, spread and cause detrimental impacts in the area of concern may potentially be solved in considering its behaviour in other areas where it has been introduced in the past. Information from the native range may also be used, including species climatic requirements, habitat preferences and dispersal abilities. Such data can be retrieved from online invasive species databases like the CABI Invasive Species Compendium (http://www.cabi.org/isc/) or the IUCN Global Invasive Species Database (http://www.issg.org), to name but two.

Box 10: Harmonia+ : a risk assessment protocol

Harmonia+ is a risk assessment scheme for introduced species that was recently developed for Belgium and neighbouring areas (D'hondt et al. 2015, Vanderhoeven et al. 2015). It is designed to be applicable to a broad range of taxa and to cover the invasion process as well as impact as completely as possible. It consists of 30 questions with predefined alternative answers. By converting answers into scores, *Harmonia*+ allows for numerical output on the risk of species. The scheme can be consulted online through http://ias.biodiversity.be.

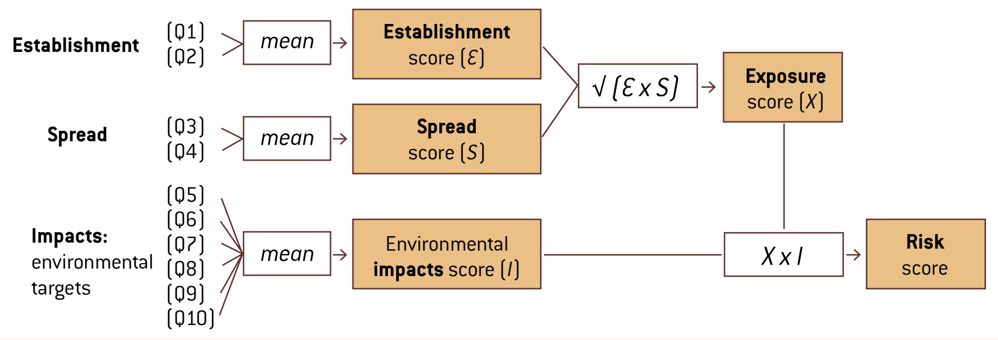
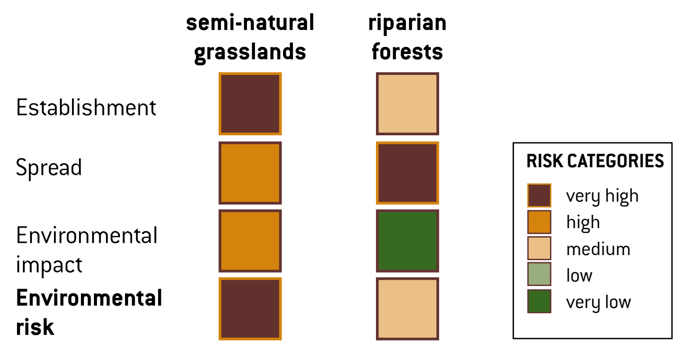


Figure 31. An overview of the *Harmonia*+ framework used to assess the invasion risk for black locust.

The assessment of black locust was performed only through the modules considered relevant here (establishment, spread and environmental impacts; Figure 31). This was done for two different habitats: once with regard to dry semi-natural grasslands, and once with regard to natural riparian forests in central Europe. The results shown in Figure 32 indicate that both types of habitat are heavily exposed to the species. Establishment capacity is more limited in riparian forests than in grasslands due to the intolerance of black locust to shade and waterlogging (Niinemets & Valladares 2006). Although its intrinsic dispersal capacity is rather limited (seeds and root suckers are rarely spread over distances exceeding 100 meters from the mother tree), black locust spreads readily through running waters, plantations and transportation of contaminated soils by man (Säumel and Kowarik 2013).



	semi-natural grasslands	**riparian forests**
Establishment	🟫	🟨
Spread	🟧	🟫
Environmental impact	🟧	🟩
Environmental risk	🟫	🟨

RISK CATEGORIES
🟫 very high
🟧 high
🟨 medium
▨ low
🟩 very low

Figure 32. Risk categories for the different stages of black locust invasion in dry semi-natural grasslands and riparian forests assessed through the *Harmonia*+ protocol (see Figure 31 for details).

The environmental impact and overall risk are far higher in dry grasslands than in riparian forests. Major differences are mainly linked to divergences in black locust's competitiveness and capacity to produce dense populations in the two habitat types as described in Box 9.

Estimating the impacts of a species or evaluating the risk encountered is for sure liable to uncertainty (Leung et al. 2012). Uncertainty can result from insufficient available information, or contrasting or contradictory results either because of the methodology used or because of context-dependent effects. The assessment and communication of this uncertainty has to be considered as an integral part of the process and is to be dealt with by the decision makers or managers at the time of action. The two protocols described here, EICAT and Harmonia+, both include uncertainty in their assessment processes (D'Hondt et al. 2015, Hawkins et al. 2015).

> *Risk management is defined by FAO and IPPC as the evaluation and the selection of options to reduce the risk of introduction and spread of introduced plant species.*

There are only a few schemes to guide managers in the choice and prioritisation of management objectives and techniques for introduced plants (but see Schmiedel et al. 2016). The main options available for decision makers and land managers are described hereafter, based on species distribution within the introduction area (Figure 33).

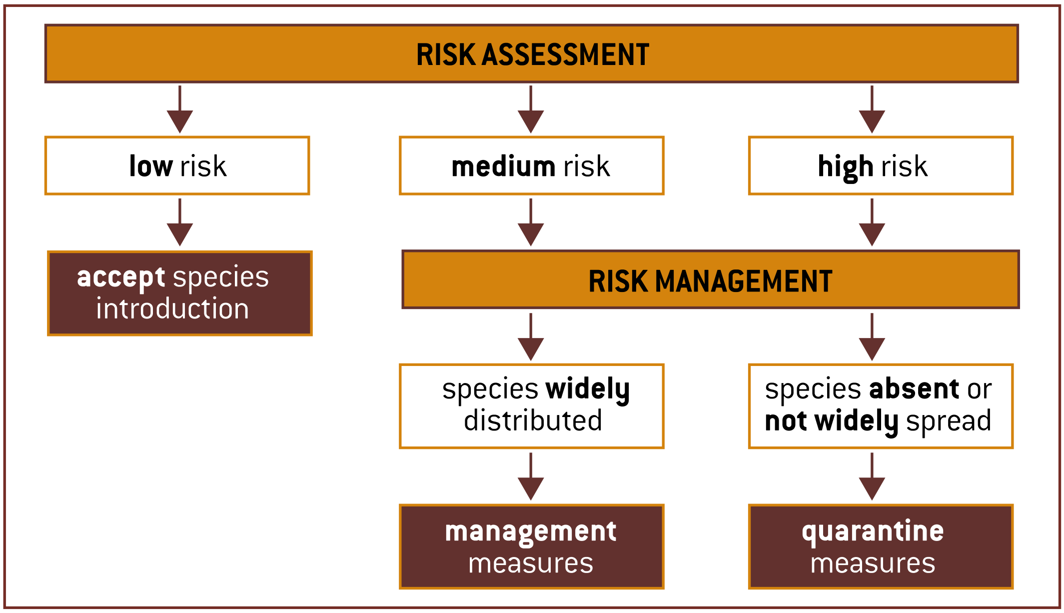


Figure 33. Risk management options for invasive plants.

IPPC guidelines and standards recommend the adoption of quarantine measures when the introduced plant is still absent or not widely distributed in the area of concern. Those measures mainly focus on prevention actions aiming at reducing species introduction and on early eradication actions (Figure 34). Prevention usually includes prohibition of import, trade and planting, the necessity and the proportionality of which need to be justified by a detailed risk analysis as requested by the World Trade Organization (WTO) agreement on the application of sanitary and phytosanitary measures. Prevention and adoption of quarantine measures may either be imposed by legislative tools or favoured by code of conduct such as on plantation forestry (Text Box II). Being as proactive as possible is becoming a necessity.

> *The selection and promotion of any new woody species in an area should discard those that may establish into the wild, spread and threaten native biodiversity.*

The approach and the assessment schemes presented in this chapter are interesting tools to be considered for the evaluation of the environmental risks encountered by the introduction of these new species.

Beyond the preventative perspective, management measures are advised by international bodies when the introduced plant is already widely distributed and cannot be eradicated anymore. This is the case for tree species that are heavily planted and provide important socio-economic benefits as a result of wood, biomass, fodder or honey production (see chapters 1.1 and 1.2). In that case, natural spread from established wild populations is much more important than establishments resulting from the international trade and quarantine measures are therefore considered as poorly effective (Branquart et al. in press). Management of widespread trees encompasses a wide range of measures that help reducing their spread and the invasion into unintended habitats. As suggested by Sitzia et al. (2016), the forestry sector may be actively involved in controlling the spread and the associated impacts of introduced trees by adopting specific plantation, silvicultural and tree harvesting techniques. The introduction of biocontrol agents from native ranges has been also proposed as a management measure, but can be considered as inappropriate in the case of introduced trees because of possible negative effect on wood production (van Wilgen and Richardson 2014).

Table 8. Quarantine (EPPO PM 5/3) and management measures (EPPO PM 3/67) proposed by EPPO to minimise the spread and the detrimental impacts of invasive introduced trees.

Quarantine measures (species absent or poorly distributed)
• Prohibition of import, trade and planting
• Obligation to monitor and report findings
• Emergency plan (i.e. action plan for local eradication if the plant is found)
Management measures (species widely distributed)
• Labelling or marking of plants in nurseries
• Restriction of conditions for planting (protection of unintended habitats)
• Obligation to report new occurrences outside the intended habitats
• Emergency plan when plant is found in unintended habitats e.g. for local eradication
• Adoption of plantation, silvicultural and harvesting techniques to minimise species spread towards unintended habitats

Figure 34. Black locust is widely planted along railway tracks to stabilise banks and reduce soil erosion. It expands readily from plantation sites by root suckering, stump sprouting and seed production and may invade neighboring natural habitats such as the rocky sites in this picture. For that specific use, black locust should be replaced as much as possible by native alternative species well known for preventing soil erosion (photo: E. Branquart).

Black locust has been largely planted across Atlantic, Continental and Mediterranean regions in Europe and is locally highly abundant. For example, in Hungary and in the Italian Piedmont, it provides important benefits related to honey production and as a source of wood. In that case, the application of quarantine and eradication measures is no longer a reasonable option. However, management may be applied to mitigate its impact on natural habitats, refraining from planting in and nearby high conservation value habitats or in areas with marginal soil conditions where its productivity would not be optimal (e.g. Vitková et al. 2015). In woodlands, limiting coppicing and clearcutting coupled with the maintenance of closed canopy forests may strongly reduce its invasion potential. Furthermore, invaded areas could potentially be restored by facilitating the establishment of late successional tree species; as the individuals of these species grow they will reduce light availability for black locust, and outcompete it (see chapters 3.6 and 5.1).

▶ *Effective communication of the dangers and opportunities associated with introduced species is essential.*

Interacting and communicating with relevant stakeholders during the whole risk analysis process is important to ensure an appropriate understanding of the decision that will result from the analyses. Additionally, information on benefits, observed impacts in forests, as well as management practices is needed throughout the process from the stakeholders. Different stakeholders and sectors, based on differences in needs and values, are affected differently by the introduced species. Thus, they will also be affected differently by any decisions made with regards to the risk and its management. If the decisions, and management measures, are to be implemented effectively, stakeholder support is crucial. Due to a potentially high influence of stakeholders' perceptions on the effectiveness of decisions taken, it is important that their perceptions are taken into account when performing risk analyses for introduced species.

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TEXT BOX I: The challenge of ash dieback – conceptual framework for practitioners based on forest management in Ortenaukreis, Germany

Bernhard Mettendorf and Daniela Vetter

The first symptoms of ash dieback caused by the fungus *Hymenoscyphus fraxineus* (see chapter 4.3) appeared in southwestern Germany in 2009. Since then, the disease has become a considerable problem for foresters, forest administration and forest owners.

The rural district of Ortenaukreis in the state of Baden-Württemberg is situated in southwestern Germany. It borders France in the West and extends up to the Black Forest and the Schwarzwald National Park in the East. The Rhine Valley lies in the West adjacent to the French border; the South-North extension of the Rhine Valley measures about 50 km in the Ortenaukreis district. Ash (*Fraxinus excelsior* L.) is a common tree species in the floodplain forests of the Ortenaukreis and occurs here on approximately 20 % of the forest area.

Some decades ago ash was thought to be a healthy and resistant tree species and therefore was deliberately planted and used as a substitute for, the then ailing, oaks (*Quercus robur* L.). As a consequence, current stands often have high proportions of ash. During recent years the ash dieback has developed rapidly (chapter 4.3). Apart from the dieback of the canopy, the disease was also found to infect tree stems. The stem infection mostly involves armillaria (*Armillaria* spp.) and leads to instability of the infected trees which subsequently may fall unpredictably.

Ash dieback poses immense challenges for forest management, e.g. regarding work safety, control of the flow of timber onto the market, and nature conservation issues. Because the disease has spread so rapidly, extraordinary action is required. The forest office of the Ortenaukreis has therefore designed a conceptual framework for management operations in relation to ash dieback. The framework was intended to support foresters in their management decisions and in the communication with the forest owners; most forests are owned by communities in the Rhine Valley.

The framework was designed by a working group of six people of the forest office Ortenaukreis. Consultancy was provided by the division Forest Economics of the FVA (Forest Research Institute of Baden-Württemberg). The framework is divided into two parts: (1) cutting operation (in the damaged ash stands); and (2) reforestation (if stands were cleared). The framework was designed to incorporate the owner's (mainly communities) objectives.

The final framework consists of the following components:

1. Decision tree (for cutting operations and reforestation).

→ see Figures 37 and 38

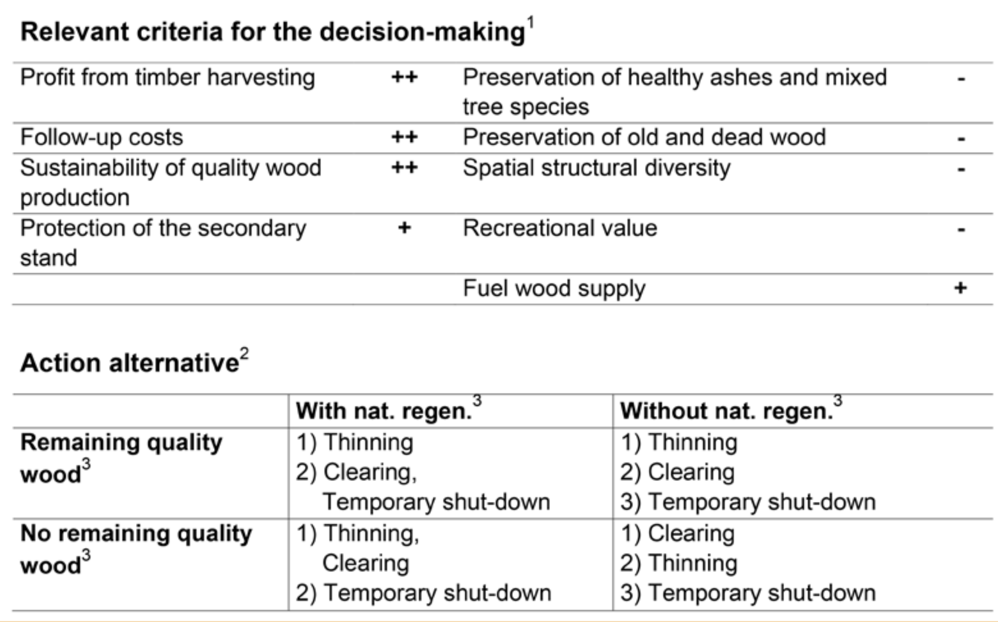
2. In each part of the decision tree, the owner's objectives form the basis for the management decision. Other important aspects (e.g. legal or operative restrictions) may lead to the exclusion of one or more alternatives.

Utility analysis of the most suitable action alternative considering the owner's objectives.

The utility analysis presents the most suitable action alternative for a specific forest owner considering the specific forest owner's objectives. Relevant criteria for decision-making and possible action alternatives were defined in advance.

⇢ see Tables 9–12 (fictitious examples that illustrate how different owner's objectives lead to different suitability ranking of action alternatives)

Table 9. Fictitious community "Profit Town" – Cutting operation



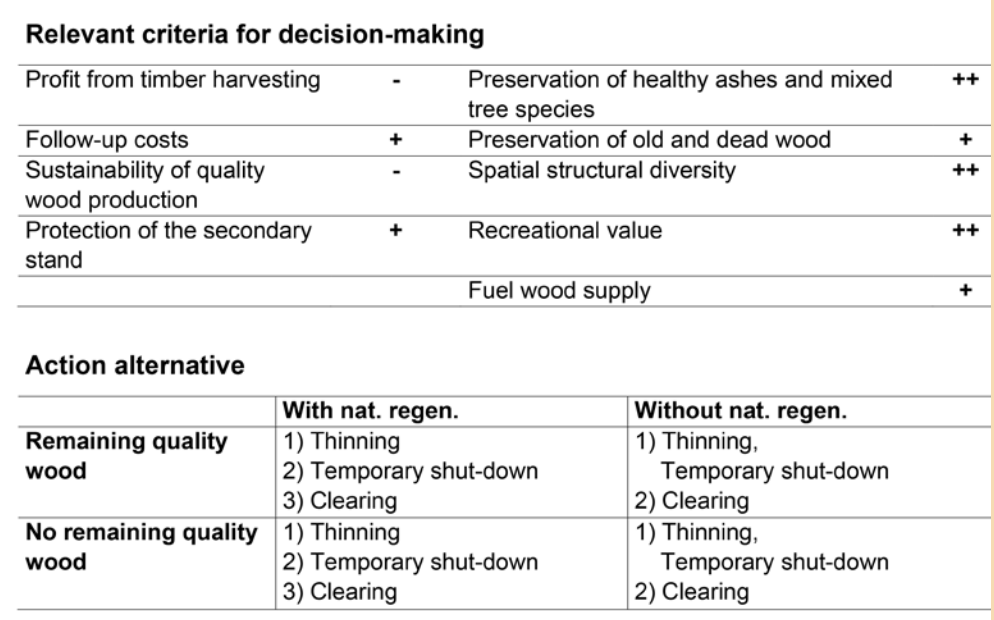
Relevant criteria for the decision-making[1]

Profit from timber harvesting	++	Preservation of healthy ashes and mixed tree species	-
Follow-up costs	++	Preservation of old and dead wood	-
Sustainability of quality wood production	++	Spatial structural diversity	-
Protection of the secondary stand	+	Recreational value	-
		Fuel wood supply	+

Action alternative[2]

	With nat. regen.[3]	**Without nat. regen.[3]**
Remaining quality wood[3]	1) Thinning 2) Clearing, Temporary shut-down	1) Thinning 2) Clearing 3) Temporary shut-down
No remaining quality wood[3]	1) Thinning, Clearing 2) Temporary shut-down	1) Clearing 2) Thinning 3) Temporary shut-down

Table 10. Fictitious community "Eco Village" – Cutting operation



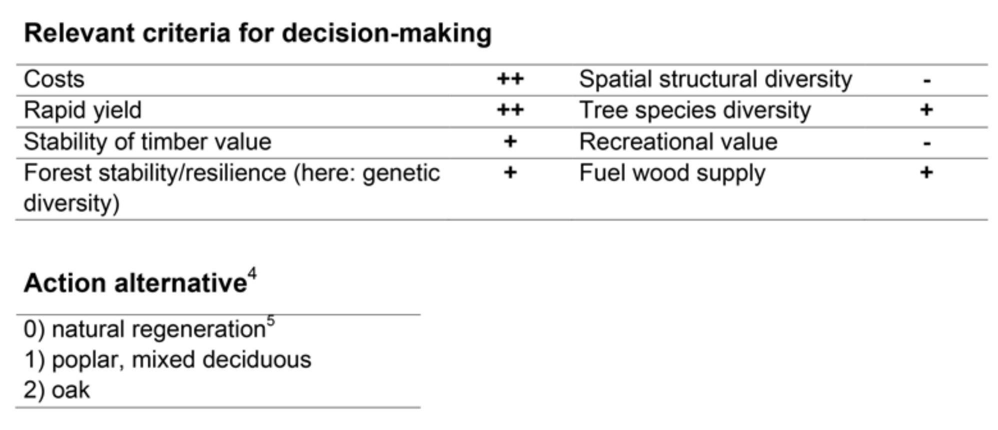
Relevant criteria for decision-making

Profit from timber harvesting	-	Preservation of healthy ashes and mixed tree species	++
Follow-up costs	+	Preservation of old and dead wood	+
Sustainability of quality wood production	-	Spatial structural diversity	++
Protection of the secondary stand	+	Recreational value	++
		Fuel wood supply	+

Action alternative

	With nat. regen.	**Without nat. regen.**
Remaining quality wood	1) Thinning 2) Temporary shut-down 3) Clearing	1) Thinning, Temporary shut-down 2) Clearing
No remaining quality wood	1) Thinning 2) Temporary shut-down 3) Clearing	1) Thinning, Temporary shut-down 2) Clearing

Table 11. Fictitious community “Profit Town“ – Reforestation



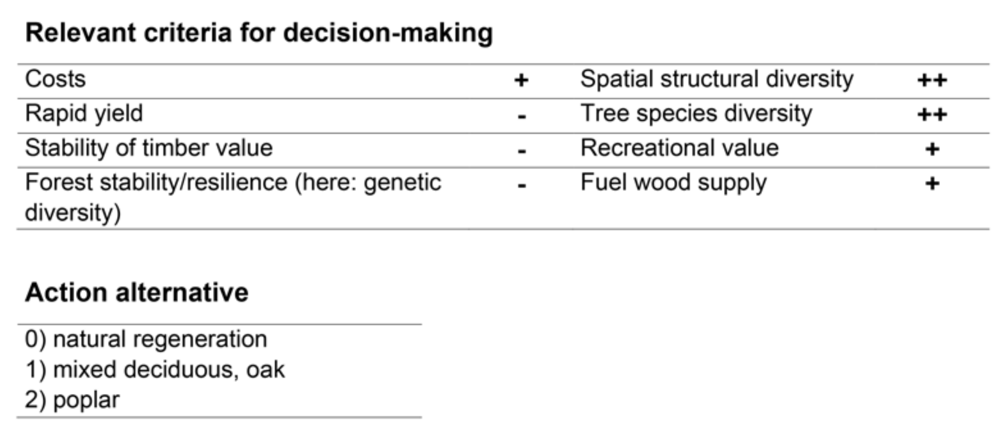
Relevant criteria for decision-making

Costs	++	Spatial structural diversity	-
Rapid yield	++	Tree species diversity	+
Stability of timber value	+	Recreational value	-
Forest stability/resilience (here: genetic diversity)	+	Fuel wood supply	+

Action alternative[4]

0) natural regeneration[5]
1) poplar, mixed deciduous
2) oak

Table 12. Fictitious community “Profit Town“ – Reforestation



Relevant criteria for decision-making

Costs	+	Spatial structural diversity	++
Rapid yield	-	Tree species diversity	++
Stability of timber value	-	Recreational value	+
Forest stability/resilience (here: genetic diversity)	-	Fuel wood supply	+

Action alternative

0) natural regeneration
1) mixed deciduous, oak
2) poplar

1 relevant criteria were defined in advance (importance for the forest owner depicted by “++” = very important, “+” = important and “-” = not important), see decision matrix with utility analysis for details and suitability values of criteria

2 see decision matrix with utility analysis for details on how action alternatives were rated; alternatives were analyzed by a utility analysis and are rated by their suitability regarding the owner’s objectives

3 suitability of alternatives may change with differing stand conditions; see decision matrix with utility analysis for detailed suitability values considering different stand conditions

4 focus on most suitable planting alternative, but mix of all three alternatives recommended; proportion of leading tree species ≤ 60 % and at least 3–5 tree species recommended

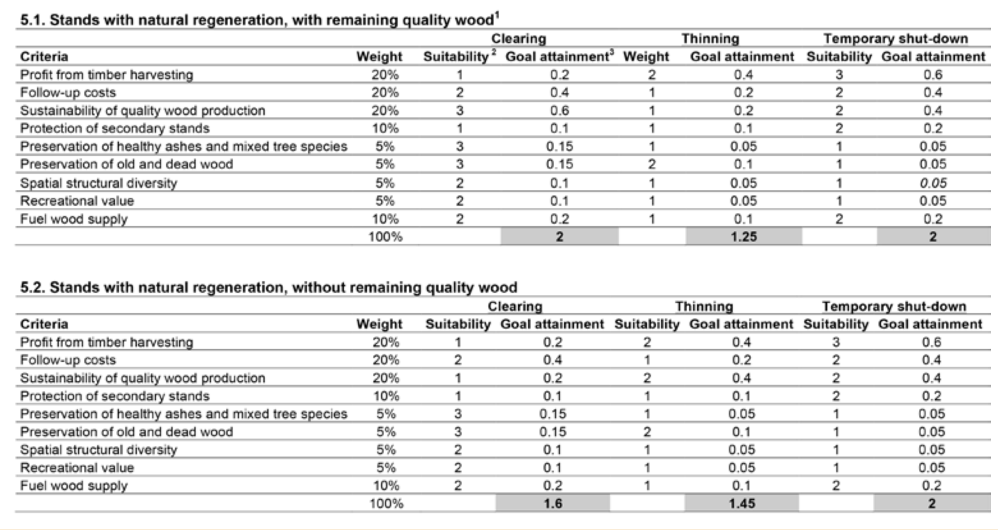
5 “0” was assigned here, because natural regeneration was not considered as an action alternative, but merely as a comparison to the planting alternatives, especially in the communication with the forest-owning communities; natural regeneration may be missing due to unfavorable (soil) site conditions or due to high roe deer densities which both cannot be influenced by the forester (hunting districts are mostly rented out to private persons by the communities)

The suitability of the alternatives was analysed by the utility analysis. The working group of the forest office Ortenaukreis defined the relevant criteria for decision-making and possible action alternatives. Also suitability values (how suitable is an alternative to meet the criteria?) were defined by the working group. The importance or weight of each criterion reflects the forest owner’s objectives.

⇢ see Tables 13–14

The developed framework will support foresters, forest administration and forest owners to handle the consequences of ash dieback. Taking into account, however, that the Ortenaukreis comprises about 3 000 ha of ash stands, the long-term consequences will be profound. 1) the income from floodplain forests is generally low. 2) the large-scale loss of forest stands will have severe financial consequences for many forest owners. There is no single tree species that is able to entirely replace ash. All potential species – e.g. oak, hornbeam (*Carpinus betulus* L.), alder (*Alnus* spp.) show some type of restriction on ash stand sites

Table 13. Decision matrix cutting operation – fictitious community "Profit Town"



5.1. Stands with natural regeneration, with remaining quality wood[1]

		Clearing		Thinning		Temporary shut-down	
Criteria	**Weight**	**Suitability[2]**	**Goal attainment[3]**	**Weight**	**Goal attainment**	**Suitability**	**Goal attainment**
Profit from timber harvesting	20%	1	0.2	2	0.4	3	0.6
Follow-up costs	20%	2	0.4	1	0.2	2	0.4
Sustainability of quality wood production	20%	3	0.6	1	0.2	2	0.4
Protection of secondary stands	10%	1	0.1	1	0.1	2	0.2
Preservation of healthy ashes and mixed tree species	5%	3	0.15	1	0.05	1	0.05
Preservation of old and dead wood	5%	3	0.15	2	0.1	1	0.05
Spatial structural diversity	5%	2	0.1	1	0.05	1	*0.05*
Recreational value	5%	2	0.1	1	0.05	1	0.05
Fuel wood supply	10%	2	0.2	1	0.1	2	0.2
	100%		**2**		**1.25**		**2**

5.2. Stands with natural regeneration, without remaining quality wood

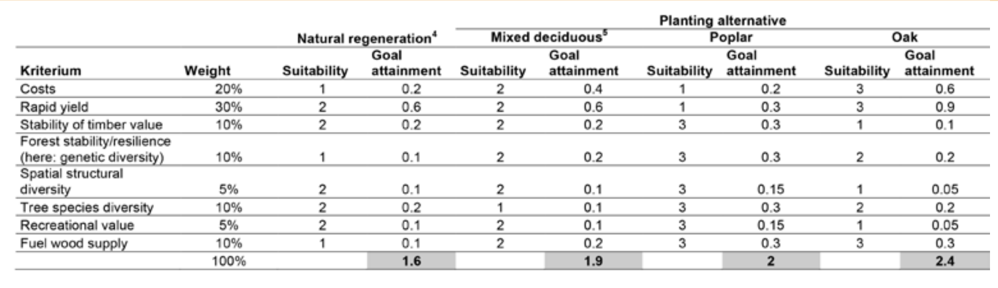
		Clearing		Thinning		Temporary shut-down	
Criteria	**Weight**	**Suitability**	**Goal attainment**	**Suitability**	**Goal attainment**	**Suitability**	**Goal attainment**
Profit from timber harvesting	20%	1	0.2	2	0.4	3	0.6
Follow-up costs	20%	2	0.4	1	0.2	2	0.4
Sustainability of quality wood production	20%	1	0.2	2	0.4	2	0.4
Protection of secondary stands	10%	1	0.1	1	0.1	2	0.2
Preservation of healthy ashes and mixed tree species	5%	3	0.15	1	0.05	1	0.05
Preservation of old and dead wood	5%	3	0.15	2	0.1	1	0.05
Spatial structural diversity	5%	2	0.1	1	0.05	1	0.05
Recreational value	5%	2	0.1	1	0.05	1	0.05
Fuel wood supply	10%	2	0.2	1	0.1	2	0.2
	100%		**1.6**		**1.45**		**2**

1 Depending on the starting position (with/without nat. regen., with/without quality wood) the suitability values (1 – good, 2 – average, 3 – poor) of the alternatives (clearing, etc) differ for the respective criteria

2 Suitability means: how suitable is an alternative to meet the criteria? E.g. suitability of clearing to achieve profit from timber harvesting, good = 1 etc.

3 Goal attainment=Weight is multiplied with suitability value and all goal attainment values per alternative are summed (results here for clearing into "2", which is to be rated inferior due to the owners' objectives (weight) than the thinning with "1.25")

Table 14. Decision matrix reforestation – fictitious community "Profit Town"



				Planting alternative					
		Natural regeneration[4]		Mixed deciduous[5]		Poplar		Oak	
Kriterium	**Weight**	**Suitability**	**Goal attainment**	**Suitability**	**Goal attainment**	**Suitability**	**Goal attainment**	**Suitability**	**Goal attainment**
Costs	20%	1	0.2	2	0.4	1	0.2	3	0.6
Rapid yield	30%	2	0.6	2	0.6	1	0.3	3	0.9
Stability of timber value	10%	2	0.2	2	0.2	3	0.3	1	0.1
Forest stability/resilience (here: genetic diversity)	10%	1	0.1	2	0.2	3	0.3	2	0.2
Spatial structural diversity	5%	2	0.1	2	0.1	3	0.15	1	0.05
Tree species diversity	10%	2	0.2	1	0.1	3	0.3	2	0.2
Recreational value	5%	2	0.1	2	0.1	3	0.15	1	0.05
Fuel wood supply	10%	1	0.1	2	0.2	3	0.3	3	0.3
	100%		**1.6**		**1.9**		**2**		**2.4**

4 Natural regeneration was included in the decision matrix to illustrate the advantages of natural regeneration to the forest-owning communities; here natural regeneration only refers to regeneration that fits the (soil) site conditions

5 e.g. maple, cherry, black walnut, lime, hornbeam

Introduced tree species may help to increase the assortment of possible alternatives to ash.

The forest district Ortenau is following a practical approach for all cases where natural regeneration in stands with ash-dieback is insufficient and the question of planting appropriate replacement trees is present. However, the choice of possible alternative species, is getting more and more restricted for different reasons. There are examples of tree species that have been already lost as a consequence of similar processes such as elms (*Ulmus* spp.) that are affected by Dutch Elm disease (*Ophiostoma novo-ulmi* Brasier) and alder (*Alnus glutinosa* L.), which is threatened locally by a *Phytophthora* fungus (*Phytophtera alni* subsp. *alni*). As a result of globalisation, various tree pests are spreading across Europe. Land use changes and climatic changes will further affect many species within their natural ranges, but also in their non-natural ranges.

Establishing healthy and diverse stands is one of the main objectives in forestry and as the choice of adequate native species will be limited in the future, a possible solution to the problem is to enlarge the portfolio of species by using appropriate non-native tree species as alternatives.

The main criteria for the selection introduced, non-native tree species are:

1. adapted to certain site conditions;
2. good increment;
3. resistance to pests and diseases spread presently;
4. good general quality of timber with existing or promising good prospects on the timber market;
5. non-invasive behaviour of the species.

The following tree genera and species were selected as a result of the selection:

- Monarch birch (*Betula maximowicziana* Regel)
- Hickory (*Carya* spp.)
- Turkish hazel (*Corylus colurna* L.)
- Black walnut (*Juglans nigra* L.)
- Hybrid walnut (*Juglans* x *intermedia* Jacques)
- Tulip tree (*Liriodendron tulipifera* L.)
- London plane (*Platanus* x *hispanica* Mill. ex Munchh.)

Hickory, black walnut and tulip tree have been tested in long-term silvicultural trial plots. For hybrid walnut and monarch birch, only short-term observations are available. There are no trials for London plane, although this tree species has been planted as a landscape element across the country. Green ash (*Fraxinus pennsylvanica* Marshall) (Fig. 34) was excluded from use because of its invasive character and because of its lack of resistance against the emerald ash borer (*Agrilus planipennis* Fairmaire, 1888), a new beetle pest on that has been spreading very fast and is currently active in Russia.

Figure 35: Stand with 55-years-old London planes in a community forest near Karlsruhe (photo: B. Mettendorf).

> *The introduction of a non-native tree species for economic purposes into silvicultural practice should be discussed and communicated openly and transparently.*

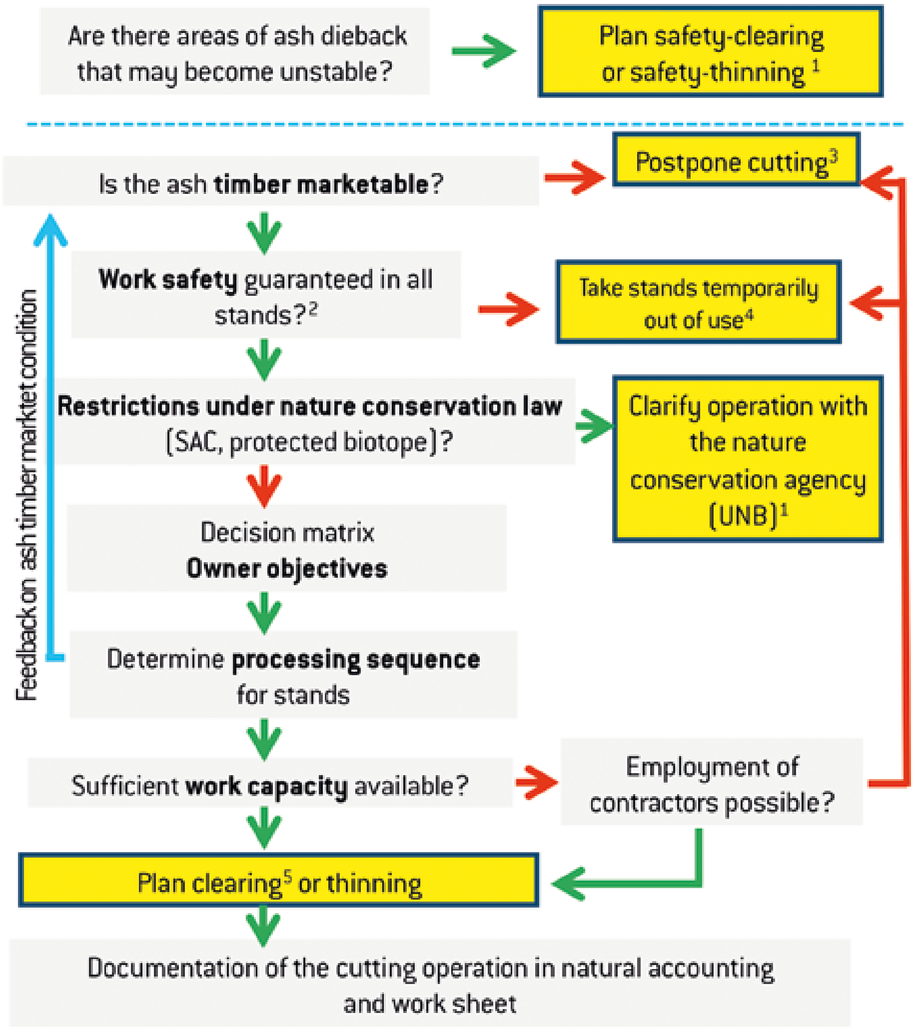
The use of the selected introduced species in forestry and silvicultural practice occurs only in minor proportions within native tree forest types such as oak and other valuable broadleaved habitat types. Planting is carried out by supplementing natural regeneration or entire replanting. The proportion of a single species planted in a single stand is limited to a maximum of 30 % (the only exception is oak for economic and environmental protection reasons). This rule results from our experiences with ash die back: if the percentage of an affected species exceeds 30 % the stand structure of the remaining stand is endangered.

As an example, the forest enterprise of Offenburg, the establishment of an oak dominated stand, which is by far the most important forest development type, can be managed while applying different methods: one option is to plant sessile oak (*Quercus petraea* (Matt.) Liebl.)

in clusters only, whereas the number of clusters per hectare can vary between 30 and 70, with 20–25 plants each in each cluster. The intermixed non-native species are planted in moderate numbers within the intermediate space. With this strategy the development of the natural regeneration is favoured, while controlling measures of the introduced species are applicable.

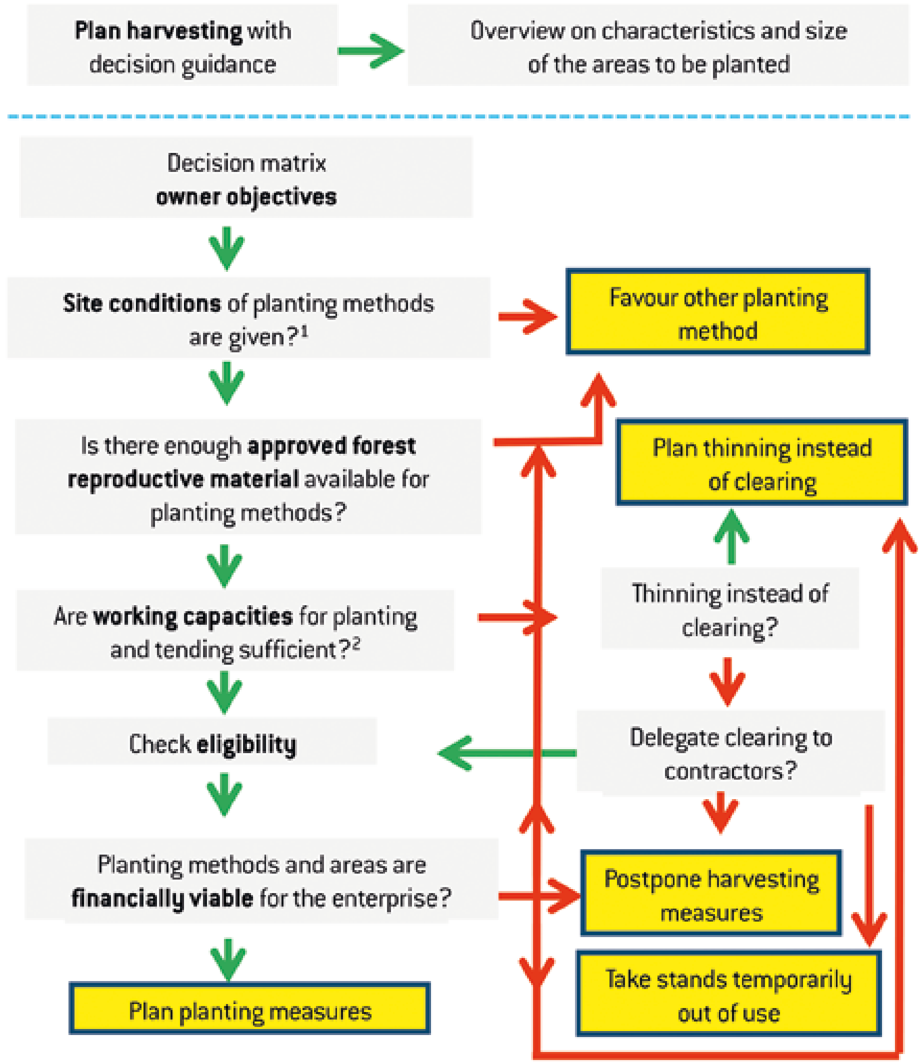
This example exhibits the need for solutions for such cases. The practical approach to apply a framework adapted to specific conditions of a forest enterprise seems a useful alternative also for companies facing similar situations and challenges.

Figure 36: Vigorous regeneration of green ash in a floodplain area in eastern Austria (photo: by F. Krumm).



[1] in particularly sensitive areas if needed press release, inform public in advance, inform nature protection officials – [2] min. work safety for harvester deployment guaranteed? – [3] postpone cutting until next season, then consider all steps again – [4] take stands out of use temporarily until collapse (ca. 15 years) – [5] before clearing consider decision tree : "reforestation"

Figure 37. Decision tree: cutting operation



[1] Compare adequacy with forest stand and site map, when the area contains FFH-habitat types check also adequacy of selected option to serve as habitat type.

[2] Additional working capacities must be made available for areas to be planted (until end of tending phase of the newly planted areas).

Figure 38. Decision tree: reforestation

3.2 European databases on invasive alien species

Annemarie Bastrup-Birk and Andreas Schuck

The capacity to identify and mitigate threats from invasive alien species (IAS) relies on accurate, updated and easily accessible information. This would help to synthesise risks and impacts of the most common and/or threatening IAS and to prevent and control biological invasions into European forests.

The EU Biodiversity Strategy 2020 (COM 2011) has dedicated an action to prevent the introduction and establishment of IAS. The EU Regulation on the prevention and management of the introduction and spread of invasive alien species, recently entered into force (EU 2014). An important aspect of this regulation is the adoption of a list of IAS of concern for Europe. It urges the Member States to:

“establish a surveillance system of invasive alien species of Union concern, or include it in their existing system, which collects and records data on the occurrence in the environment of invasive alien species by survey, monitoring or other procedures to prevent the spread of invasive alien species into or within the Union” (see Box 12).

> ▶ *There is an urgent need for information on the presence and distribution of IAS across all ecosystems in Europe.*

To date some 40 online information portals and databases have been developed at global, European, regional and national levels. Regarding terrestrial IAS, relevant information systems include the database of the European and Mediterranean Plant Protection Organization (EPPO) as well as the databases of the Global Biodiversity Information Facility (GBIF), the Global Invasive Species Information Network (GISIN) and the International Union for Conservation of Nature (IUCN) (see Box 10). The DAISIE database (Delivering Alien Invasive Species Inventories for Europe) is one of the most comprehensive European databases on invasive alien species with more than 12 000 entries. Two further regional databases are to be explicitly mentioned among several others that inventory the terrestrial IAS in Europe: the NOBANIS (more than 20 European countries) and the REABIC focussing on the Euro-Asian region.

> ▶ *A European Information System on Invasive Alien Species, EASIN, has been set up as the new tool for supporting the implementation of the EU Regulation.*

The European Information System on Invasive Alien Species (EASIN) builds on experiences and tools developed of already existing databases such as DAISIE, NOBANIS and EPPO PQR – see also Box 10.

BOX 10. Selected portals and databases addressing IAS at global, European, regional and national levels.

- Global Biodiversity Information Facility (GBIF) at http://www.gbif.org
- Global Invasive Species Information Network (GISIN) at http://www.gisin.org/
- International Union for Conservation of Nature (IUCN) Species Survival Committee (SSC) – Invasive Species Specialist Group (ISSG) at http://www.issg.org/index.html
- Global Register of Introduced and Invasive Species (GRIIS) at http://www.griis.org/
- Delivering Alien Invasive Species Inventories for Europe (DAISIE) at http://www.europe-aliens.org
- European Network of Invasive Alien Species (NOBANIS) at http://www.nobanis.org/
- European and Mediterranean Plant Protection Organization-Plant Quarantine Data Retrieval System (EPPO-PQR) at http://www.eppo.org/
- Regional Euro-Asian Biological Invasions Centre (REABIC) at http://www.reabic.net/
- European information system on Invasive Alien Species (EASIN) at http://easin.jrc.ec.europa.eu
- National Institute for Invasive Species Science (NIIS) at http://www.niiss.org
- CABI Invasive Species Compendium at http://www.cabi.org/isc/

EASIN aims to facilitate the exploration of existing alien species information from distributed resources through a network of inter-operable web services, following internationally recognised standards and protocols. It integrates and harmonises the many online information systems relevant for IAS in Europe. EASIN acts as an up-to-date and extensive inventory of alien species within terrestrial, coastal and marine regions of Europe with detailed information on each species and their invasiveness (Katsanevakis et al. 2015). Additional information addresses taxonomy, pathways of introduction, range and distribution, reproduction and spread, biology and impact and diagnostic tools.

DAISIE has contributed with comprehensive information on invasive or potentially invasive species that threaten the European environment and introduced species as well as their distribution in each country based on experts‘ advice (DAISIE 2012). However, DAISIE has not been updated recently and does not include more than 30 % of the IAS in Europe (Gatto et al. 2012). Therefore, EASIN datasets have been used for pan-European or regional assessments of pathways and gateways of alien invasions supporting the prevention and management of the introduction and spread of invasive alien species in Europe.

Forest- and tree-dependent invasive alien species threatening biodiversity are found in all European countries (EEA 2012, 2016).

Until recently, tree species have not been considered as important IAS (Richardson et al. 2014). A list of 751 species (434 tree species and 317 shrubs) has been compiled by Rejmánek and Richardson (2013) although it represents only a small proportion of the world's woody plant flora (estimated to about 60 000 tree species). Of this list, Europe hosts currently 73 invasive alien tree species of which 28 are used in forestry. DAISIE and EPPO indicate that four tree species are of severe concern: silver wattle (*Acacia dealbata* Link), tree of heaven (*Ailanthus altissima* (Miller) Swingle), black cherry (*Prunus serotina* Ehrh.) and black locust (*Robinia pseudoacacia* L.) (Schmid 2014, Sitzia et al. 2016).

Some non-native species have been intentionally introduced to provide economic, environmental or social benefits (e.g. Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco – see Box 11.2). Some of these species that have been introduced outside their native ranges, have escaped to become serious threats to forests and other ecosystems (FAO 2011). This is a considerable concern in the forest sector since many of the tree species used for agroforestry, commercial forestry and desertification control are non-native to the area. Black locust is listed among the worst 100 invasive species in Europe as it modifies soil properties and replaces local biodiversity in particular in riparian forests (see chapter 5.1). In particular, white willow (*Salix alba* L.), ash (*Fraxinus excelsior* L.), black poplar (*Populus nigra* L.) and black alder (*Alnus glutinosa* (L.) Gaertn.) are affected (Benesperi et al. 2012, Della Rocca 2016). In other regions such as in south-western France, black locust has actually been planted to increase the biodiversity of 'Les Landes', a region in south-western France.

It is vital to ensure that such species serve the purposes for which they were introduced and do not cause negative effects to native ecosystems. Such examples include various pine species (e.g. maritime pine (*Pinus pinaster* Aiton) and Monterey pine (*Pinus radiata* (D. Don)) that have been planted on large areas and have become naturalised (Brundu et al. 2016).

Forestry in Europe is expected to be increasingly affected by the threat of IAS. The introduction of pathogens and invertebrate pests on imported wood and other forest products may lead to high economic implications and severe ecological damage. It has been estimated that 109 invasive alien insect pests of woody plants have been introduced to and have established in Europe: 57 of these species are from North America and 52 are from Asia (Eyre et al. 2013). The Asian long-horned beetle (*Anoplophora glabripennis* Motschulsky, 1854) is an example of a harmful insect that has been introduced as a consequence of expanding intercontinental trade. Since autumn 2011, the presence of this beetle has been documented on numerous forest sites across Europe and has manifested itself as one of the most harmful IAS for deciduous trees.

Recently, considerable attention has been given to a North American pest, the pine wood nematode – PWN (*Bursaphelenchus xylophilus* (Steiner & Buhrer 1934, Nickle 1970). In 1999, the PWN was detected close to Lisbon in Portugal (Mota et al. 1999). Previous surveys in Europe had suggested that PWN was absent from the region (EPPO and CABI 1990). Several new outbreaks have been identified since 2008 in other parts of Portugal, as well as in Spain. Scots pine (*Pinus sylvestris* L.) is at risk from this pest in both northern and central Europe; black pine (*Pinus nigra* J.F. Arnold) and maritime pine are threatened in central and southern Europe.

Box 11. Example of a non-native introduced species: Douglas fir (San-Miguel-Ayanz et al. 2016).

Douglas fir is a conifer species native to North America. The tree was introduced to Europe in 1827. It was initially planted as an ornamental tree and over time became a major economic species due to its fast growth rate and good quality timber (see chapters 4.1, 5.2 and 5.3). By the end of the 19th century, Douglas fir was an accepted tree species in forestry. After the Second World War, it was also planted in Western Europe. More than 80 % of Douglas fir in Europe are found in France, Germany and the United Kingdom. It is the most abundant non-native tree species in central European forests (Essl 2005, San-Miguel-Ayanz et al. 2016). Further introduction of exotic organisms associated with Douglas fir in its native range may be more problematic than the introduction of Douglas fir itself, in case of host jump affecting other native tree species (Schmid et al. 2014). According to Richardson and Rejmánek (2011) it may display the potential of becoming invasive in Germany, Austria, Bulgaria and United Kingdom, given the right circumstances. For this reason, silver fir (*Abies alba* Mill.) has been suggested as a sustainable European alternative to Douglas fir to substitute for the drought sensitive Norway spruce (*Picea abies* (L.) H. Karst.) under global warming conditions (Tinner et al. 2013).

Figure 39. Giant Douglas fir tree (photo: A. Bastrup-Birk).

National customs authorities in Europe responsible for imported timber and wood products have long been aware of the risk of PWN introduction. PWN has been designated as a quarantine organism and strict control measures on trade of potentially affected tree species have been imposed to limit further spread of this dangerous pest. Such control measures have added significantly to the costs aside from destroying affected pine trees and stands.

The chestnut blight fungus (*Cryphonectria parasitica* (Murrill) M.E. Barr) is another example of a hazardous IAS. This fungus originated in Asia and has expanded, at a slow, yet steady, rate since it was found in Italy in 1938 (Robin and Heiniger 2001). It has devastated large plantations of sweet chestnut (*Castanea sativa* Mill.) in southern Europe.

Reliable, detailed information on the main IAS in Europe is an essential tool for preventing their spread and harmonised, and for applying effective and appropriate control strategies.

▶ *Additional data and scientific information is required for continuously build-up a reliable database to ensure fact based responses.*

Several studies analysing different IAS databases in Europe identified considerable differences in the data, and consequently their analysis and resulting recommendations

(Chytrý et al. 2008, Katsanevakis et al. 2015). Information on the distribution and estimated impacts of IAS may vary for and between countries. In some countries a species may appear on the IAS list but is not yet considered as invasive. Thus, caution should be taken when applying collated data from different sources.

Europe should ensure maintenance, update and expansion of a central pan-European database on IAS such as EASIN (see also Box 12). Streamlining and harmonisation of the national and regional systems that collate data on alien species are recommended to prevent existing knowledge from disappearing or becoming unavailable. Avoiding the pitfalls of different definitions and criteria, which may lead to incomparability of data also needs to be addressed. Core elements of such a database are the common data standards and information protocols. These allow interoperability, compatibility and coordination among initiatives operating at the national, regional and global levels. This includes robust definitions regarding status, impact and invasion of alien species. They should be the basis for commonly approved formats and standards for recording information across alien taxa in marine, freshwater and terrestrial ecosystems.

Box 12. EU Regulation on the prevention and management of the introduction and spread of invasive alien species

The situation

At present there are estimated to be more than 12 000 alien plants, animals, fungi and micro-organisms in the European Union and in other European countries (EC 2014a). Out of those 10–15 % are considered to be invasive with their numbers increasing. By either suppressing or eliminating indigenous species, invasive alien species are considered one major contributor to biodiversity loss. It is estimated that they have cost the European economy €12 billion per year over the last 20 years (EC 2014b). They also affect a wide range of ecosystem services, infrastructures and can have serious implications for human health.

In forest ecosystems currently 134 species (71 trees, 61 shrubs and 2 defined tree or shrub) are regarded as invasive in Europe (Rejmánek and Richardson 2013).

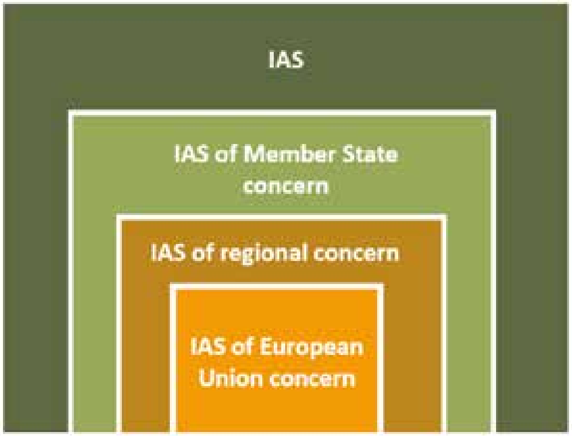


Figure 40. Invasive alien species have impact at different geographic levels.

Elaborating on a European Union regulation

Due to such alarming developments, along with the Member states, EU jointly elaborated on a regulation on invasive alien species. It entered into force on 1st January 2015 and is the result of an extensive consultation process, expert reviews and impact assessments (visit EC Website on 'Invasive Alien Species' for more details http://ec.europa.eu/environment/nature/invasivealien/). The regulation is aimed at addressing consequences resulting from invasive alien species in a holistic and comprehensive manner within the EU. It seeks to protect native biodiversity and ecosystem services, while minimising and mitigating the impacts such species may have on human health and economy. The regulation addresses only species of overall European Union concern and not as such at the regional or national levels.

Key elements of the Regulation

List of invasive alien species of Union concern

The European Commission and EU Member States are able to propose invasive alien species to a list of invasive alien species of Union concern based on a set of criteria (see 2: 'selection criteria' below). A scientific forum then reviews the scientific robustness of the provided information while a designated committee ensures compliance with the criteria. The list will be regularly updated by either adding new species or removing such that no longer meet the criteria for inclusion on the list. The first invasive alien species list was entered into force on 3rd August 2016.

Selection criteria for invasive alien species

In order to be included to the invasive alien species list of Union concern all of the following criteria need to be met:

- they are found, based on available scientific evidence, to be alien to the territory of the Union excluding the outermost regions;
- they are found, based on available scientific evidence, to be capable of establishing a viable population and spreading in the environment under current conditions and in foreseeable climate change conditions in one biogeographical region shared by more than two Member States or one marine sub-region excluding their outermost regions;
- they are, based on available scientific evidence, likely to have a significant adverse impact on biodiversity or the related ecosystem services, and may also have an adverse impact on human health or the economy;
- it is demonstrated by a risk assessment carried out pursuant to Article 5 Regulation (EU) No 1143/2014 that concerted action at Union level is required to prevent their introduction, establishment or spread;
- it is likely that the inclusion on the Union list will effectively prevent, minimise or mitigate their adverse impact.

Intervention types

For those species that are listed as invasive the regulation foresees three types of measures based on the particular circumstances. They are described in detail under the respective 'Regulation Articles' and thus only a few key facts are listed below:

- **Prevention** regulates intentional introduction, storing, breeding, transport as well as unintentional introduction. It elaborates on permits and authorisations, the establishment of a list of invasive alien species, implementation of emergency measures in case of eminent threat, action plans on pathways of invasive alien species.
- **Early detection and rapid eradication** as laid out in the regulation include the establishment of surveillance systems, official controls, early detection notifications, and measures and derogations for rapid eradication at an early stage of invasion.
- **Management of established invasive alien species** that are widely spread require management measures to mitigate impacts. Also the implementation of restoration measures to assist recovery of degraded or even destroyed ecosystems are part of the Regulation.

The European Commission‘s financial support system

The European Commission supports action on invasive alien species through existing financing instruments. Some of the main funding instruments are: (1) the EU’s financial instrument supporting environmental, nature conservation and climate action (LIFE); (2) Horizon 2020; (3) the EU’s rural development policy (2014–2020); and (4) the European Regional Development Fund (ERDF).

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TEXT BOX II: Code of Conduct on planted forest: recommended management for introduced and invasive tree species

Giuseppe Brundu and David M. Richardson

Planted forests comprising of introduced tree species make significant contributions to local and national economies and provide multiple products and ecosystem services that support livelihoods and biodiversity (e.g. Brockerhoff et al. 2008). However, many widely used introduced tree species have become invasive – i.e. they have spread from planted sites into the neighbouring areas where they caused substantial damage. The challenge is to manage existing and future planted forests dominated by introduced tree species in order to maximise current and future benefits while minimising present and future negative impacts. In many countries or regions, introduced tree species planted for timber production or other purposes often lead to conflicts of interest but also to negative impacts on ecosystem services, nature conservation, etc., not only when they become invasive (e.g. Dodet and Collet 2012).

Introduced tree species currently dominate 4.4 % of the European forest area with tree species that are considered to be invasive currently occupying 0.5 % of Europe's forests (FOREST EUROPE 2015). Nowadays, many introduced tree and woody species are restricted in their use in some European countries due to national legislations and listings such as ash-leaved maple (*Acer negundo* L.), acacias (*Acacia* spp.), tree of heaven (*Ailanthus altissima* (Mill.) Swingle), pines (*Pinus* spp.), black cherry (*Prunus serotina* Ehrh.), northern red oak (*Quercus rubra* L.) and black locust (*Robinia pseudoacacia* L.).

In addition to other general guidelines (Annex 1), and to encourage national authorities to implement specific principles of prevention and mitigation of the risks posed by invasive introduced tree species into their national environmental policies, the Council of Europe has promoted the preparation of a Code of Conduct on Planted Forest and Invasive Alien Trees (Brundu and Richardson 2016).

The Code of Conduct on Planted Forest and Invasive Alien Trees is addressed to all relevant stakeholders and decision-makers in 47 member states of the Council of Europe. It aims to enlist the co-operation of various stakeholders of the forest sector (i.e. trade and industry, national forest authorities, certification bodies and environmental agencies) and associated professionals in preventing new introductions. In addition, the Code recommends practices that would reduce, control and mitigate negative impacts of introduced tree species in planted forests. It complements the Code of Conduct on Horticulture and Invasive Alien Plants published by the Council of Europe (Heywood and Brunel 2011) aimed at the horticultural industry and trade, and the European Code of Conduct for Botanic Gardens on Invasive Alien Species (Heywood and Sharrock 2013). The Code does not replace any statutory requirements under international or national legislation. It should be considered as a complementary document on prevention and management of the introduction and spread of invasive species.

The Code of Conduct consists of fourteen major principles that are clustered into five groups:

1. Awareness
   - 1.1. Awareness regarding regulations concerning invasive tree species of non-native origin
   - 1.2. Awareness of which introduced tree species are invasive or which may become invasive
   - 1.3. Development of platforms for information sharing and training programmes

2. Prevention and containment

- 2.1. Promote – where possible – the use of native tree species
- 2.2. Adopt good nursery practices
- 2.3. Modify plantation practices to reduce possible issues with invasive non-native tree species
- 2.4. Revise general management practices of planted forests
- 2.5. Implement suitable practices for harvesting and timber haulage
- 2.6. Adopt good practices for habitat restoration

3. Early detection and rapid response

- 3.1. Promote and implement early detection and rapid response programmes
- 3.2. Establish or join a network of sentinel sites

4. Outreach

- 4.1. Engage with the public on the risks posed by invasive non-native trees, their im pacts and on options for their management

5. Forward planning

- 5.1. Consider developing research activities on invasive non-native trees species and becoming involved in collaborative research projects at national and regional levels
- 5.2. Take global change trends into consideration

Although environmental and socio-political factors in Europe demand unique approaches for dealing with non-native tree invasions, developments from elsewhere, especially regarding ways of dealing with conflicts of interests and effective engagement with multiple stakeholders provide many useful lessons. For these reasons, and also because the role of "forestry in the Anthropocene" in general is being actively debated (e.g. Lugo 2015), the Code will need to be revised regularly.

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Annex 1 – A selection of existing international forest guidelines providing indications on the use of introduced tree species in planted forests.

- **Non-Legally Binding Authoritative Statement of Principles for a Global Consensus on the Management, Conservation and Sustainable Development of All Types of Forests**
  A document produced at the United Nations Conference on Environment and Development (UNCED), informally known as the Earth Summit, Rio de Janeiro, 3–14th June 1992: (6.a "*the potential contribution of plantations of both indigenous and introduced species for the provision of both fuel and industrial wood should be recognized.*").
- **Forest Europe**
  The brand name of the Ministerial Conference on the Protection of Forests in Europe. forty-seven signatories (46 European countries and the European Union).
- **General guidelines for sustainable forest management in Europe (Resolution H1)**
  Second Ministerial Conference on the Protection of Forests in Europe 16–17th June 1993, Helsinki, Finland: (*"9. Native species and local provenances should be preferred where appropriate. The use of species, provenances, varieties or ecotypes outside their natural range should be discouraged where their introduction would endanger important/valuable indigenous ecosystems, flora and fauna. Introduced species may be used when their potential negative impacts have been assessed and evaluated over sufficient time, and where they provide more benefits than do indigenous ones in terms of wood production and other functions. Whenever introduced species are used to replace local ecosystems, sufficient action should be taken at the same time to conserve native flora and fauna"*).
- **General Guidelines for the Conservation of the Biodiversity of European Forests (Resolution H2)**
  Second Ministerial Conference on the Protection of Forests in Europe 16–17th June 1993, Helsinki, Finland: (*"4. Where possible the establishment of taxa which are naturally associated with those that occur most frequently in the forest should be encouraged, and a variety of structure within stands should be favoured, where the natural dynamics of such associations permit"*).
- **Pan-European Operational Guidelines for Sustainable Forest Management**
  Third Ministerial Conference on the Protection of Forests in Europe, 2–4th June 1998, Lisbon/Portugal: (4.2.b *"For reforestation and afforestation, origins of native species and local provenances that are well adapted to site conditions should be preferred, where appropriate. Only those introduced species, provenances or varieties should be used whose impacts on the ecosystem and on the genetic integrity of native species and local provenances have been evaluated, and if negative impacts can be avoided or minimised"*).
- **Conserving and enhancing forest biological diversity in Europe (Vienna Resolution 4)**
  Fourth Ministerial Conference on the Protection of Forests in Europe, 28–30th April 2003, Vienna, Austria: (*"14. contribute to the development of a Pan-European strategy which prevents and mitigates the impacts of invasive alien species that threaten ecosystems, in accordance with the decisions of the CBD"*).
- **Non-Legally Binding Instrument on All Types of Forests (forest instrument)**
  The General Assembly of the United Nations adopted (resolution 62/98) in December 2007, the most widely, inter-governmentally agreed definition of Sustainable Forest Management.

- **Pan-European Guidelines for Afforestation and Reforestation with a special focus on the provisions of UNFCCC**
  Document adopted by the MCPFE expert Level Meeting on 12–13th November, 2008 and by the PEBLDS Bureau on behalf on the PEBLDS Council on 4th November 2008: (*"21. Species, provenances, varieties or ecotypes outside their natural range should only be used where their introduction would not endanger important and/or valuable indigenous ecosystems, flora and fauna. Those that are likely to invasive should be avoided using the CBD Guiding Principles …" – "22. A precautionary approach should be taken to the use of genetically modified trees …"*).
- **Protection of forests in a changing environment**
  Draft Madrid Ministerial Resolution 2, Protection of forests in a changing environment, adopted by the Expert Level Meeting on 1st July 2015 for consideration by the ministers at the FOREST EUROPE Ministerial Conference Madrid 20–21th October 2015: (*"14. share expertise in the region and reinforce the collaboration between countries on … … as well as handling invasive species"*).

3.3 Assessment of invasive tree species in nature conservation and forestry – contradictions and coherence

Torsten Vor, Stefan Nehring, Andreas Bolte, Anke Höltermann

▶ *Invasiveness of plant taxa is differently defined and assessed.*

While the general principles and processes of plant invasion are well-known, the more nuanced issues of human values, perceptions and attitudes are less widely recognised (Rotherham and Lambert 2011). It is evident that people understand natural phenomena in different ways according to their knowledge, to their experience or simply according to their attitude. Thus, what is an invasion by native or alien species is rather challenging to define in a consistent way (Figure 41. Heger et al. 2013). Several definitions of the term 'invasive species' have been available and there is a lot of variation amongst individual definitions. While initially an invasion into ecosystems was defined as an immigration of an essential part of a population (Schaefer and Tischler 1983), the wording of some definitions has been more specific than in other cases (please see *Introduction* of this book). In modern ecology, an invasive species refers to an alien species, which has been directly or indirectly favored (imported) by humans, and has established self-reproducing populations with higher numbers of individuals (Kowarik 2010, Schaefer 2012). This definition does not take anthropocentric valuations into account.

Figure 41. Natural regeneration of Douglas fir together with other tree species following a windthrow event (photo: J. Bauhus).

After the United Nations Conference on Environment in 1992 in Rio de Janeiro, nature conservation policies and many federal laws emphasised the threat to biodiversity by invasive species and the requirement to control these species. In the German Act on Nature Conservation and Landscape Management (Federal Nature Conservation Act – BNatSchG) Article 7 defines an invasive species as *a species whose populations outside of its natural range have a significant threatening potential to the naturally occurring ecosystems, biotopes or species in the reference area*. In the North American literature, the traits of invasive species were described in a similar way: *biotic invaders are species that establish a new range in which they proliferate, spread and persist to the detriment of the environment* (Mack et al. 2000). Therefore, a risk assessment for invasive species in Europe was established (in coherence with *EU Regulation 1143/2014*) in order to prevent threats to the native species and ecosystems.

In Germany, the 'German-Austrian Black List Information System' (GABLIS) for invasive species was developed as an assessment tool by the German Federal Agency for Nature Conservation (BfN). Nine alien commercial tree species were assessed as invasive according to this assessment tool (Nehring et al. 2013b). Nonetheless, an alternative assessment approach by a group of forest scientists, partly using different methodology, found only four tree species to be invasive (Vor et al. 2015). Within this chapter, the contradictions and coherences of these two assessment schemes are presented and discussed. Moreover, a joint approach of nature conservationists and forest scientists towards a proper management of Douglas fir as one of the most important alien tree species in central Europe shows an example to overcome conflicts between nature conservation and forest management aims.

> ▶ *The key criteria for invasiveness from the perspective of nature conservation law is that the species has a 'significant threatening potential' to biodiversity.*

With the exception of species covered by the mandate of the European and Mediterranean Plant Protection Organization (EPPO) (Brunel et al. 2010), until recently there has been no coherent risk assessment for alien species at the national level in Europe. However, in 2010, Nehring et al. (2010) published a comprehensive risk assessment tool for alien species in Germany (including tree species). The tool was developed in the context of a reform of the Federal Nature Conservation Act, which came into an effect on 1st March 2010. The methodology of the assessment was developed in close cooperation between the German Federal Agency for Nature Conservation (BfN) and the Austrian Environment Agency (UBA) and is called GABLIS (as mentioned above) (Essl et al. 2011).

GABLIS is an international and taxonomically universal risk assessment system, which takes into account the detrimental effects of alien species – not only tree species – on biodiversity. Invasiveness of individual taxa is assessed by a defined and transparent procedure developed on the basis of a set of specific criteria. Economic and health issues posed by individual invasive species are included in the assessment but they are not part of the evaluation process itself. The overall assignment of an alien species to a list category in GABLIS is based on the level of threat to native biodiversity, which is assessed using five main criteria:

- Interspecific competition

- Predation and herbivory
- Hybridisation
- Vectors of pests and diseases
- Other negative impacts on ecosystems

Additional criteria considered within GABLIS include:

- Status of the current distribution
- Existence of emergency measures to eradicate the species
- Other management options

A third set of criteria focuses on biological or ecological traits of the assessed species and it includes:

- Occurrence in natural, close-to-nature or protected areas
- Reproduction capacity
- Spread capacity
- Current spread history
- Monopolisation of resources
- Facilitation by climate change

However, the effects of species traits are context, habitat and invasion phase dependent (Pyšek and Richardson 2007). Therefore, prognoses of detrimental effects based on species traits are only possible to a limited extent (Rejmánek et al. 2007). Therefore, in GABLIS, traits are used for classification only within a certain range.

Data used for the assessment may originate from scientific reports and peer-reviewed publications as well as from expert judgement, and they may refer either to a reference area or to climatically and ecologically similar areas. It is mandatory to document the data source to ensure transparency, reliability and replication of the results. This is required for a consistent interpretation of GABLIS assessment results, which may become legally binding in the future.

In order to consider species as invasive under GABLIS, the species must first pose a scientifically documented threat to naturally occurring ecosystems, habitats or species. However, due to the lack of accurate data, in most cases, the damage threshold for GABLIS is determined by qualitative indicators only. The alien species is confirmed as a threat if at least one population of a native species is locally endangered by the alien species. Further, if its invasion into new areas is likely to increase the risk of extinction of the native species in large parts of its range. This includes the expectation of the eventual upgrading or inclusion of native species in the Red List of endangered species.

In accordance to the German Federal Nature Conservation Act (Box 13), GABLIS does not provide any site-specific exemptions for the assessment of alien tree species as handled by other assessment approaches (e.g. Vor et al. 2015). This reflects the fact that rare sites often have high-value features in terms of nature conservation (e.g. boulder fields).

Moreover, it is important to note, that the knowledge of effective countermeasures (e.g. silvicultural management options) does not preclude per se the classification of a species as invasive. Therefore, according to GABLIS the necessity of countermeasures may be a possible consequence of its invasiveness. In this respect GABLIS differs significantly from the alternative methodology presented by Vor et al. (2015) who includes the means of silvicultural control in the invasiveness assessment of alien tree species.

The term 'significant threatening potential' in the German Federal Nature Conservation Act states that it is not necessary to have documented damage by an alien species to the reference area for an alien species to be classified as invasive. The sole possibility of the species having harmful effects is sufficient for it to be considered as invasive. GABLIS meets this important prerequisite. For alien species not yet present in the reference area or for alien species at the beginning of their spread, GABLIS assesses the risk by assessing the experience gained from invasions in climatically and ecologically similar areas. The criterion of 'being invasive elsewhere' is one of the most important and most appropriate prerequisites for carrying out predictive risk assessments (see Pyšek and Richardson 2007).

GABLIS is recognised by national and international nature conservation communities and is used by many institutions in Germany as well as by several EU member states. Since the first publication of GABLIS in 2010, BfN has assessed alien species of all taxonomic groups in Germany and published assessments of alien fish species (Nehring et al. 2010), vascular plants (Nehring et al. 2013b) and other vertebrate groups (Nehring et al. 2015b).

Eighty vascular plant species were assessed by GABLIS and 38 were found to be invasive (Nehring et al. 2013b, Table 15), which also includes nine tree species. All invasive tree species are listed on so called 'management list', none of these species is in the phase of early expansion, and needs urgent eradication. Measures against widely spread species should be aimed to minimise/mitigate the negative impact in e.g. protected areas, nature reserves or to safeguard endangered native species (Essl et al. 2011, Nehring et al. 2015a). The GABLIS assessments were later also confirmed by the German Coordination Centre for Invasive Plants in protected areas of Saxony-Anhalt (KORINA 2014).

In order to better protect native biodiversity, ecosystem services, economic values and human health, the European Union adopted the Regulation 1143/2014 on invasive alien species (active since 1st January 2015). The regulation differentiates between three types of interventions: (1) prevention, (2) early detection and rapid eradication, and (3) management – corresponding to the different lists of GABLIS for invasive species (warning list, action list, management list). The European Commission is legally bound to prepare a draft list of invasive alien species of Union concern (the so-called 'Union list') within one year based on risk assessments and scientific evidence. On 4th December 2015 the first Union list, which includes 37 invasive species (no tree species), was adopted by the competent Committee. Twenty days after its publication in the Official Journal of the European Union (EU 2016), the first Union list was entered into force on 3th August 2016. However, EU Member States can submit requests to the European Commission to include further invasive species into the Union list at any time (see Chapter 3.2.).

Box 13. German Act on Nature Conservation and Landscape Management

(Federal Nature Conservation Act – BNatSchG) of 29th July 2009 – unofficial translation, from http://www.bmub.bund.de/fileadmin/Daten_BMU/Download_PDF/Naturschutz/bnatschg_en_bf.pdf

Article 40 – Non-native, alien and invasive species

1. Suitable measures must be taken to counter threats to ecosystems, biotopes and species presented by non-native or invasive species of plants and animals.

2. Where there are indications that species could be invasive species, the relevant species are to be monitored.

3. The competent Federal and State authorities shall immediately take suitable measures aimed at eliminating, or preventing the spread of, newly appearing plants and animals of invasive species. In the case of invasive species that have already spread, they shall take measures to prevent the species' further spreading and to mitigate the impacts of the existing spreading, to the extent that such measures seem likely to succeed and the relevant success is not disproportional to the relevant required effort and expense. Sentences 1 and 2 shall not apply to plants within the meaning of (4) Sentence 3 No 1 that are cultivated in agriculture and forestry.

4. Planting of alien species of plants, and release of alien species of animals, in natural surroundings shall require a permit from the competent authority. Artificially propagated plants shall not be deemed alien if their genetic origins are found in the relevant area. Such a permit shall be denied if a threat to Member States' ecosystems, biotopes or species cannot be ruled out. The following shall be exempt from the permit requirement:
    1. the cultivation of plants in agriculture and forestry,
    2. the release of animals
        a) of non-alien species,
        b) of alien species, provided their release requires a permit under plant protection legislation which makes allowance for the interests of species conservation, for the purposes of biological plant protection,
    3. the introduction of animals of non-alien species that are subject to laws on hunting or fishing, the planting of woody plants and seeds outside of their natural ranges, through 1st March 2020; until that time, preference should be given to planting woody plants and seeds, in natural surroundings, only within their natural ranges.

Article 22 of Directive 92/43/EEC must be observed.

5. With regard to species not yet occurring within the boundaries of the national territory, permits pursuant to (4) shall be issued by the Federal Agency for Nature Conservation (BfN).

6. The competent authority may order the elimination of animals or plants that have been placed in natural surroundings without relevant permits, of plants spreading unintentionally in natural surroundings or of animals that have escaped into natural surroundings, if such elimination is needed to ward off threats to ecosystems, biotopes or species.

GABLIS provides a valuable scientific basis for the German input to the Union list. It was approved as an assessment protocol compliant with the main requirements of the EU Regulation (Roy et al. 2014). In 2015, BfN submitted a list of potential candidates to be included on the Union list to the German administration for further consultation within the body. The BfN list includes eight out of the 38 invasive plant species identified by GABLIS (underlined in Table 15). All of the listed species are considered to be at an early stage of invasion.

Table 15. Invasive plant species in Germany according to Nehring et al. (2013b) are shown in bold. Invasive species proposed by BfN as German contribution to the Union list of EU Regulation No. 1143/2014 are underlined. Invasive tree species (including one shrub-like species) as assessed by GABLIS are highlighted in red.

Acer negundo
Ailanthus altissima
Allium paradoxum
Ambrosia artemisiifolia
Amorpha fruticosa
Artemisia verlotiorum
Asclepias syriaca
Azolla filiculoides
Bidens frondosa
Buddleja davidii
Bunias orientalis
Claytonia perfoliata
Cotoneaster dammeri
Cotoneaster divaricatus
Cotoneaster horizontalis
Crassula helmsii
Cynodon dactylon
Dianthus giganteus
Echinocystis lobata
Echinops shaerocephalus
Eleagnus angustifolia
Elodea canadensis
Elodea nuttallii
Epilobium ciliatum
Fallopia bohemica
Fallopia japonica
Fallopia sachalinensis
Fraxinus pennsylvanica
Galeobdolon argentatum
Gleditsia triacanthos
Helianthus tuberosus
Heracleum mantegazzianum
Hydrocotyle ranunculoides
Impatiens balfourii
Impatiens edgeworthii
Impatiens glandulifera
Impatiens parviflora
Lagarosiphon major
Lonicera henryi
Lonicera tatarica
Ludwigia grandiflora
Ludwigia x kentiana
Lupinus polyphyllus
Lycium barbarum
Lysichiton americanus
Mahonia aquifolium
Miscanthus sacchariflorus
Miscanthus sinensis
Myriophyllum aquaticum
Myriophyllum heterophyllum
Paulownia tomentosa
Phedimus spurius
Phytolacca americana
Pinus nigra
Pinus strobus
Pistia stratiotes
Populus canadensis
Prunus laurocerasus
Prunus serotina
Pseudotsuga menziesii
Quercus rubra
Rhododendron ponticum
Rhus typhina
Robinia pseudoacacia
Rosa rugosa
Rubus armeniacus
Rudbeckia laciniata
Sarracenia purpurea
Senecio inaequidens
Solidago canadensis
Solidago gigantea
Spartina anglica
Symphoricarpos albus
Symphyotrichum lanceolatum
Symphyotrichum novi-belgii
Syringa vulgaris
Telekia speciosa
Vaccinium atlanticum
Vallisneria spiralis
Viburnum rhytidophyllum

Forest science pleads to emphasise the spreading potential of alien tree species as well as options for their management.

The GABLIS assessment of vascular plants classified 13 tree species (red species in Table 15) as invasive or potentially invasive (Nehring et al. 2013b). These 13 species include several commercial tree species such as Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and northern red oak (*Quercus rubra* L.) that have a tradition of more than a hundred years of being used in forestry in central Europe with almost no indications for threatening natural ecosystems, habitats or species.

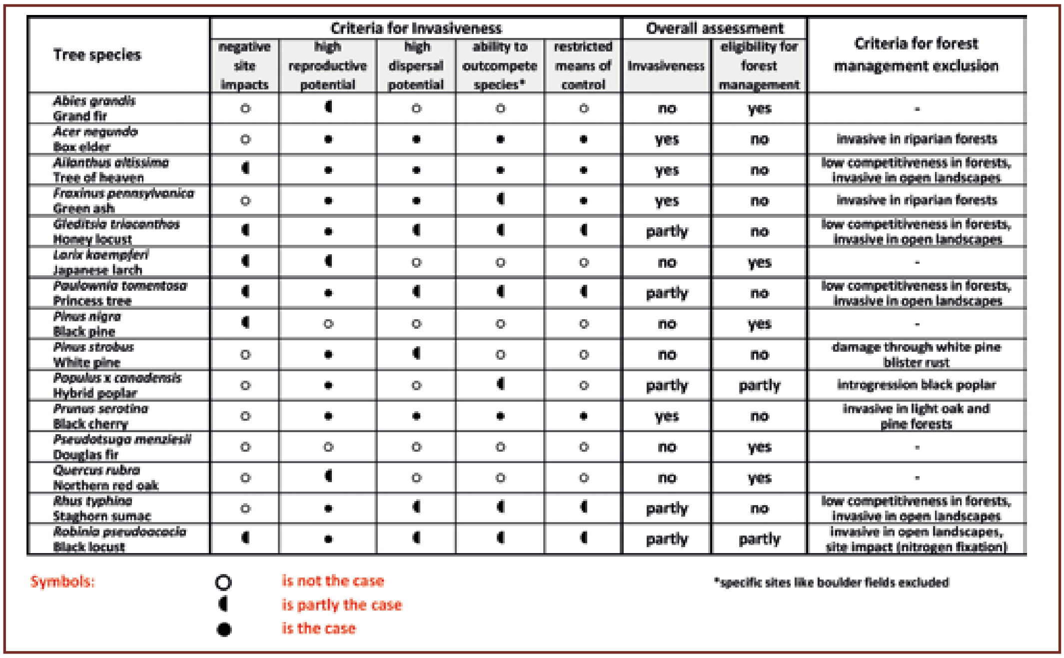
Therefore, a group of forestry scientists have objected to the GABLIS assessment of the alien tree species used for forestry purposes. They have argued that most of the listed tree species do not meet the legal criteria of presenting a 'significant threatening potential' to forest ecosystems (German Federal Nature Conservation Act) (Ammer et al. 2014). Ammer et al. (2014) criticised the GABLIS methodology, arguing that it is mainly based on selective criteria, and does not adequately consider biological processes of plant expansion and recruitment. Moreover, some criteria combine processes such as competition and negative ecosystem effects that overlap and occur at different ecosystem scales. Therefore, Ammer et al. (2014) suggested an alternative approach for assessing the invasiveness of tree species that includes management options preventing further spread of the invasive species. Introduced tree species behaving invasively and posing a threat to native biodiversity should be controlled by using specific forest management practices. It is also important to note that invasive tree species that can be controlled by using specific silvicultural approaches pose a lower threat to other species and ecosystems than those that can be managed only by a limited set of management approaches.

Due to the contrasting views, 28 forest scientists from Germany and Switzerland published an alternative evaluation of 15 alien tree species with regards to their potential to pose risks to forest ecosystems. This report was also focusing on nature conservation issues, including two additional important alien tree species; i.e. grand fir (*Abies grandis* (Douglas ex D. Don) Lindley) and Japanese larch (*Larix kaempferi* (Lamb.) Carr.) (Vor et al. 2015). The indicators used to assess the invasiveness of these species following an extensive literature review were:

- Site impacts;
- Reproductive potential;
- Dispersal potential;
- Ability to outcompete native species;
- Means of control and management.

The species were categorised according to their overall threat potential. Invasions of specific sites and habitats as for instance open rocky screes, shallow and nutrient-poor ridges (see below) were not included in the assessment but they were mentioned where there are examples for individual tree species. Such sites need protective management measures applied on a regular basis as well as the special protection against invasions of alien species, which is one issue among many others with regards to these specific environments. Furthermore, the 15 selected alien tree species where classified with regard to their suitability for use in forestry. The assessment resulted in four of the investigated tree species being classified as invasive, five being classified as partly invasive, mainly due to their invasive traits in open landscapes, and six species being classified as not invasive (Table 16).

Table 16. Evaluation of ecological traits of alien tree species in Germany according to Vor et al. (2015).



Tree species	Criteria for Invasiveness					Overall assessment		Criteria for forest management exclusion
	negative site impacts	high reproductive potential	high dispersal potential	ability to outcompete species*	restricted means of control	Invasiveness	eligibility for forest management	
Abies grandis Grand fir	○	◖	○	○	○	no	yes	-
Acer negundo Box elder	○	●	●	●	●	yes	no	invasive in riparian forests
Ailanthus altissima Tree of heaven	◖	●	●	●	●	yes	no	low competitiveness in forests, invasive in open landscapes
Fraxinus pennsylvanica Green ash	○	●	●	◖	●	yes	no	invasive in riparian forests
Gleditsia triacanthos Honey locust	◖	●	◖	◖	◖	partly	no	low competitiveness in forests, invasive in open landscapes
Larix kaempferi Japanese larch	◖	◖	○	○	○	no	yes	-
Paulownia tomentosa Princess tree	◖	●	◖	◖	◖	partly	no	low competitiveness in forests, invasive in open landscapes
Pinus nigra Black pine	◖	○	○	○	○	no	yes	-
Pinus strobus White pine	○	●	◖	○	○	no	no	damage through white pine blister rust
Populus x canadensis Hybrid poplar	○	●	○	◖	○	partly	partly	introgression black poplar
Prunus serotina Black cherry	○	●	●	●	●	yes	no	invasive in light oak and pine forests
Pseudotsuga menziesii Douglas fir	○	○	○	○	○	no	yes	-
Quercus rubra Northern red oak	○	◖	○	○	○	no	yes	-
Rhus typhina Staghorn sumac	○	●	◖	◖	◖	partly	no	low competitiveness in forests, invasive in open landscapes
Robinia pseudoacacia Black locust	◖	●	◖	◖	◖	partly	partly	invasive in open landscapes, site impact (nitrogen fixation)

Symbols:
○ is not the case
◖ is partly the case
● is the case

*specific sites like boulder fields excluded

> *Joint concepts for the management of alien tree species are possible and Douglas fir in Germany can be considered as an example.*

Douglas fir is the most important alien coniferous tree species in Germany; it was classified as *invasive* by the Federal Nature Conservation Act (by BfN) according to Nehring et al. (2013b) (based on GABLIS) and as *not invasive* in the report by Vor et al. (2015). Although there are persistent controversies about the two methodologies defining invasiveness, there were shared ideas about how to manage Douglas fir to minimise any potentially negative effects on biodiversity. Consequently, a joint management concept for Douglas Fir was developed by scientists from the BfN and the German section of the International Union of Forest Research Organisations (DVFFA) – disregarding the conflicting definitions of invasiveness. The group published the following statements illustrating a common agreement for Douglas fir management (DVFFA and BfN 2016):

1. On the vast majority of forest sites in Germany the management of Douglas fir does not pose a significant threat to biodiversity and ecosystem services on the national level according to the current state of scientific knowledge.
2. At special habitats, such as open rocky screes, shallow and nutrient-poor ridges, xeric grasslands and thermophilic forest (i.e. thermophilic oak forest) communities, Doug-

las fir should not be grown in order to protect rare and endemic species. Such sites, which are mostly protected by law and do not represent large areas, should be kept free of Douglas fir by: removing natural Douglas fir regeneration; converting neighbouring Douglas fir stands into stands of native species; and avoiding the establishment of new Douglas fir stands. In addition to these general recommendations, in protected areas specific legal regulations in respect of alien tree species apply.

3. Generally, Douglas fir should be mixed with other native tree species, like European beech (*Fagus sylvatica* L.).

These recommendations may not be applicable to the whole of Europe and must be adapted to the specific conditions in other regions. However, in general, such recommendations provide an example of how to protect native biodiversity and to reduce impacts of alien tree species while bearing in mind the significance of forestry sector.

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3.4 Eradication as an option for managing invasive tree species in protected areas

Livia Zapponi, Raffaele Cavalli, Emma Minari and Franco Mason

Introduced tree species used in commercial and ornamental forestry may represent a threat when they spread in natural habitats where they can affect ecosystem functions (Richardson 1998). Therefore, it is fundamental to assess the impact of introduced tree species have on biodiversity of protected areas; it is important to carefully identify conservation goals and prioritise the strategies to manage the species as well as rank the species considering their potential impact and the feasibility of their control. Addressing the impact of introduced tree species that exhibit invasive behaviour is particularly important (DAISIE 2009) as invasive tree species may threaten endemic and native species through competition and interspecific hybridisation (Cox 2009).

Effective management strategies need to be species- and site-specific and take into consideration important factors such as propagule pressure.

The effects of removal of introduced tree species on the native re-vegetation is rarely assessed (Kettenring and Adams 2011). However, such management approaches should be properly monitored in order to evaluate the recovery of native populations and the costs involved, and to eventually establish complementary conservation measures (Genovesi and Shine 2004). Unfortunately, eradication projects are mainly published as technical reports, thus with limited dissemination and replication.

In the case of eradication, multiple factors contributing to the persistence and expansion of invasive tree species need to be taken into consideration. Effective strategies need to be species-specific, considering propagule pressure, and site-specific, since not all recipient habitats react in the same way to the invasions (Höfle et al. 2014) but the factors that drive their spread are insufficiently understood Eradication methods should be calibrated taking into account regeneration strategies of target species, and in particular, the occurrence of sexual and vegetative reproduction. The techniques applied to control and eradicate introduced and invasive tree species include mechanical and chemical treatments as well as a combination of both.

Combined strategies where tree growing stages are considered may be required for invasive introduced tree species.

Integrated strategies may be needed to limit the impact of the different tree growing stages. Seed-bearing trees should be eliminated as well as the younger individuals before they reach the reproductive stage. Despite their potential negative side effects, herbicides have been applied in some protected areas (e.g. in Canada, Hungary, Italy, Spain). Application of glyphosate on stumps has been used as a method to remove the tree of heaven (*Ailanthus altissima* (Mill.)) late in the growing season, when the leaves are completely unfolded, using a paintbrush (rather than spraying) to ensure precise application to the target species. This method does not prevent the formation of shoots but reduces their biomass, decreasing the competitive ability of the species, thus this should be followed by afforestation with native tree species (Constán-Nava et al. 2010). In general, canopy gaps close to forest margins and in areas more prone to invasions should be limited in order to avoid the expansion of pioneer species. Increasing the proportion of shade-bearing species as well as increasing the age could be considered as successful strategies to limit the dispersion of black cherry, red oak (*Quercus rubra* L.), ash-leaved maple (*Acer negundo* L.) and black locust (*Robinia pseudoacacia* L.) (Höfle et al. 2014).

Box 14. Mechanical treatments: sustainability and efficacy

- **Girdling** is a method used to kill trees. A ring of bark around the circumference of the tree stem is removed down to and including the cambium using a chainsaw (or other tools) and the phloem transport between canopy and roots is interrupted. The cut should not be so deep that it affects the stability of the stem in strong winds. It is a common technique that, when compared to other methods, is relatively inexpensive and has limited impacts on the topsoil. However, it presents several limitations as conifers and diffuse-porous trees can remain alive for many years (Zimmermann 1983), or may even survive girdling (Thomas 2004). The mechanical damage caused by girdling may trigger the production of sprouts (Del Tredici 2001). Therefore, girdling should be adapted to the species, considering optimal timing and location. The sprouting of the suppressed buds below the cut is frequent for some broadleaved trees, and may compromise the success of the eradication.

- **Root removal** reduces the propagation on re-sprouting trees. However, it has high costs and considering the impact of heavy machinery on soil surface, it is generally not applicable in protected areas (Constán-Nava et al. 2010).

- **Mulching** (application of, usually, organic material to the soil surface) could increase the effectiveness of hand-pulling, but may damage native vegetation and alter the soil properties (Meloche and Murphy 2006).

- With **waterlogging** the availability of soil oxygen decreases, which affects the survival and regeneration of other species (see Glenz et al. 2006 for flooding tolerance of tree species). For example, considering that black cherry (*Prunus serotina* Ehrh.) benefits from well-drained soils (Closset-Kopp et al. 2010), artificial waterlogging could represent a suitable strategy in eradicating this species.

For introduced tree species that do not re-sprout and whose seedlings do not find suitable conditions for regeneration, eradication provides an opportunity for the creation of habitat trees.

Where removal of introduced tree species is a management objective, there is an opportunity to increase the availability of microhabitats as they may be artificially created, as it was demonstrated in a study focusing on removal of London plane trees (*Platanus hybrida* Brot.) in a protected area in northern Italy (Cavalli and Donini 2003, Zapponi et al. 2015). Examples of microhabitats that may be created are hollows for cavity-nesting birds or basal pockets for the development of aquatic saproxylic larvae. With regards to microhabitat creation, introduced tree species may also be used to increase deadwood volumes (i.e. standing and fallen dead trees), creating snags or uprooted trees that are key elements of old-growth forests and of fundamental importance for the conservation of forest biodiversity (Mason 2003).

Box 15. Chemical treatments and their effect on non-target species

The effectiveness of girdling can be increased using chemical substances. The most used is glyphosate, a highly water-soluble herbicide that has been commonly applied in agriculture and forestry. Herbicides can be applied on bark, wounds generated by cutting and girdling, and leaves (Wittenberg and Cock 2001). Spraying should be avoided as it is likely to have a more significant impact on other species than other methods of herbicide application (Collin and Dumas 2009). Furthermore, herbicides may affect non-target species and their use must, therefore, be in accordance with relevant legislation. Its detrimental effects on non-target species are more frequently studied with regards to agricultural applications usually concluding that glyphosate has the potential to affect other organisms present in the ecosystem, e.g. woodfrogs (Lanctôt et al. 2014), earthworms (Gaupp-Berghausen et al. 2015) or soil microbial communities (Helander et al. 2012). Although it has been argued that its application in northern forest ecosystems is not likely to be problematic (Newton et al. 2008), others (e.g. Helander et al. 2012) have indicated that the slow degradation of glyphosate in cold climates and its abundance in freshwater reservoirs, where the herbicide's accumulation can cause problems, represent a considerable concern.

Plant growth regulators are natural or synthetic compounds (e.g. hormones or their synthetic equivalents) influencing developmental or metabolic processes in higher plants (Rademacher 2015). The synthetic auxin NAA (α-naphthaleneacetic acid) belongs to this category and has been historically used to control shoot production in fruit trees (e.g. Looney and Jackson 2010). According to the Environmental Protection Agency (EPA 2007), it does not pose a risk of affecting non-target organisms, such as mammals, birds, aquatic organisms and non-target plants. The application of a NAA compound has been used to limit shoot formation in red oak and the preliminary results (Minari et al. 2015) suggested that applying a solution of NAA using a pruning paste (to avoid affecting non-target species) on the surface of the stump of girdled red oak significantly reduces their shoot biomass (Figure 42).

Figure 42. Experimental application of NAA to reduce shoot formation in red oak, associated to different types of girdling: a) double ring girdling with NAA, b) double ring girdling without NAA, c) notch girdling with NAA and d) notch girdling without NAA. (Photos: L. Zapponi)

> *Island ecosystems are particularly vulnerable to the invasion of introduced species: they may provide useful insights on management approaches.*

The severity of the impacts of invasive tree species (e.g. *Acacia* spp., *Eucalyptus* spp., *Pinus* spp.) in islands (Brundu 2014) brought the development of intensive strategies that were often carried out with the support of the LIFE financial instrument. For more information see Regulation (EC) No 614/2007 of the European Parliament and of the Council of 23rd May 2007 concerning the Financial Instrument for the Environment LIFE+.

An example of eradication measures of introduced tree species from an island ecosystem is the case of the isle of Anholt (Denmark) where the aim was to re-establish the lichen-rich communities of the northern grey dunes, dominated by *Corynephorion canescentis* (L.)

Beauv. This required the complete removal of mountain pine (*Pinus mugo* Turra) trees, including needles and cones. In addition, mosaic burning, grazing and hand removal of mountain pine regeneration was carried out (Doody 2013) to increase pH and reduce water accumulation, in order to facilitate the conservation of coastal heath vegetation where the lichen is an important component (Christensen and Johnsen 2001). The isle of Montecristo (Italy) is another example of eradication from an island environment: it is a nature reserve established to preserve a rich flora, with 304 vascular species in only 10.4 km^2, including species characteristic of low Mediterranean maquis and coastal garigue (e.g. *Quercus ilex* L., *Erica arborea* L., *E. scoparia* L.) (Paoli and Romagnoli 1976). The botanical diversity of this island was threatened by the introduction of several species and a LIFE project was developed to eradicate the tree of heaven, which was sprayed, painted or injected with glyphosate, according to the height and age of the plants (Zanichelli et al. 2014).

In general, the number of attempts to completely eradicate introduced species on islands in Europe is still rather modest (224 eradication programmes on 170 islands, mainly focusing on animal species). Genovesi and Carnevali (2011) suggest that two reasons for this are: (i) the presence of endemic species on European islands, which imposes restrictions on the methods that can be used to eradicate the invasive species; and (ii) the limited public awareness of the problem suggesting there is a general lack of public support for eradication programs.

In a meta-analysis of publications involving control of invasive plant species, Kettenring and Adams (2011) found that less than a third of the studies evaluated the costs of treatments. A more complete evaluation of the costs and benefits of eradication treatments should be considered in experimental studies and assessments to allow the managers of protected areas to establish which approaches are most appropriate (Kettenring and Adams 2011).

> *Several factors, such as the morphology of the terrain, characteristics of the trees, human and equipment efficiency influence the costs of each intervention.*

Comparison of the costs of the different interventions could aid managers choosing the most suitable approach. Girdling could be rapidly executed by notching the external circumference of the stem with two oblique converging cuts, 4–5 cm deep, using a chainsaw. Furthermore, for the methods requiring a tractor and a winch, any optimisation of the supplementary operations (e.g. fixing of the winch cable to the tree using a modular stepladder in a light alloy for climbing up the tree) increases the total cost of the intervention. For instance, the increase of available deadwood creating fallen snags or leaning dead trees requires using a tractor with a winch as well as the application of girdling, which results in higher costs compared to artificially creating either uprooted trees (tractor and winch) or dead standing trees (girdling). The topography of a site must also be considered; on flat or gently sloping terrain an excavator with tracks would be appropriate, and on steeper slopes, a wheeled-legged excavator should be used. Due to the different mobility of the two vehicles, the time required for moving from one tree to another can affect the productivity and hence the cost of the entire intervention.

The costs of flooding a site as a means of getting rid of an introduced species (i.e. waterlogging) are mainly determined by soil characteristics and terrain topography, as these factors determine the amount of water that must be used to keep the soil sufficiently saturated. This method requires creating a water delivery system (i.e. presence of a permanent channel network and possibility) to provide the required amount of water either through the gravity fed irrigation or using of a pump. Even if the gravity fed irrigation is more intensive in terms of labour, the pumping system tends to be more expensive because of the cost of the pump required for this method and its energy consumption.

It is important to stress that the management of introduced invasive species in protected areas should include not only their eradication, but also restoration of the ecosystem. Active re-establishment of native biodiversity may increase the resilience of the given ecosystem, which may act as protection against new invasions (Genovesi and Shine 2004). Restoration measures should also prevent side effects generated by eradication measures, such as creating areas that could be re-colonised or invaded by other species that may have greater impact (Hiebert 1997). To accomplish this task, managers should focus on clear goals: rather than pursuing a vague concept of naturalness, the native biodiversity should be protected and ecological integrity should be enhanced (Randall 2010). Larios and Sunding (2013) identified three pathways for ecological restoration: (i) spontaneous succession, (ii) technical reclamation, and (iii) assisted succession, which is a combination of the previous approaches (i) and (ii). Practical examples of the last two approaches are described in Box 16.

Box 16. Eradication and restoration in the Bosco Fontana Nature Reserve

The Bosco Fontana Nature Reserve in Italy is an ancient woodland of 200 ha on the flood plain of the Po River. The woodland is characterised by coppice with standards (*Carpinion betuli* association) where two species with different ecology occur: the shade-bearing (sciophilous) hornbeam (*Carpinus betulus* L.) and the light-demanding (heliophilous) pedunculate oak (*Quercus robur* L.). Following the excessive cuts that took place during the World Wars and following an extensive windthrow in 1949, a reforestation with introduced tree species (red oak, black walnut (*Juglans nigra* L.) and London plane) was carried out between 1949 and 1952. In only 40 years, both red oak and London plane reached a standing volume of roughly 1500 m^3 for the whole reserve. In 1995, an average diameter at breast height (dbh) of more than 50 cm was recorded for these introduced tree species, whose crowns were already occupying the highest layers of the canopy competing with native tree species (Mason 2004). Mason (2002) found that that the entomological saproxylic fauna supported by red oak was relatively poor in terms of diversity as only three out of 27 species of jewel beetles (Coleoptera Buprestidae) that are normally found in forest stands dominated by native oaks, were present in stands of non-native oaks. The methods that were implemented to eradicate red oak and to favour the restoration of the native flora were adapted to local conditions. In areas where red oak dominated, the eradication was associated with the creation of gaps of at least 200–250 m^2 in size where 2- to 3-year-old pedunculate oaks were planted. Other native species (e.g. hornbeam) that limited the development of pedunculate oak seedlings were also removed in order to enlarge the gap to allow the establishment of a small nucleus. In the most favourable situations, the native residual vegetation included pedunculate oak seed-bearing trees, which allowed for natural regeneration that was assisted by creating elliptic gaps oriented east to west in order to maximise the availability of light reaching the gap floor. The optimal position of the seed-bearing trees is shown in Figure 43, where a gap of 200–250 m^2 allows enough light to reach the floor for at least ten years, and thus sustain the growth of pedunculate oak seedlings.

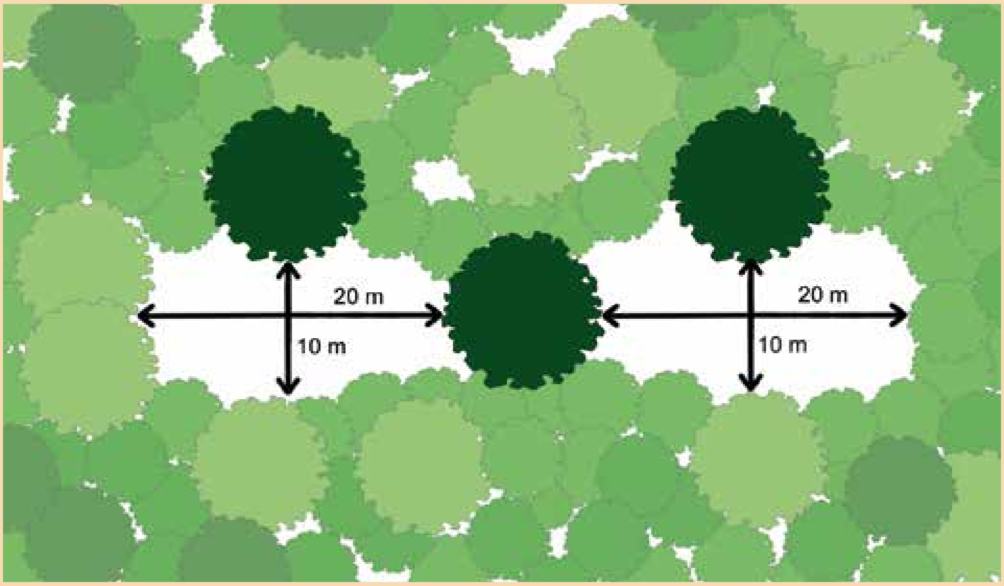

Figure 43. Canopy gap creation in the Bosco Fontana Nature Reserve; the selected seed-bearing trees are showed in dark green.

In conclusion, eradications of invasive tree species require the use of several methods, often used in combination, at the same time considering the ecology and growing stage of the species. There have only been a few studies that have applied their findings to build mitigation strategies and to establish best management practices (Hulme et al. 2014). It is also important to note that there is currently no formal coordination among nature reserves and countries on methods and priorities for eradication of invasive tree species (Brunel et al. 2013). The challenge for the future is, therefore, the creation of a platform where strategies could be shared, where the impacts would be monitored and assessed, and long-term results would be used to support best practices.

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3.5 Introduced species in Polish National Parks: distribution, abundance and management approaches

Anna Gazda and Jerzy Szwagrzyk

The abundance of introduced tree species in Polish forests is generally very low; their combined share is less than 1 % (Gazda 2013). The largest group of introduced species in the National Parks (hereafter NP) in Poland is formed by perennial (33 %), annual (28 %) and herbaceous plants with woody plants, i.e. trees and shrubs, accounting for 25 % of introduced species (Bomanowska et al. 2014). Many of these species are able to naturally regenerate and to disperse throughout the forests where mature individuals of introduced species are not present (Gazda and Augustynowicz 2012).

The most common introduced tree species in Polish state forests is northern red oak (*Quercus rubra* L.) (Gazda 2013). If all forests are taken into consideration, including the private and state ownership, the most common introduced tree species is black locust (*Robinia pseudoacacia* L.) (Czerepko 2008). Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) is the most common introduced coniferous tree species. However, its share in forest stands is much lower than northern red oak or black locust (Chylarecki 2004).

▶ *Introduced tree species are present but not abundant in Polish National Parks.*

Despite their relatively low abundance, introduced tree species are well-dispersed in Poland; they are currently present in all 430 forest districts in Poland (Gazda 2013). This makes their potential future spread quite likely as the seed sources are already present in every region of the country. However, to establish themselves in forest communities, introduced tree species need to compete with native trees. In forest communities dominated by shade-tolerant species like European beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Mill.) and hornbeam (*Carpinus betulus* L.), the chances of success for introduced tree species are rather small. In habitats dominated by open-canopy forests, like riparian woods, the chances of successful invasion by introduced tree species (e.g. ash-leaved maple (*Acer negundo* L.) are greater (Danielewicz 2008). Forest stands dominated by native Scots pine (*Pinus sylvestris* L.) and where the light intensity below the canopy is high may also be susceptible to invasion by introduced tree and shrub species (Jagodziński et al. 2015).

Many of NPs in Poland were established by conversion of a forest district (or parts of several forest districts) into NPs. For decades, black cherry (*Prunus serotina* Ehrh.) has been planted under canopies dominated by Scots pine to enrich the litter, thus improving soil conditions. Currently, black cherry grows in high numbers, both within managed and protected forests, usually as a shrub or a small tree, forming a dense sub-canopy layer. Therefore, apart from formerly managed forest stands, the NPs also inherited the admixture of introduced tree species.

Introduced tree species are also associated with human settlements; since villages and small towns are located within borders of some NP in Poland (e.g. Kampinos NP, Wielkopolska NP, Ojców NP), the urban settlements may be considered as seed sources of introduced tree species. However, with the exception of English walnut (*Juglans regia* L.), it is difficult to identify species that have escaped from gardens into surrounding forests (Gazda 2013).

> *Many forest stands within National Parks are susceptible to invasion by introduced species.*

Introduced tree species are absent or rare in seven out of 23 Polish NPs (the grey dots in Figure 44). Ten NPs have at least five introduced tree species present, but the species are not abundant there (orange dots in Figure 44). Six NPs have more than ten introduced tree species, and some of the species cover larger areas and pose a serious threat of rapid expansion (the red dots in Figure 44).

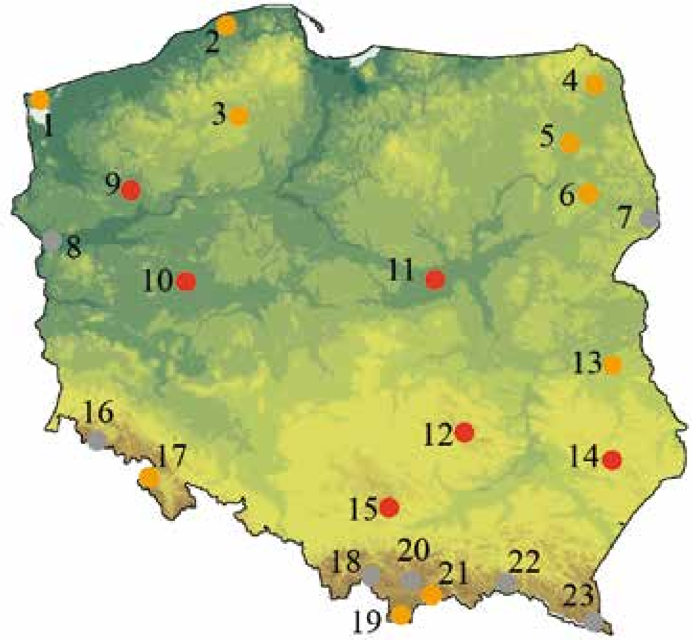

Figure 44. Distribution of non-native tree species within Polish NPs (red – abundant presence of introduced tree species; orange – several introduced tree species present, but not very abundant; grey – introduced tree species are rare or absent); 1. Wolin NP; 2. Słowiński NP; 3. Tuchola Forest NP; 4. Wigry NP; 5. Biebrza NP; 6. Narew NP; 7. Białowieża NP; 8. Ujście Warty NP; 9. Drawno NP; 10. Wielkopolska NP; 11. Kampinos NP; 12. Świętokrzyski NP; 13. Polesie NP; 14. Roztocze NP; 15. Ojców NP; 16. Karkonosze NP; 17. Góry Stołowe NP; 18. Babia Góra NP; 19. Tatra NP; 20. Gorce NP; 21. Pieniny NP; 22. Magura NP; 23. Bieszczady NP.

Black cherry, red oak and black locust are the most commonly occuring introduced tree species in NPs in Poland and their range is expanding – this is especially the case for Wielkopolska NP.

Wielkopolska NP (No. 10 in Figure 44) is situated near Poznan, and is the NP most invaded by introduced tree species (Table 17); the number of introduced trees is high, mostly due to ornamental tree species being grown in yards, gardens and along streets in a town that is located within the NP. Black cherry is the most abundant introduced tree species in this NP where it ranks as the second most common woody species, after native Scots pine. Black cherry showed a rapid expansion during the last few decades; although it was found in only eight forest compartments in 1947, it was present in 629 compartments in 2007 (Purcel 2009). The second most abundant introduced tree species in Wielkopolska NP is black locust that was already abundant in 1947 (recorded in 114 compartments) and extended its range to 337 compartments by 2007 (Purcel 2009). The third abundant introduced species in the NP is northern red oak with the fourth being ash-leaved maple. Other introduced tree species are present in rather low numbers.

Kampinos NP (No. 11 in Figure 44) (Table 17) is located near the city of Warsaw. It is the second largest among Polish NPs (almost 40 000 ha) with villages and small settlements within its proximity where introduced woody species are also found. Black cherry is the most common introduced tree species in Kampinos NP where it forms a dense understory in Scots pine stands in vast areas along the southern edge of the NP. Second most commonly occurring introduced tree species is northern red oak with the third being jack pine (*Pinus banksiana* Lamb.), which reflects the fact that mostly poor habitat types associated with inland sand dunes are found in Kampinos NP.

Roztocze (No. 14 in Figure 44) (Table 17) is a NP where thirteen introduced woody species are recorded. Two of the species, growing mostly as shrubs deserving special attention: i.e. black cherry, occurring currently in an area of about 700 ha (almost 10 % of the park), and low juneberry (*Amelanchier spicata* (Lam.) K. Koch) also occurring in large numbers. Black locust growing mostly in secondary forests was established in former agricultural areas and covers an area of slightly over 70 ha. Although black locust re-sprouts vigorously, it does not regenerate sexually, and this limits its spread to larger areas. Northern red oak currently occurs on 15 ha of forest area where it regenerates naturally; more than half of the northern red oaks are young individuals growing under canopy of other tree species. The remaining nine introduced tree species present in Roztocze NP can only be found in single locations and in small numbers.

Eleven introduced tree species are found in Świętokrzyski NP (No. 12 in Figure 44) (Table 17) with northern red oak being the most commonly occurring species (Sikora and Sobieraj 2015). Other species such as European horse chestnut (*Aesculus hippocastanum* L.), green ash (*Fraxinus pennsylvanica* Marshall), English walnut, black cherry, jack pine, black pine (*Pinus nigra subsp. nigra* J. F. Arnold), eastern white pine (*Pinus strobus* L.), black locust, staghorn sumac (*Rhus typhina* L.), and ash-leaved maple – are also found in the NP but mainly occur along the roads or at forest margins.

Table 17. Occurrence and impact of introduced tree species in Polish National Parks: 1 – one or few individuals growing within habitats changed by man; 2 – more individuals growing within habitats changed by man; 3 – frequent occurrence of species but mainly within changed habitats changed by man, but several individuals observed in natural habitats; 4 – more individuals present but not abundant in natural forests; 5 – introduced tree species very abundant in natural forests.

Introduced tree species	**Wielkopolska**	**Kampinos**	**Roztocze**	**Świętokrzyski**	**Ojców N**	**Drawno**	**Biebrza**	**Narew**	**Tuchola Forest**	**Słowiński**	**Wigry**	**Wolin**	**Polesie**	**Stołowe Mountains**	**Pieniny**	**Tatra**	**Białowieża**	**Karkonosze**	**Babia Góra**	**Bieszczady**	**Gorce**	**Magura**	**Ujście Warty**
Prunus serotina	5	4	5	1	2	1	3	2	2	1	3	1	1				1						
Quercus rubra	3	2	2	4	3	1	1	1	2	1	2		1	1			1	1					
Robinia pseudoacacia	3	2	3	1	1	1	1	1	2	1		1	1		1							1	
Pseudotsuga menziesii	1	1	1	1	1	1				1		1		1		1		1			1		
Aesculus hippocastanum	2	1	1	1	1	1	1	1				1		1	1								
Acer negundo	1	2	1	1		1	1	2			2						1						
Pinus strobus	1	1	1	1	1	1				1				1				1	1	1			
Pinus banksiana	1	1	1	1	1	1	1						1										
Pinus nigra	1	1	1	1						1					1	1							
Fraxinus pennsylvanica	1	1	1	1		1			1														
Juglans regia	1	1		1	1	1	1																
Populus x canescens	1	1				1		1							1								
Rhus typhina	1	1		1	1				1														
Larix kaempferi	1	1				1										1							
Pinus rigida	1	1	1																				
Thuja occidentalis					1	1						1											
Acer ginnala	1	1																					
Acer saccharinum		1			1																		
Acer tataricum	1	1																					
Pinus contorta		1														1							
Thuja plicata		1										1											
Abies concolor	1																	0**					
Picea pungens						1												0*					
Picea sitchensis										1								0*					
Ailanthus altissima	1																						
Betula nigra		1																					
Betula papyrifera		1																					
Carya gabra	1																						
Carya opata	1																						
Chamaecyparis pisifera					1																		
Juglans cinerea			1																				
Morus alba							1																
Tsuga canadensis			1																				
Abies grandis																		0**					

* individuals eradicated during the last few years
** dying trees

Ojców NP (No. 15 in Figure 44), the smallest NP in Poland, covering only slightly over 2000 ha has the highest number of native tree species (37) from all NPs in Poland (Gazda et al. 2015) reflecting the diverse topography and variability in habitats in this NP. There are 12 introduced tree species occurring in Ojców NP; most of them grow close to human settlements in the village of Ojców, which is located in the centre of the Park (Barabasz-Krasny et al. 2004). Nonetheless, four introduced tree species are found in forest stands in the NP: northern red oak, European horse chestnut, black locust and English walnut. Northern red oak is the most common one, especially among the young cohort of trees.

Drawno NP (No. 9 in Figure 44) in the north-western part of the country has over ten introduced tree species. However, none of the introduced tree species recorded in the park are considered abundant with only two of them (black cherry and black locust) occurring in natural or near natural habitats (Table 18).

▶ *National Parks that situated close to big cities have relatively high densities of introduced tree species.*

Białowieża NP (No. 7 in Figure 44) has a very low number of introduced tree species (i.e. three: northern red oak, ash-leaved maple and black cherry) as it comprises mostly of natural and near natural forests that have been strictly protected for a long time. There are only several introduced tree species and shrubs that appear within the forest margin; i.e. in the yard of the former forester's lodge that is situated within the NP's boundaries (Adamowski et al. 2002). Other NPs with low numbers of introduced tree species are located in the mountain areas of southern Poland where some eastern white pine is found (Babia Góra NP No. 18 in Figure 14; Bieszczady NP No. 23 in Figure 44). Some Douglas firs are present in Gorce NP (No. 20 in Figure 44) and Magura NP (No. 22). No introduced tree species are found in the Ujście Warty NP (No. 8 in Figure 44) as this NP comprises mostly of meadows and wetlands with the forested area accounting for less than 2 % of the NP's area.

All NPs in Poland are required to have a management plan in place that is checked and approved by the Ministry of Environment (Anonymous 2009). All management approaches are described in the management plan, which may also include eradication of introduced tree species. Until the end of the 20th century any attempts to eliminate or restrict introduced tree species in the NPs were only sporadic. The new legal act on nature conservation (passed in 2004) allows for more regular action plans. This had led to a development of management actions restricting the expansion of introduced species that is currently in place in sixteen NPs in Poland. In most cases, these plans focus on invasive herbaceous species such as giant hogweed (*Heracleum mantegazzianum* Sommier & Levier), Sosnowsky's hogweed (H. sosnowskyi Manden.), Japanese knotweed (*Fallopia japonica* (Houtt.) Ronse Decr.), giant knotweed (*F. sachalinensis* (F. Schmidt) Ronse Decr.) and Bohemian knotweed (*Fallopia × bohemica* (Chrtek & Chrtkov) J.P.Bailey). There are only a few cases where the management plan includes introduced tree species such as black cherry (in six Parks) and red oak (in three Parks) (Najberek and Solarz 2011). The most popular methods to manage introduced woody species include the manual removal of seedlings, cutting saplings and felling bigger trees and in some cases (e.g. black cherry) a combination of cutting and spraying with herbicides (e.g. Roundup). Discontinuity of these management approaches as well as their side effects may cause some problems; especially since there are still no available data on the effectiveness of management approaches against introduced tree species in the Polish NPs.

Table 18. The most expansive introduced tree species (ITS) in natural habitats.

No. on the map*	National Park	Park size (ha)	Altitude (m asl)		Altitude range (m)	Dominant forest type	No. of ITS in natural habitats	No. of ITS in habitats transformed by human	The most widespread ITS in forests
			min	max					
10	Wielkopolska	7584	100	132	32	Pine/Oak	4	23	*P. serotina* *R. pseudoacacia* *Q. rubra* *A. negundo*
11	Kampinos	38549	70	105	35	Pine	5	23	*P. serotina* *Q. rubra* *P. banksiana*
14	Roztocze	8483	220	350	130	Pine/Oak/ Beech/Fir	3	12	*R. pseudoacacia* *Q. rubra* *P. serotina*
12	Świętokrzyski	7626	280	612	332	Fir/Beech/ Pine/Oak	3	12	*Q. rubra* *P. serotina*
15	Ojców	2146	300	473	173	Beech/Fir/ Pine/Oak	5	11	*Q. rubra*
9	Drawno	11342	70	105	35	Pine/Beech	2	15	*P. serotina* *R. pseudoacacia*
5	Biebrza	59223	100	127	27	Pine/Alder	3	8	*A. negundo* *P. serotina* *R. pseudoacacia*
6	Narew*	7350	108	161	53	Alder	2	6	*P. serotina* *Q. rubra*
3	Tuchola Forest	4613	145	175	30	Pine	2	5	*P. serotina* *Q. rubra*
2	Słowiński	21573	0	115	115	Pine	1	7	*P. nigra*
4	Wigry	15000	126	183	57	Spruce/Pine/Oak	3	3	*P. serotina* *A. negundo* *Q. rubra*
1	Wolin	8133	0	116	116	Pine/Beech/Oak	1	6	*P. menziesii*
13	Polesie	9764	167	200	33	Pine/Oak	3	4	*P. serotina* *R. pseudoacacia* *Q. rubra*
17	Stołowe Mountains	6340	400	919	519	Spruce	0	4	
21	Pieniny	2346	450	982	532	Beech/Fir	0	4	
19	Tatra	21197	900	2499	1599	Spruce	0	4	
7	Białowieża	10517	140	176	36	Spruce/Oak/ Hornbeam/Pine/ Alder	0	3	
16	Karkonosze	5581	700	1602	902	Spruce	0	3	
18	Babia Góra	3391	700	1725	1025	Spruce/Beech	0	1	
23	Bieszczady	29177	650	1346	696	Beech	0	1	
20	Gorce	7031	700	1310	610	Beech/Fir/Spruce	0	1	
22	Magura	19439	350	846	496	Beech/Fir	0	1	
8	Ujście Warty NP	8074	15	45	30	Alder	0	0	

*Figure 44

In some Polish NPs, no specific management actions directed towards the elimination of introduced tree species have been undertaken. In Tatra NP (No. 19 in Figure 44), for example, where the introduced tree species are relatively rare, and their locations are well known, they are not considered to be dangerous and are treated as curiosities.

One of the largest efforts to eliminate introduced tree species, especially black cherry, was conducted in Wigry NP (No. 4 in Figure 44) and Roztocze NP (No. 14 in Figure 44). This management action was coordinated by the Wigry NP and financed by external resources (i.e. the funding was not provided by the Ministry of Environment). This project was rather large as only in Roztocze NP, the area subjected to various treatments was over 300 ha. Scientists from several universities jointly developed the action plan; the project was designated as a large-scale experiment assessing the effectiveness of different methods used to remove introduced tree species (various treatments replicated in several NPs). The crews conducting individual treatments in the field were thoroughly instructed by the project coordinators; those that monitored the effectiveness of various treatments were also given precise instructions. In addition, the local communities were informed about this project and individual management actions carried out. The results are presented in Krzysztofiak and Krzysztofiak (2015).

Another well-designed action plan directed against black cherry was conducted in Kampinos NP (No. 11 in Figure 44) (Namura-Ochalska and Borowa 2015). Black cherry trees were felled and removed and the stems were cut at various heights. In addition, seedlings of native deciduous tree species were planted to encourage development of a dense canopy of these species. The removal of the whole trees turned out to be effective, but very labour-intensive. Cutting stems at a height of 80 cm above the ground resulted in less vigorous re-sprouting than cutting stems just above the root collar. However, the frequency of fungal infestations on black cherry cut at 80 cm was higher than in case of cutting at the ground level. The method of cutting black cherry at 80 cm above the ground combined with planting of native deciduous trees is the recommended eradication management as it appears to be the most promising method of eliminating black cherry from the stands in the Kampinos NP (Namura-Ochalska and Borowa 2015).

Efforts directed towards elimination of introduced species from National Parks are still in the experimental phase.

Black cherry and ash-leaved maple are currently the most commonly occurring introduced tree species in Polish NPs. Northern red oak and black locust are abundant but their progress in terms of invading the NPs is relatively slow. Introduced coniferous species have not yet shown any tendency towards expansion, and some of them – especially introduced pines, spruces and firs – are already dying out. Attempts to control or to eradicate non-native tree species in Polish NPs are still in the experimental phase. In the NPs, where some of the introduced trees are already very abundant (e.g. Wielkopolska and Kampinos NPs), their reduction requires a long and persistent effort, which depend on a steady and long-term funding. In NPs where introduced tree species are only sparse, on the other hand, and confined to single individuals or small groups of trees (e.g. Babia Góra or Bieszczady NPs), their immediate eradication should be relatively easy. However, the NP authorities do not currently feel compelled to do so. It is very likely that the introduced tree species will be sooner rather than later outcompeted by native species in the NPs with low abundance of introduced tree species, especially those NPs located in mountain areas.

> *A successful elimination of introduced tree species from Polish National Park need a close cooperation with managers of national forests.*

Although planting of introduced tree species is currently not allowed in the Polish NPs, there is no tendency to eliminate them from managed stands; some of these species are already regenerating naturally and spreading. Opinions among forests are diverse, with many of them strongly supporting planting of introduced tree species. Therefore, solving the problem of the presence of introduced tree species in Polish NPs would probably need concerted efforts from managers of public forests as well as from private forest owners.

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3.6 Silvicultural strategies for introduced tree species in northern Italy

Fabio Meloni, Renzo Motta, Etienne Branquart, Tommaso Sitzia and Giorgio Vacchiano

> *More than 1000 non-native plant species have been introduced to Italy since 1492; this equates to more than 13 % of the total number of native species.*

Italy has a long history of human impact; the destruction of the former lowland forests and the country's position at the center of the main trade routes since ancient times greatly facilitated towards introduction and establishment of many non-native plant species in the country, which dates back thousands of years. A recent survey in Italy listed 1023 introduced plant species, 163 of which classed as permanently established having negative impacts on ecosystems or society (Celesti-Grapow et al. 2009). More than half of these species are found exclusively in man-made habitats such as artificial surfaces, agricultural land, forest plantations and artificial water bodies. Human disturbance plays an important role in increasing the richness of non-native flora and promoting its establishment. Artificial habitats, particularly cities, act as sources of introduced (both deliberately and accidentally) species that can be further spread by humans, for example through planting for ornamental purposes in parks and gardens (Kowarik 2003). Infrastructures, such as roads and railways, also provide opportunities for secondary dispersal of introduced species (Von der Lippe and Kowarik 2008). Some of the species introduced and facilitated by the above-mentioned means can cause negative impacts including toxicity to animals or humans, modifications of nutrient cycling and disturbance regimes, reduced provision of ecosystem services, or direct damage to man-made structures (e.g. Celesti-Grapow and Blasi 2004).

The bio-deterioration of the historical heritage (Figure 45) by fast growing and vigorous introduced tree species, and the reduction of native diversity, mostly in riparian, forest, wetland, and coastal habitats are considered amongst particularly relevant impacts for Italy. According to a recent survey of EU Life+ projects (Silva et al. 2014), the introduced tree species most often targeted for eradication by conservation projects across Europe are black locust (*Robinia pseudoacacia* L.), tree of heaven (*Ailanthus altissima* (Mill.) Swingle), red oak (*Quercus rubra* L.), and black cherry (*Prunus serotina* Ehrh.) (Silva et al. 2014). In this chapter, we report on the few field experiences and success stories of silvicultural control of these introduced tree species in urban and natural habitats in northern Italy.

There is broad evidence that silvicultural practices can either enhance or hamper biological invasions. Planting introduced tree species for uses such as wind breaks, biomass production, or fire protection and erosion control increases the probability of invasion (Cierjacks et al. 2013). Management practices such as clearcutting, group cutting, and coppicing can also promote the regeneration of some introduced tree species (Radtke et al. 2013).

Forest managers can apply silvicultural options to alter interspecific competition to suppress unwanted regeneration of introduced species at a local level and thus support the desired tree species composition.

Figure 45. Tree of heaven on roofs of the Alessandria Citadel (18th century), a monument in the Tentative list for UNESCO World Heritage sites(photo: T. Tobia, released under Creative Commons Attribution-Share Alike 3.0 Unported license. https://commons.wikimedia.org/wiki/File:La_Cittadella_di_Alessandria_04.JPG).

However, shelterwood or selection systems may be considered as a promising means towards reducing invasion risks while preserving native communities (Sitzia et al. 2012). Even the simple maintenance of continuous tree cover can prevent, or at least slow down, the spread of some introduced tree species (Table 19). While there is a wealth of information available to forest managers on some species such as black locust, the effect of silvicultural strategies has been much less studied for other equally, or even more aggressive species, such as tree of heaven or black cherry, which suggests a large research potential.

Table 19. Silvicultural measures aimed at reducing the spread of introduced tree species in Italy (modified from Sitzia et al. 2016)

Species	**Examples of silvicultural measures**
Tree of heaven (*Ailanthus altissima* (Mill.) Swingle)	Avoid coppicing (Radtke et al. 2013) Cut seed trees (Skowronek et al. 2014) Underplant or seed shade-tolerant native species (Skowronek et al. 2014) Prescribed burning (Rebbeck et al. 2014) Protective belt of native trees (ECORICE 2015)
Black cherry (*Prunus serotina* Ehrh.)	Avoid clearcutting and openings (Terwei et al. 2013) Mowing suckers (Caronni 2009) Conversion of coppice to high forest (Caronni 2009) Underplant or seed shade-tolerant native species (Skowronek et al. 2014) Ageing with absence of treatments (allowing other tree species to follow in the succession without any other treatment) (Starfinger et al. 2003) Maintain or facilitate closed canopy (Annighöfer et al. 2015) Promote native species (Annighöfer et al. 2015) Girdling (Annighöfer et al. 2012) Single tree selection or group selection (Annighöfer et al. 2015)
Red oak (*Quercus rubra* L.)	Underplant or seed shade-tolerant native species (ECORICE 2015) Repeated spring or summer coppicing Soil tillage (ECORICE 2015)
Black locust (*Robinia pseudoacacia* L.)	Avoid coppicing (Radtke et al. 2013) Coppice ageing (Motta et al. 2009) Promote native species Conversion of coppice to high forest Release high number of standards in coppices (Radtke et al. 2013) Drill-and-fill (holes are drilled into trees and filled with herbicide) (Michigan Department of Natural Resources 2012) Avoid clearcutting and openings (Terwei et al. 2013) Girdling (Maetzke 2005) Protective belt of native trees (Giambastiani et al. 2005) Single tree selection or group selection (Terzuolo and Canavesio 2010) Pollarding (Maltoni et al. 2012)

> ▶ *Prevention: in the initial stages of invasion, an uneven-aged, multilayered forest structure with high permanent canopy cover can slow down and push back the invasion.*

Promoting the growth and crown expansion of native species, especially if fast-growing, helps to prevent invasion by most of the introduced tree species, as they are light-demanding and their growth is limited by shading (with the exception of black cherry). Highly competitive native species, e.g. fast-growing, root-sprouting aspen (*Populus tremula* L.), white poplar (*Populus alba* L.) or willows (*Salix* spp.) in lowland forests, or slower-growing but shade-tolerant hornbeam (*Carpinus betulus* L.), maples (*Acer* spp.), and hazel (*Corylus avellana* L.) in upland mixed hardwood forests, can be planted in gaps, under the cover of introduced species or in dense protective belts around sites that have been invaded. In Natura 2000 areas and other sites of high conservation values, prevention can be achieved by avoiding opening of canopy gaps and ensuring regeneration of native species by under-planting.

Control: removal of seed trees (using the drill-and-fill technique, felling, or girdling and applying subsequent stump chemical treatment where necessary) and avoiding the creation of large gaps are very important in avoiding the natural regeneration of introduced tree species.

Chemical treatments can be a reasonable complementary method to silvicultural measures, depending on the situation. The drill-and-fill technique involves drilling a hole into a tree at a downward angle (towards the pith), and filling the hole with herbicide. The bigger the tree, the more holes and herbicide are needed. This technique can be applied on a limited number of stems since its application is expensive.

Girdling (Figure 46) has provided diverse results (e.g. 30–50 % of girdled trees still produced root shoots; Silva et al. 2014) and has been considered more effective on larger trees. A ring of bark must be completely removed from the whole circumference of the tree; local experience showed that the ring should be at least 15–20 cm wide for this technique to be effective. The removal of the ring, especially if carried out at the beginning of the growing season, prevents movement of water and metabolites around the tree, blocking first root growth and then water and nutrient uptake. The tree wilts and the part of the tree above the ring-barking zone dies. However, the technique may induce a large seed crop in the last year before the tree death occurs (Maetzke 2005). Mechanical treatment to control regeneration of introduced species (e.g. uprooting seedlings and repeated mechanical cleaning of suckers) is feasible only in low-invasion areas.

No management at the last invasion stage; i.e. refraining from management by allowing other tree species to follow in the succession without applying any other treatment in areas with low propagule pressure.

Figure 46. Girdling on black cherry (photo: Wisconsin Dept. of Natural Resources, released under Creative Commons 2.0 License. https://www.flickr.com/photos/widnr/6588710907).

In heavily invaded forests, silviculture can be less effective and more expensive; a viable option is to refrain from management; i.e. letting the invasion cohort mature and grow old (assuming that propagule pressure is not high). The following control strategies are applicable only at small scales, and should always be complemented by planting native species:

1. **Seed trees:** cutting or girdling, supplemented by chemical treatment where necessary (e.g. drill-and-fill, stem injection or stump spraying).

2. **One to two year-old:** mechanical removal or coppicing, repeated as often as necessary during the growing season in order to deplete carbohydrate reserves in the stump and roots. The best timing for this technique to be applied is in spring or summer when the reserves are concentrated in the shoots.

3. **Seedlings (< 2 m height):** uprooting (manual or mechanical) or chemical treatment; dense regeneration clumps can be removed by soil chopping or mastication, but only for species incapable of root-sprouting (e.g. red oak; Table 19).

4. **Pole stage or coppice:** shorten coppice rotation, i.e. 5–15 years, or shorter than the age of sexual maturity (Figure 47) followed by 1) or 2) to suppress stumps and shoots.

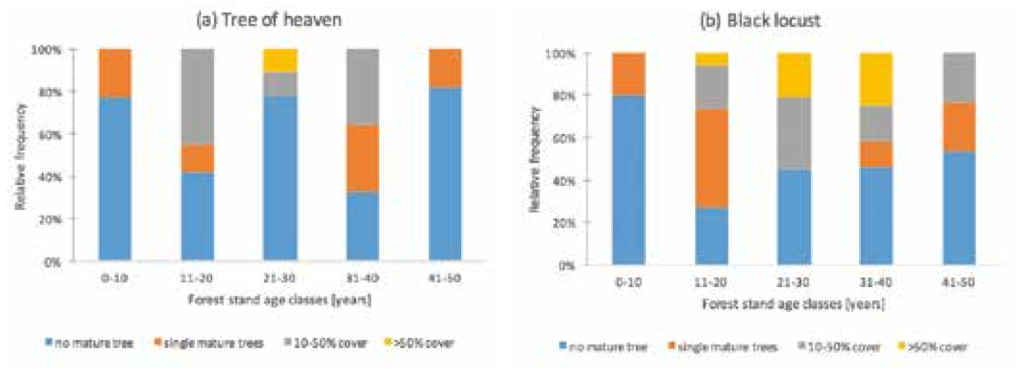

Figure 47. Abundance of tree of heaven (a) and black locust (b) in the canopy (in classes) per forest stand age class, frequency of cases over 113 plots in the upper Etsch Valley in South Tyrol, northern Italy (amended from Radtke et al. 2013).

In highly invaded Natura 2000 sites, small scale eradication could be attempted by the removal of all individuals (including as many the roots as possible), tillage, planting and seeding of a native herbs-shrubs-tree mixture, and intensive tending for the duration of five years. A slower but more extensive control measure is single tree thinning combined with under-planting using e.g. poplar (*Populus* spp.) or shade-tolerant species also utilising mechanical control of natural regeneration. If eradicating invasive species proves impossible or too expensive, a novel ecosystem might therefore be acknowledged and managed for any ecosystem services it may provide; this may be referred to as potential integration stage (see Box 17: Silviculture of black locust).

Species-specific strategies based on experiences in northern Italy – black locust

Black locust is a highly light-demanding species (Huntley 1990). Disturbances like clearcutting may result in suckering of black locust's stumps or in the germination of seed-banks (the seeds of black locust are particularly long-lived in forests). The replacement of native temperate forests by black locust is usually associated with tree felling, clearcutting, coppicing, forest decline or other perturbations (Motta et al. 2009).

However, the competitiveness of black locust is much less pronounced in closed canopy forests as well as in various habitats on mesic and nutrient-rich soils (Sitzia et al. 2012). For this reason, although capable of altering natural ecosystems, invasion can be effectively contained by silvicultural practices. Thirty-three EU LIFE projects that were carried out between 1997 and 2014 in stands invaded by black locust yielded some common experiences (Silva et al. 2014):

- Mechanical control is difficult and costly; simple cutting of the aboveground parts aggravates the sprouting of shoots. Cutting or burning generally increases sucker and sprout production and it should be therefore avoided, unless a repeated treatment is applied. However, this is an expensive option and the sites are often treated only once and the problem of invasion at the site is assumed to have been solved. Follow-up treatments are required for all these operations.

- Cutting and chemical control was often extremely effective (Riparia-Ter LIFE08 NAT/E/000072 and Proyecto Estany LIFE08 NAT/E/000078). The application of herbicides to live standing young trees has shown best success. However, sprouting may occur after chemical application; therefore, a follow-up treatment is usually necessary.
- Cutting and grazing by goats or sheep was effective in some projects (GrassHabit LIFE05 NAT/H/000117 and HUNVIPURS LIFE04 NAT/ HU/000116); in North Carolina (USA), for instance, after four seasons of browsing by a combination of cattle and domestic goats, all black locust died (Michigan Department of Natural Resources 2012). Goats have been reported to be a better grazing animal for the control (Stone 2009). Since black locust can be toxic to cattle, caution is thus advised.

BOX 17: Silviculture of black locust

Black locust is a widespread species in northern Italy (where it covers 233 000 ha, which equates to 2.3 % of forests nationwide, but up to 11 % in some regions; e.g. Piedmont) and a potentially important source of timber and energy.

In severely invaded stands where no ecosystem service is at risk, management can be oriented towards timber production (using coppice and/or high forest with long rotations), especially in stands dominated by black locust and where its annual growth can exceed 12 m^3/ha (Terzuolo and Canavesio 2010).

Other potential uses include biomass, poles for agriculture and slope stabilisation works, and honey production (with yield exceeding 400 kg/ha in 10–20 years old forests). Even nature conservation goals can be attained by e.g. managing linear formations and riparian belts as ecological corridors (coppice with 6–10 year rotation) or lowland stands as bird nesting areas (coppice with 15–20 year rotation and release of 200 reserves trees/ha). In invaded stands where no treatment has been applied for 40 years and where the shrub layer of elder (*Sambucus nigra* L.) and hazel, is well developed (1500 stems/ha), such sites are considered to be ideal for e.g. bird foraging due to light canopy cover by black locust (Pividori and Grieco 2003). Shrubs may also act as nursing sites for more shade-tolerant herbaceous species, which are otherwise absent in black locust stands.

The opportunities offered by black locust, as well as the relative facility of its control, require that management strategies are differentiated according to specific objectives in terms of resource exploitation, habitat conservation or local eradication goals, which do not necessarily contradict each other.

To prevent invasion, edges of native forests and openings in a close proximity to black locust stands can be planted with native species and maintained by irrigation and mowing in order to create protective belts that are at least 20 m wide (Giambastiani et al. 2005). The canopy of these forest stands makes it more difficult for the light-demanding black locust to naturally regenerate and become established.

Refraining from all management may be the most effective strategy to induce a decline of black locust and facilitate the recovery of local tree species. Monitoring of the stand dynamics in invaded forests in northern Italy showed that the relative stand basal area represented by black locust decreased – after no treatment being applied – from 100 % to only 28 % (Figure 48) (Pividori and Grieco 2003). In invaded forests, when other species occur and can disperse, refraining from cutting can be more effective and less expensive as opposed to an active removal of black locust. In turn, however, no management may lead to mechanical instability of trees, especially if competition for light is intense, and thus lower the soil protection.

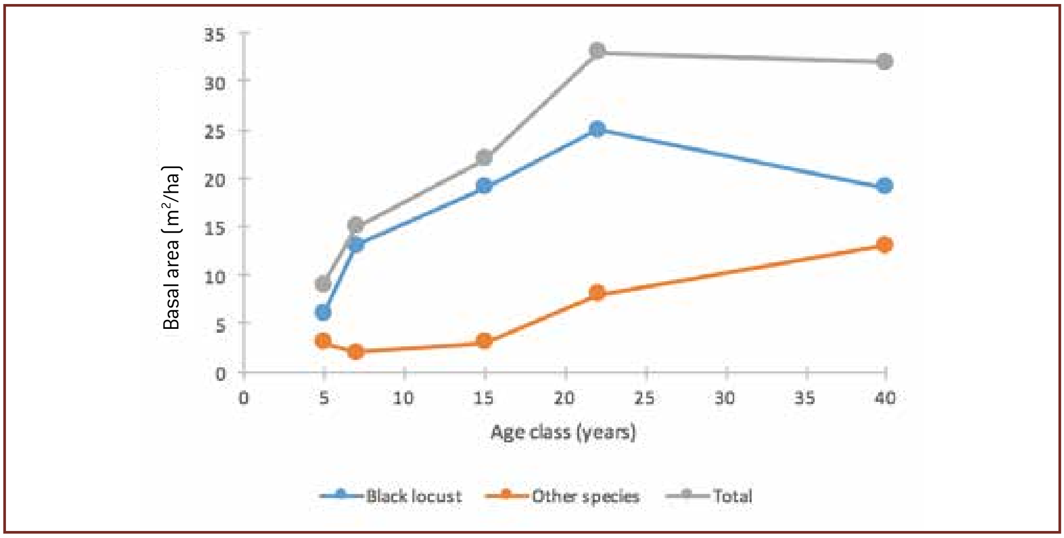

Figure 48. Basal area of black locust and native species in a chronosequence of invaded coppices in Piedmont, Italy (amended from Pividori and Grieco 2003).

In areas that are particularly significant for biodiversity (e.g. nature parks) or recreation, local eradication can be favoured by irregular thinning or selection cutting to promote native species and driving the forest towards an uneven-aged, continuous cover stand structure, accompanied by underplanting of shade-tolerant species (Terzuolo and Canavesio 2010). Large openings should be avoided or planted with native fast-growing species such as hop-hornbeam (*Ostrya carpinifolia* Scop.), hazel, maples, black poplar (*Populus nigra* L.) and white poplar; seed trees around openings could be treated mechanically (cutting/girdling) and/or chemically (if allowed).

In coppice stands dominated by black locust, clearcutting of black locust may enhance its vegetative regeneration; it is important to note that vegetative offsprings are more shade-tolerant than black locust seedlings (Knapp and Canham 2000). Their growth can be hindered by avoiding clearcuts and reducing the light availability by conversion into high forest by applying 2–3 selection thinnings on individual shoots at 20 and 30 years. The second possibility could be to prolong the rotation as much as possible, then release a high number of standards at clearcut (Radtke et al. 2013). In mixed-species coppices or mixed coppice and high-forest stands, black locust should be coppiced 0–10 years before the thinning of the dominant native canopy to limit invasive potential by maintaining some cover formed by the native species. A highly effective method to reduce the cover of black locust is to maintain the vegetation cover, especially where such management is a priority in order to provide protection against landslides and rock fall (e.g. on slopes) (Jancke et al. 2009). As sprouting is regulated by auxins, coppicing in June is the most effective way of reducing the number of vegetative sprouts since auxins are at high concentrations and located in the shoots with carbohydrate reserves in the roots being at the lowest point (Sterrett and Chappell 1967). An effective form of control is pollarding at the height of 2.5–3 m. This reduces crown vigor and root sucker production (Maltoni et al. 2012).

The growth rate of certain native tree species must also be carefully considered; sweet chestnut (*Castanea sativa* Mill.) can produce a fast growth after coppicing and thinning is applied with oak species usually growing much slower. If possible, there should be a dominant oak canopy prior to cutting (e.g. when converting to high forest) and black locust should be coppiced before the oak component is thinned. The interval between subsequent treatments should be prolonged considering under-planting with native species as a useful method. In Mediterranean areas, holm oak (*Quercus ilex* L.) and pines (*Pinus* spp.) usually show rapid growth with the former being particularly effective in outcompeting black locust due to casting high shade and creating a competitive shrub layer (Maltoni et al. 2012).

Species-specific strategies based on experiences in northern Italy – tree of heaven

Tree of heaven is a ubiquitous species (see Chapter 5.7) currently established from the lowland area to the montane belt in northern Italy, with a preference for warmer sites. Tree of heaven tolerates dry and saline soils but it does not grow well on sites that are prone to flooding. Although capable of very fast growth rates (height increment up to 4 m per year), it is not particularly light-demanding and it is therefore able to establish in even small gaps under a closed forest canopy. Seed production starts between 3 to 5 years of tree's age and is considered rather abundant every year. Sprouts are promoted by allelopathic root exudates produced by the parent tree.

Suggested control strategies include the manual removal of individual trees in the earliest phases of the development, which is recommended in less intensively invaded areas when the native vegetation can still benefit and out-compete the invader. The application of girdling is considered to be more effective if carried out in spring on mature trees and when combined with slash disposal or burning (Box 18).

Prescribed burning can reduce competitiveness of tree of heaven relative to more fire-resistant native species (Rebbeck et al. 2014). Biological methods such as grazing, natural competitors or enemies or enhancement of native species competition are generally not effective due to tree of heaven's resistance to parasites, low palatability of its foliage, and its ability to rapidly surpass its competitors. In invaded riparian forests in Natura 2000 site (Habitat 91E0), control measures were successfully combined with the planting and tending of 'protective' belts of native tree species and shrub vegetation (Figure 49) around invasion nuclei in order to prevent further spread (ECORICE 2015).

Experience on silvicultural management of tree of heaven is still rather limited with most management measures showing only partial effectiveness. Prevention of spread to uninvaded areas and monitoring of invasion below a closed canopy are the only experience-based recommendations that can be formulated at this point.

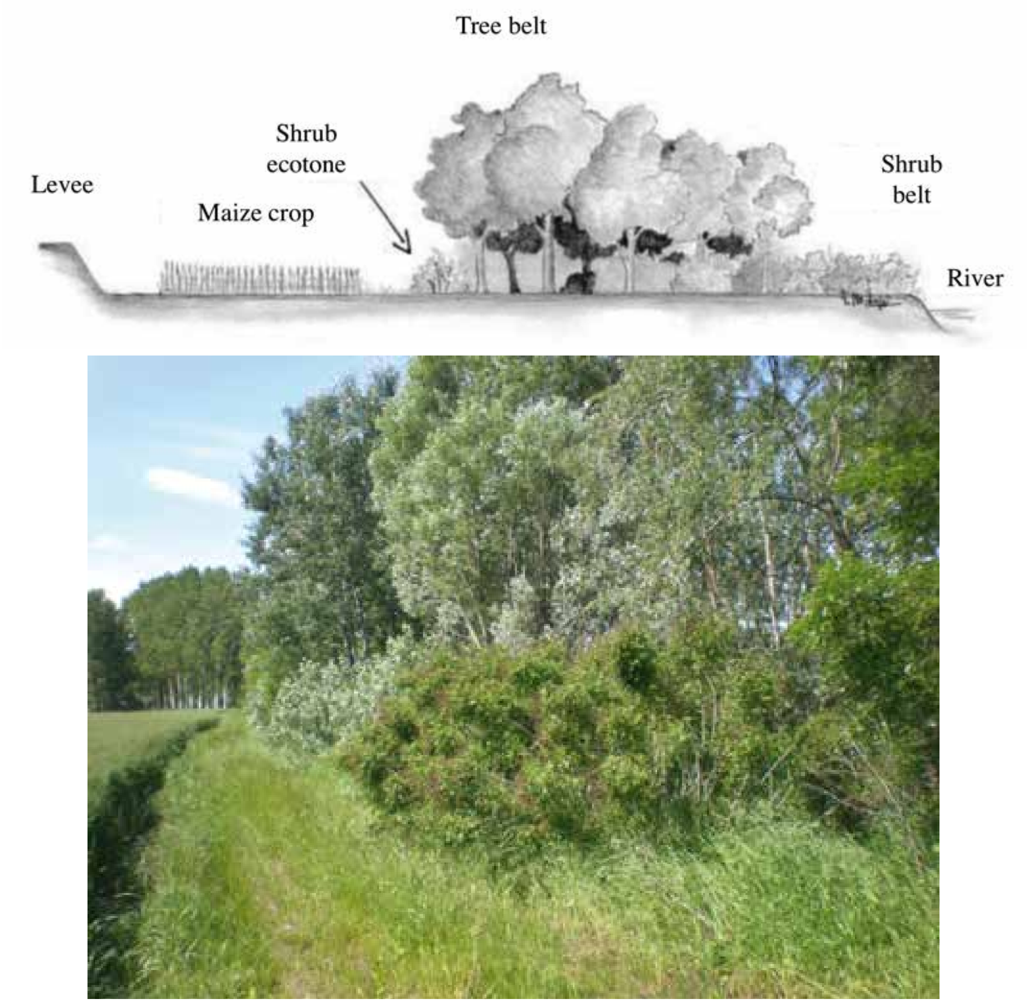

Figure 49. Protective shrub and tree belt to prevent spreading of introduced tree species to river ecosystems (a); protective tree belt in Piovera (AL, Italy) along the Po river (b).

BOX 18: Managing slash to contain introduced tree species

Management of slash is a complex and sensitive part of the process of cutting and mowing operations that are used to control the spread of introduced and invasive tree species. If not correctly disposed of, vegetative parts, fruits, or seeds of introduced tree species can be transported to uninvaded sites and facilitate future colonisation (Figure 50).

Slash can be effectively piled and burned on site or at wood production facilities provided that all regulations for fire prevention and smoke emissions are carefully followed (LIFE09 NAT/IT/000118 2015). Incinerating the disposed slash is considered to be the safest strategy for destroying the vegetative parts, seeds, and fruits of introduced and invasive species. Disposal at dumps must be avoided since the waste is not always properly sealed and the seeds or vegetative parts can be spread by the wind into the surrounding areas.

Other methods include anaerobic digestion or composting (never for tree of heaven), which must be carried out in authorised industrial facilities that comply with existing regulations (e.g. D.M. 5-2-1998 in Italy). Aerobic transformation must be ensured in such case; i.e. the thermophilic stage must take place (55°C must be maintained for > 72 hours). This process stabilises organic matter and completely decomposes the seeds and vegetative parts of the invasive plants. Unintentional dispersal of slash during temporary storage and transport should be avoided.

Figure 50. Tree of heaven re-sprouts even after herbicide use (photo: released under Creative Commons Attribution-Share Alike 4.0 International license. https://en.wikipedia.org/wiki/File:Tree_of_Heaven_Re-sprouting.jpg).

Species-specific strategies based on experiences in northern Italy – red oak

Red oak thrives on acidic sites and it is able to tolerate compacted and seasonally flooded soils. However, it does not grow well in clay, limestone soils and on drier sites. Its seedlings are shade-tolerant and can establish below a closed canopy. Red oak acorns are produced in mast seeding years that occur every 3 to 5 years after the age of about 25 years with a limited viability of the seeds between the age of 25 and 50.

The natural regeneration of red oak is denser closer to the parent trees, where the accumulation of litter is greater as it favours the preservation and germination of the acorns (Garcia et al. 2002). The thick litter of dead leaves is essential for protection of the acorns against weathering; it further inhibits regeneration of other tree species. The natural regeneration of red oak is hampered under the canopies of tree species with particularly dense canopies such as hornbeam. Forests most threatened by red oak invasion are bottomland oak-hornbeam forests of the plains and interior hills (EU Habitat 9160), sweet chestnut forests, mixed floodplain and alluvial forests of alder (*Alnus* spp.) and willow species.

Repeated and frequent coppicing of sprouts in spring or summer (at least 1–2 cuts per year) can exhaust the stump. The possibility of vegetative growth from the stump increases with the size of the tree to up to the age of 60 years. The ability to produce sprouts is reduced by 50 % at the age of 80 years. These measures may be accompanied by tillage and under-planting or seeding with fast-growing native species such as aspen or birch (*Betula pendula* Roth) (ECORICE 2015). Based on these experiences, repeated coppicing and underplanting is recommended in order to avoid natural regeneration from seed and to gradually deplete red oak's capacity to vegetatively regenerate.

Species-specific strategies based on experiences in northern Italy – black cherry

Black cherry displays a high resistance to drought. In Italy, this species does not grow well in waterlogged or calcareous soils. Black cherry can also tolerate high shade and its saplings often develop a 'sit-and-wait' strategy; once released by a disturbance-induced gap, they grow rapidly into the canopy also producing large amounts of seed.

In disturbed areas with low propagule pressure, the germination and establishment of black cherry can be hindered by brambles (*Rubus* spp.). In such case, although the overtopped black locust saplings die, they can subsequently re-sprout from roots and stumps. The absence of disturbances often leads to a reduction in the number of individuals during the succession process.

Silvicultural control measures have not been effective due to black cherry's high tolerance to shading and capability to reproduce vegetatively or from the seed. Black cherry has been difficult to control; in Parco del Ticino in northern Italy, for instance, black cherry successfully invaded 514 ha. Although the entire area was continuously treated over 10 years by a mix of control measures (i.e. complete stem removal, repeated mowing, simultaneous conversion of native coppices to high forests, and planting native species, which cost €830 000), the species re-appeared within the next few years (Caronni 2009). The recommendation based on the experience from Parco del Ticino is therefore to concentrate all eradication efforts on the edges of the invaded area. The following management actions can also be considered in a light of black cherry eradication: e.g. conversion of coppice to high forest, total removal of adult trees, maintenance of a closed canopy, mowing of suckers (repeated for the duration of 3 to 5 years), application of herbicide (Triclopyr), and under-planting with shade-tolerant native species.

Cutting black cherry stems proves to be ineffective as observational studies in Italy showed that re-sprouting occurred on all felled trees. In highly invaded stands, disturbances that may activate the soil seed bank should be minimised (Skowronek et al 2014). With the support of a recently developed simulation model based on diameter class demography through time, it has been suggested that felling only the largest trees could be effective in reducing the abundance of black cherry and result in positive revenues for the landowners. On the other hand, intensive harvesting should be avoided because it could lead to a substantial depletion of nutrients from the soil and produce canopy openings that would be conducive for the pioneer characteristics of black cherry (Annighöfer et al. 2015).

Regulating stand density, seedbed and microclimate by using specific silvicultural treatments can be effective in preventing or mitigating the spread of some invasive tree species causing low impact to the environmental.

The need to choose an appropriate management strategy to address invasions by introduced tree species belongs a the set of possible measures associated with each invasive species trait, invasion stage, and site and environmental condition (Simberloff 2014). This requires a systematic valuation of the methods' efficiency across different regions and ecosystem types. Furthermore, appropriate silvicultural measures applied to native forest habitats can help maintain or improve their resistance to invasions. In all cases, the most effective results are obtained when suitable prevention and eradication measures, continuous monitoring, and awareness-raising campaigns are carried out.

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TEXT BOX III: Insights into certification in relation to introduced and invasive tree species

Marion Karmann, Owen Davies and Antonio Brunori

Management responses to introduced and invasive tree species do not depend solely on environmental factors; they also depend on economic factors and social attitudes. Forest certification schemes, which bring together environmental, economic and social interests, therefore play an important role in determining how such species are managed. Invasive species present a threat to many of the values promoted in forest management certification, particularly the conservation of biodiversity. However, introduced species may have a role in delivering other values, particularly economic ones. Certification schemes and their national standards are thus likely to include requirements controlling new introductions as well as managing the impacts of already present introduced and invasive species.

The approaches of two certification schemes, the Forest Stewardship Council (FSC) and the Programme for the Endorsement of Forest Certification schemes (PEFC), are described and the requirements in different national standards are compared.

> *The international basis for certification standards and the development of national indicators varies.*

PEFC sets international Sustainable Forest Management benchmarks (PEFC 2010), on the basis of which national stakeholders develop their own national standards with the open participation of interested parties in a consensus-driven decision making process. FSC, on the other hand, which is based on broad stakeholder consensus, develops a set of globally applicable Principles and Criteria for forest stewardship, along with generic indicators (FSC 2015). To make the FSC criteria operational for national or regional forest management certification, national standard development groups with representatives from social, economic and environmental chambers negotiate and decide upon appropriately adapted indicators (Karmann et al. 2016).

FSC in Germany

With less than 4 % of the forest area comprised of introduced tree species, forestry in Germany does not rely heavily on such tree species; although Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) accounts for 1.7 % of the forest area in Germany and locally generates substantial financial returns (BMVEL 2004). FSC Germany expands the aspiration of the global FSC Principle 6 to maintain and enhance biodiversity, and refers to close-to-nature forestry. The national standard (FSC Germany 2012) requires forest management to approximate the tree species composition, structure and dynamics of natural forests, utilising natural processes as much as possible, and incorporating features such as old trees and deadwood.

PEFC in Italy

Italy is one of the European countries most affected by the invasion of introduced species since it has been a centre of intense exchange and colonisation of non-native biota as a result of human trade and migrations ever since ancient times (Blasi et al. 2007). Introduced species are estimated to dominate 2.7 % of Italian forests with black locust (*Robinia pseudacacia* L.) being the most widespread species (Rizzo and Gasperini 2011). There are specific indicators in the national standard (PEFC Italy 2015) regarding the management of introduced tree species suggesting they should not exceed 30 % of the entire forested area of the certified forest. The standard further states that the area dominated by introduced tree species cannot increase by more than 5 % for the duration of the management plan.

FSC and PEFC in the United Kingdom

The United Kingdom is unusual in having an independent forest stewardship standard (the UK Woodland Assurance Standard; UKWAS 2012), which is approved by both FSC and PEFC. Centuries of deforestation left a forest cover of only 5 % at the beginning of the 20th century; the increase to the current level of 13 % was achieved largely by planting introduced coniferous species. Conifers now account for around half of all woodland in the UK, and half of the conifer area is stocked with a single introduced species, Sitka spruce (*Picea sitchensis* (Bong.) Carr.) (Forestry Commission 2015). The UK national standard implicitly recognises the importance of introduced species to the forest industry; some restrictions on introduced species explicitly exclude introduced tree species, and the preferential use of native species is limited to new woodlands and semi-natural woodlands.

> ▶ *There are differences in these three certification standards presented (i.e. FSC Germany 2012, PEFC Italy 2015 and UKWAS 2012), which reflect national circumstances and stakeholder attitudes.*

Regarding deliberate introductions, FSC Germany and PEFC Italy impose area restrictions, with further restrictions applied in areas of high conservation value in the case of Germany. In the UK, there are no restrictions on the introduction of non-native tree species except in natural and semi-natural woodlands; other non-native plant and animal species may be introduced only if they are not classed as invasive.

All of the national standards require monitoring of the impacts of introduced species although they vary considerably in the specificity of their requirements. Regarding measures to control invasive species, both FSC Germany and PEFC Italy severely restrict soil cultivation and the use of pesticides with the latter only being permitted for specific phytosanitary uses. FSC Germany also restricts the use of biological control agents. In the UK, FSC and PEFC allow the use of pesticides and biological control agents, with restrictions, but also require that forests be designed to reduce the impact of invasive species and that invasive species be managed in cooperation with neighbouring land managers.

> ▶ *Certification standards in individual countries differ in the way they approach the management of introduced and invasive tree species.*

While there are clear similarities in the treatment of introduced and invasive species in the national standards of FSC Germany, PEFC Italy, and FSC and PEFC in the United Kingdom, such as in requirements for monitoring, there are also some significant differences which reflect national circumstances and stakeholder attitudes. Generally speaking, the standards for Germany and Italy are far more restrictive than that for the UK, where introduced tree species have a predominant role in the forest industry. The UK standard is also less restrictive on the use of pesticides, and so may permit more options for the control of invasive species. Despite the national differences, all of the standards impose some restrictions on the introduction of non-native species and require the monitoring of the impacts of invasive species, thus ensuring that these issues are considered by the managers of certified forests. It remains to be seen whether time will lead to further convergence or divergence of national requirements.

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3.7 Occurrence of introduced tree and shrub species in Italian regions in relation to the extent of planted and coppiced forests

Sabina Burrascano, Laura Celesti-Grapow and Carlo Blasi

In Europe, invasive trees and shrubs are considered as potential drivers of the alteration of both open and forest habitats, with some being reported causing severe economic and ecological damage (www.europe-aliens.org, www.eppo.int). The early stages of succession, which are characterised by a high degree of resource availability and by reduced competition, offer great colonisation opportunities and are more susceptible to invasions than the late-successional stages (Catford et al. 2012). Indeed, open habitats are often those affected most by the establishment of introduced species. This is one of the reasons why the occurrence of introduced trees in Europe has mainly been studied in open habitats, particularly in man-made ecosystems (Kowarik et al. 2013). There is, however, an increasing number of studies on their establishment in forests (e.g. Chabrerie et al. 2008) since some invasive species have colonised forest habitats (Lambdon et al. 2008).

The occurrence of introduced trees and shrubs may depend on forest origin and management strategy.

The vast majority of European forests are subjected to production-oriented harvesting activities, each of which represents a disturbance event (Roberts and Gilliam 1995). Since management strategies may differ substantially with regard to the proportion of trees harvested and the rotation period, managed forests are characterised by a wide variety of disturbance extent, intensity and frequency. Therefore, the vulnerability of forests to invasion by introduced plants may vary greatly depending on the management regime. For instance, the number of standards released after harvesting, the rotation period, the life-history traits of the native dominant species and the varying intensities of competition may determine the likelihood and the extent of the establishment of introduced species, as well as of their subsequent spread.

The relationships between forest management strategies and the establishment of introduced trees has been highlighted by a substantial body of scientific evidence, with a wealth of knowledge being formed in recent years in Europe on how introduced species respond to a range of forestry interventions (Sitzia et al. 2015). For instance, coppiced stands have been found to be particularly prone to the establishment of tree of heaven (*Ailanthus altissima* (Mill.) Swingle) and black locust (*Robinia pseudacacia* L.) in northern Italy (Radtke et al. 2013). The time elapsed since the last disturbance event has also proved to be highly relevant in determining the abundance and recruitment of black locust in northern Italy (Motta et al. 2009). Management strategies may favour or control the establishment of introduced tree species (Dodet and Collet 2012), depending on, among other things, those actions carried out to establish and manage plantation forests

(Brundu and Richardson 2016). Owing to the selection of highly productive species, the high propagule pressure and the proximity of the planting sites to natural or semi-natural vegetation, plantation forestry has proved to be one source of introduced tree species in natural and semi-natural habitats (Donaldson et al. 2014) as it fosters the establishment and spread of introduced species in the wild, thus increasing the risk of negative environmental impacts and the threat to the conservation of biodiversity (Dodet and Collet 2012).

Approximately one third of the surface of Italy is covered by forests. The marked environmental and cultural heterogeneity of the country has determined the presence of substantially different land management strategies that are also apparent within forested areas. Depending on the site productivity and on the dominant tree species, forests in different regions in Italy are either largely managed as coppices or as high forests. Some studies provide information on the introduced flora in forest habitats in Italy (Banfi and Galasso 2010), although an assessment of the main patterns of plant invasion in forests at the national scale is still needed. Within this broader perspective, an assessment of the relation between the number of established introduced tree and shrub species in each region and the extent of forest plantations and the share of forests subjected to different management types, i.e. coppice vs. high forest was made within the current chapter. Latitude was also included among the explanatory variables since this geographical gradient is known to affect introduced plant species richness in different regions across the country (Celesti-Grapow et al. 2010).

A comprehensive national survey on introduced plant species in Italy was compiled in 2009, and the results of the survey were integrated with those from the national forest inventory to assess regional occurrence of introduced trees and shrubs in Italian forest (Celesti-Grapow et al. 2009).

▶ *The integration of national databases on the introduced vascular flora with the national forest inventory may effectively contribute to assess regional occurrence of introduced trees and shrubs in forests.*

Information on introduced tree and shrub species in forest areas was obtained from the database of the introduced Italian vascular flora (Celesti-Grapow et al. 2009), which has been constantly updated since then, thanks to the growing attention being paid to biological invasions. The database provides detailed information on each taxon of the Italian introduced spontaneous flora, including life form, distribution of each species in the administrative regions and occurrence in the land cover types, according to the CORINE Land Cover classification system. Following the system standardised on a nationwide scale by the working group on the introduced flora of Italy (Celesti-Grapow et al. 2009), each species in the dataset is also designated on the basis of its establishment status within the country as either casual (those that do not form self-replacing populations and rely on repeated introductions for their persistence) or established (naturalised, i.e. those that had become established and thus sustained self-replacing populations by undergoing a widespread dispersal and becoming incorporated within resident flora without the contribution of new propagules from human interventions).

The list of all established introduced tree and shrub species reported in forests was extracted from the latest version of the database; i.e. the CORINE land cover category 3.1.

Neophytes. Both trees and shrubs were considered because some species are classified as either the former or the latter depending on the source flora. We extracted presence/absence data for each taxon for each of the 21 administrative regions.

We used a national land cover map (CLC2000) to derive the total forest area in each region and used this information in the model to account for the species/area relationship and to coarsely investigate the effect of the degree of connectivity among forest ecosystems. Data on the extent of the various forest types were obtained from the most recent Italian National Forest Inventory (INFC 2005), and were used as explanatory variables. We focused on the proportion across the forested area of each region of: (i) forests managed as coppice; and (ii) plantation forests. Lastly, we calculated the latitude of the centroid of each region.

Data were analysed using Generalised Linear Models with a log-link function (assuming a Poisson distribution of errors) following the indications included in Zuur et al. (2013) to investigate the drivers of established tree species richness in forest areas across Italian regions. After checking explanatory variables for collinearity, the total forest area and the proportion of coppiced and of plantation forests were used as explanatory variables; the total forest area of each region was used as an interaction term. The proportion of forests managed as high forests was excluded since it was highly correlated with the proportion of coppiced area (Spearman coefficient of –0.9). We included latitude as an additional explanatory variable. All the explanatory variables were standardised to a 0/+1 scale before analysis. All the analyses were run in R 3.2.2 using the packages 'stats' and 'vegan'.

In total, 21 established introduced tree species and 28 established shrub species were recorded in Italian forests. The most widely distributed invasive species were tree of heaven, black locust, ash-leaved maple (*Acer negundo* L.), bastard indigo (*Amorpha fruticosa* L.) and paper mulberry (*Broussonetia papyrifera* (L.) Vent.), which were recorded in almost all the regions; additionally, among the most widespread, black cherry (*Prunus serotina* Ehrh.) and red oak (*Quercus rubra* L.) occur in most of the northern temperate regions, whereas blue-leaf wattle (*Acacia saligna* (Labill.) H.L.Wendl.) and silver wattle (*A. dealbata* Link.) occur in most regions of southern Italy. These species largely correspond to those listed among the most studied and widespread invasive trees and shrubs in Europe (Starfinger et al. 2003).

The occurrence of introduced tree and shrub species across regions strongly responds to the portion of forest occupied by planted and coppiced forests.

Introduced tree and shrub species strongly respond to the portion of forest occupied by plantation and coppiced forests in each administrative region (Figure 51, Table 20). The final model explained 79.5 % of the deviance (obtained as the ratio between the difference between null and residual deviance and null deviance). All predictors were significant. The model was validated by calculating its dispersion (2.38) and by checking that the fitted values did not yield any clear pattern when plotted against the residuals.

Table 20. Results of the GLM in which the number of established species per region is used as response variable and the data derived from the national forest inventory (forest area, coppiced area, plantation area) and the latitude of the centroid of each region are used as explanatory variables. Asterisks indicate p-value thresholds of 0.05 (*); 0.01 (**); 0.005 (***).

	Estimate	Std. error	p-value	
Intercept	0.8976	0.3619	0.0131	*
Coppiced area (%)	1.2974	0.4096	0.0015	**
Plantation area (%)	1.4626	0.4377	0.0008	***
Forest area	3.8437	1.0218	0.0002	***
Latitude	1.4494	0.2000	0.0000	***
Coppiced area (%):Forest area	-4.0986	1.2468	0.0010	**
Plantation area (%):Forest area	-2.3120	0.8814	0.0087	**

The positive association between the number of introduced tree and shrub species and the proportion of forest area represented by plantations in each region confirms that plantation forests promote the introduction and establishment of introduced plants (Dodet and Collet 2012). Establishment of introduced species is most often intentional through the planting of seedlings or seeds; however, establishment may also be unintentional through the unintended regeneration of species outside the planted area (Martin et al. 2009). It should also be borne in mind that non-native species introduced for forestry purposes are generally planted in order to maximise self-sustainment and establishment. Such species usually originate from regions where the climate resembles the introduced range; they are selected on account of their tolerance of a wide range of conditions, and they are planted repeatedly in very large numbers so as to maximise their chances of establishment by exploiting close environmental matches and high propagule pressure (Donaldson et al. 2014).

While plantation forests may certainly act as a means of introduction and establishment of introduced species, it is even more important to consider the potential consequences of this process for the surrounding landscape. Indeed, one of the main issues regarding the introduction of non-native species through plantations is that they often are in close contact with natural and semi-natural areas. Once introduced, this proximity provides opportunities for such populations to invade adjacent ecosystems and have substantial negative environmental impacts (Donaldson et al. 2014). Particular attention should be paid to contexts in which invasive species spread into forest habitats because time lags in forests may be particularly long (Essl et al. 2011) and invasions may occur at a very slow rate of the canopy turnover; hence, the long-term effects should be monitored (Martin et al. 2009). Trees in particular can become dominant reaching very high densities and act as 'transformers', thereby radically changing vegetation structure, nutrient cycling, hydrology and fire regimes in the invaded sites (van Wilgen and Richardson 2014).

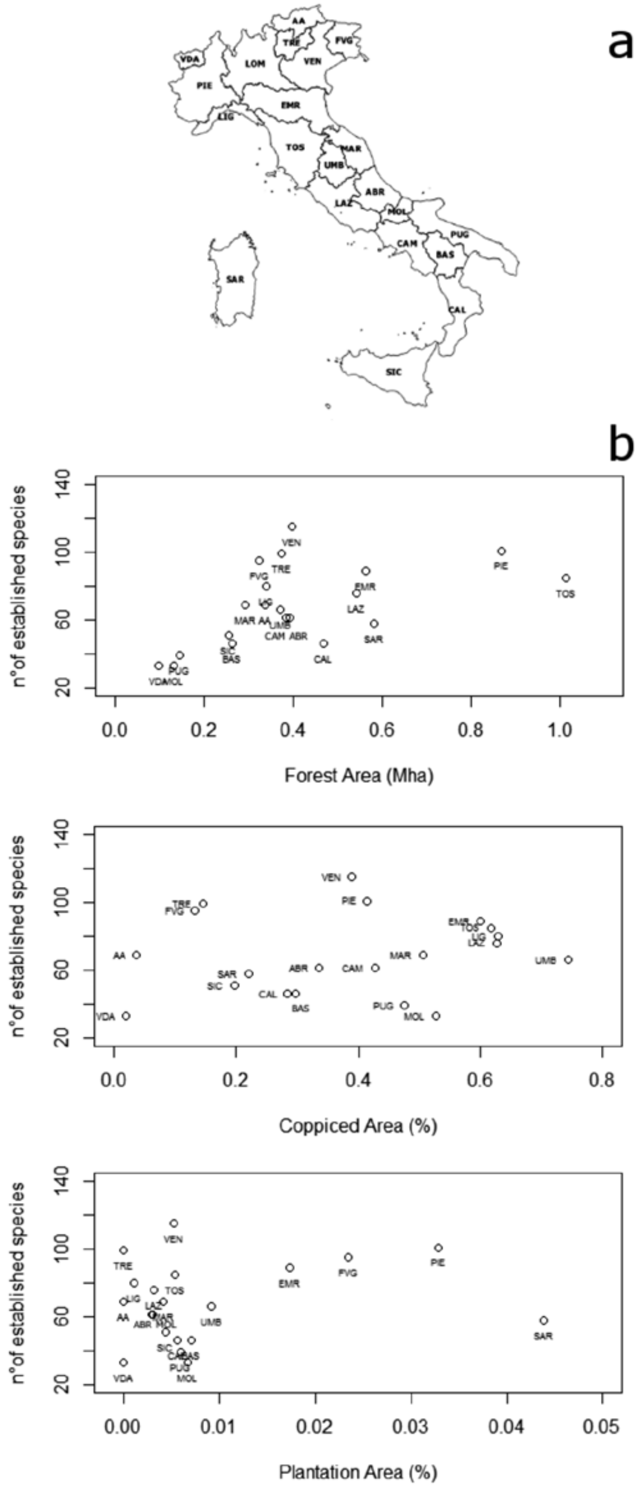

Figure 51. a) – legend of the acronyms used for the administrative regions; b) – scatterplots of the number of established tree and shrub species vs. the most relevant explanatory variables in the GLM.

In addition to the abundance of forest systems and to the proportion of plantation forests in each region, the established introduced tree and shrub species respond to the portion of forest managed as coppices in comparison to high forests. The most noticeable effect of coppice practices is the high frequency and broad-scale canopy disturbance. Indeed, disturbance is a well-known primary factor in promoting plant invasion in different habitat types (Davis et al. 2000) and in particular in forest ecosystems in which it creates clearings with a temporary increase in resource availability (Essl et al. 2011). It should also be remembered that many introduced tree species are pioneer, light demanding, early successional species in their native ranges since they are selected on account of a series of life-history traits, such as fast growth, precocious and prolific seed production and vegetative reproduction, which make them efficient colonisers in disturbed areas and confer a competitive advantage over other species in open-canopy forests (Dodet and Collet 2012, Richardson et al. 2014). In the last decades, coppices, as well as high forests, were often subjected to abandonment, especially in those regions where many forests are difficult to access and are therefore less profitable than others. Unfortunately, the national forest inventory does not report the area of abandoned forests; these are included in the general category ‘undefined management type’ and valuable information is therefore lost.

The significant interaction terms suggest negative interactions between forest area and the percentage of coppices and plantations. This may be explained by two different types of interaction: on one hand, when forest area is high, the effect of coppice and plantation area may be reduced since they are included in a highly connected forest landscape. On the other hand, if the proportion of coppice and plantation area is very high, forest area may interact to a limited extent with their effect on the number of introduced species.

▶ *Latitude has a positive relation to the number of introduced tree and shrub species occurring in forest areas.*

Another noteworthy finding that emerged is that the number of introduced tree species that occur in forest areas decreases significantly in parallel with decreasing latitude. Such a trend, which was previously reported for the total introduced flora of Italy (Celesti-Grapow et al. 2010) and of Europe (Lambdon et al. 2008), is acknowledged to reflect the lower richness of introduced vascular flora in the Mediterranean region than in the temperate region (Chytrý et al. 2009).

The latitudinal gradient may assume a different ecological meaning depending on the region where it is studied and on the specific stress that affect plant communities in different regions. Indeed, the type and degree of stress to which plant communities are subjected are particularly relevant in determining the patterns of occurrence of introduced plant species with harsh sites being in general less invaded (Zefferman et al. 2015). In this view the positive relation we found between the number of introduced tree and shrub species and latitude may be interpreted as a consequence of the more stressful drought conditions in the southern regions of Italy since forestry and horticulture has generally selected and introduced fast-growing, shade-intolerant trees and shrubs that thrive in base-rich, mesic sites rather than species adapted to dry sites (Martin et al. 2009).

Although the representation of introduced species might not be high in terms of species numbers, the impact of invasive species in the Mediterranean region should not be over-looked. Indeed, the invasive spread of some species poses a severe threat to the conservation of plant diversity (see for instance Pretto et al. 2012) in this area where particularly high number of endemic species underlies the existence of one of the most important hotspots of biodiversity globally.

In view of the importance of prevention measures in the management of invasive species, as was stressed in the recent EU regulation on invasive alien species (Sitzia et al. 2015), a concerted effort should be made to focus on forest management strategies as they have been shown to affect more than one step in the invasion process in forests, including the introduction, establishment and subsequent invasive spread of invasive species to adjacent natural areas.

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3.8 Asian knotweeds – an example of a raising threat?

Fanny Dommanget, Paul Cavaillé, André Evette and François-Marie Martin

Asian knotweeds (*Fallopia* spp.) are herbaceous plants originating from south-eastern Asia that were introduced to Europe at the end of the 19th century for ornamental purposes. They are now widespread across Europe and North America, and are currently considered to be one of the worst invasive species in the world (IUCN 2011). The Asian knotweed complex is mainly composed of three taxa:

1. Japanese knotweed (*Fallopia japonica* (Houtt.) Ronse Decr.);
2. Giant knotweed (*F. sachalinensis* (F. Schmidt) Ronse Decr.);
3. Hybrid knotweed (*F. x bohemica* (Chrtek & Chrtková) J.P. Bailey).

F. japonica has also been designated as *Reynoutria japonica* Houtt. and *Polygonum cuspidatum* Sieb. & Zucc. in the scientific literature, *F. sachalinensis* as *R. sachalinensis* (F. Schmidt) Nakai and *P. sachalinense* F. Schmidt, and *F. x bohemica* as *R. x bohemica* Chrtek & Chrtková or *P. x bohemicum* (Chrtek & Chrtková) Zika & Jacobson.

> *Asian knotweeds are highly productive rhizomatous species that quickly spread through various habitats.*

Asian knotweeds develop a dense network of rhizomes that can laterally spread over distances such as 20 m (Beerling et al. 1994) with the underground biomass representing up to two thirds of the total biomass (Figure 52) (Price et al. 2001). Ramets (i.e. individual members of a clone) from the same individual are interconnected through the rhizomes and seem to share resources through clonal integration (Aguilera et al. 2010). This mechanism enables individual ramets in less favourable microenvironments to benefit from resources acquired by ramets in more favourable microenvironments (De Kroon and Hutchings 1995). Asian knotweeds are characterised by a high growth rate that can be up to 15 cm a day (Urgenson et al. 2009) allowing them to rapidly dominate the areas where they become established. The segmented and ramified ramets (Figure 52) of Japanese knotweed can reach a height of 3 m, with giant knotweed growing to 5 m, and hybrid knotweed having an intermediate morphology (Bailey and Wisskirchen 2006).

Figure 52. Underground system (a), flowers (b) and growing ramets (c) of *Fallopia japonica* (photos: F. Dommanget).

If sexual reproduction also occurs in the wild (Forman and Kesseli 2003), Asian knotweeds' reproduction is mostly vegetative, especially in Japanese knotweed for which only one male-sterile clone has been identified in Europe (Krebs et al. 2010) and only four in the USA (Gammon and Kesseli 2010). Giant knotweed and hybrid knotweed have a more complex genetic variability (Hollingsworth et al. 1999) as sexual reproduction exists between Japanese and giant knotweeds and between the hybrid and its two parents (Tiébré et al. 2007). But vegetative reproduction is very efficient as it only takes a small fragment of a rhizome (Sásik and Eliáš Jr 2006) or stem to produce a new individual (Bímová et al. 2003). Small white flowers appearing in summer from July to September (Figure 52) are situated in terminal and axillary panicles and are pollinated by insects (Beerling et al. 1994). Asian knotweeds produce achenes of variable viability depending on the clone (e.g. Buhk and Thielsch 2015) that spread along rivers thanks to their good buoyancy and ability to germinate after immersion (Rouifed et al. 2011). The propagules disperse via e.g. watercourses (Bímová et al. 2004) or through construction vehicles (Rouifed et al. 2014) or backfill materials (Beerling 1991).

Asian knotweeds have a broad environmental range (e.g. Rouifed et al. 2012) and they can therefore be found in a diverse variety of habitats; they are able to grow on old mine spoil, alluvial soils, quarries and waste zones, but also in open woodlands (Beerling et al. 1994). However, they are more frequently found on disturbed habitats along riverbanks or along roads and railways (Tiébré et al. 2008). Hybrid knotweed has also been found around Mediterranean Basin where extreme weather events such as summer droughts do not seem to be limiting for the hybrid (Bailey and Wisskirchen 2006). Hybrid knotweeds have also colonised southern Scandinavia and mountainous areas (Bailey and Wisskirchen 2006). Moreover, with climate change causing increases in temperatures and a decrease in the number of early frost days (e.g. Groeneveld et al. 2014), Asian knotweeds are expected to spread to higher altitudes and latitudes.

Invasive Asian knotweeds impact ecosystem functioning as they negatively affect species diversity and the growth and abundance of other species, in particular tree regeneration and modify biogeochemical processes.

In areas where they invade, Asian knotweeds displace native plant species, affect fauna and modify soil functioning. Their high growth rate and high biomass production allow them to dominate open spaces, forming a dense layer that prevents light reaching the ground layer, and thereby reducing both richness and abundance of other plant species (Siemens and Blossey 2007). However, light obstruction is not the only mechanism explaining their dominance; Asian knotweed litter has been shown to reduce seed germination of other species (Beerling et al. 1994). Moreover, they produce phytotoxic compounds negatively affecting seed germination (e.g. Vrchotová and Šerá 2008) and growth of neighbouring species (e.g. Dommanget et al. 2014).

Asian knotweeds have also been reported to affect fauna as it changes the composition of soil macroorganisms. Gerber et al. (2008) found that total biomass of invertebrates in grassland and shrub-dominated habitats was almost twice as high than that in habitats invaded by Asian knotweeds, and that species richness was also negatively affected in areas infested by Asian knotweed. Kappes et al. (2007) investigated the effect of Asian knotweed infestation on different groups of soil and litter-dwelling fauna: herbivore generalists (slugs and snails), detritivores (Isopoda; e.g. woodlice, Diplopoda, millipedes) and predators (Opiliones; harvestmen). Snails were generally found to be more negatively affected than slugs by knotweed infestation, the abundance of Isopoda was decreased, whereas Diplopoda were not affected, and abundance, species diversity and diversity of predatory Opiliones were greater in knotweed infested stands. Kappes et al. (2007) conclude that knotweed infested habitats are characterised by a shift to a detritus based food chain. Such modifications to the composition and the abundance of invertebrate communities affect higher trophic levels. Maerz et al. (2005) observed a decline of green frog (*Rana clamitans* Latreille) in areas invaded by Asian knotweeds and hypothesised that knotweed degrades habitat quality for frogs by reducing arthropod abundance. Hajzlerová and Reif (2014) found that understory birds species richness in riparian communities was reduced in areas invaded by Asian knotweeds in the Czech Republic.

The litter of Asian knotweeds has a low nutritional value when compared with other plants. Knotweeds are able to transfer nitrogen from the aerial parts to rhizomes for storage before the leaf fall; resorption of nitrogen from knotweed leaves into the rhizomes was more than 75 % whereas in red alder (*Alnus rubra* Bong.) it was only 5 % (Urgenson et al. 2009). This results in soils under knotweed cover containing less organic matter and with slower mineralisation rates (Koutika et al. 2007), which in turn can lead to the replacement of key tree species (e.g. *Alnus*) (Urgenson et al. 2009). Asian knotweeds induce changes in soil microbial communities, which leads to the reduction in the potential denitrification enzyme activity (Dassonville et al. 2007). It is important to note that the impacts of Asian knotweeds on nutrient concentrations depend on the site initial conditions (Dassonville et al. 2008). However, the presence of Asian knotweeds may lead to edaphic conditions becoming rather homogeneous.

In riparian environments Asian knotweeds can, after reaching a certain threshold of spread, alter the physical and chemical quality of stream water (Claeson et al. 2014) and modify stream macroinvertebrate assemblages (Lecerf et al. 2007). Finally, by reducing the regeneration of native woody species, knotweed can have lasting effects on the structure of riparian forests and the amount of large woody debris; this is of the utmost importance for sediment dynamics and stream morphology and, consequently, for plant development along river banks (Urgenson et al. 2009).

Control methods to eradicate or impede further spread of Asian knotweeds are usually expensive and often insufficient.

Various methods to control Asian knotweeds have been tested but they are often largely inefficient and expensive. However, one of the most efficient methods is the early uprooting and disposal requiring a constant monitoring of areas at risk. Other mechanical solutions were developed to locally eliminate Asian knotweeds; i.e. rhizome extraction and their deep burial, rhizomes removal and their elimination or their crushing and covering with tarpaulin to accelerate their decomposition (Boyer 2003). Cutting and mowing are commonly used solutions to eradicate or at least reduce Asian knotweeds' vigour in conservation and protected areas. However, they are labour-intensive requiring repeated treatment, and are therefore expensive (Delbart et al. 2012).

Biological control has also been investigated as a means to control Asian knotweeds. Trials by Shaw et al. (2009) and Grevstad et al. (2013) indicated that the psyllid (*Aphalara itadori* Shinji) has potential as a biocontrol agent in Great Britain and in North America; the psyllid greatly reduced knotweed growth, and was observed to be a specialist feeder on knotweed, with a low occurrence of development on other plant species.

Another method is the use of chemical herbicides. Bashtanova et al. (2009) reviewed various methods to eradicate Japanese knotweed using a variety of herbicides and found that none of them resulted in eradication. Delbart et al. (2012) found consistent results, testing the efficiency of different active substances, concentrations and application methods (injected and sprayed). In some cases, where Asian knotweeds have invaded, the use of chemical herbicides is not recommended (e.g. along roads) or is forbidden (e.g. along rivers) as the herbicides could leach into the groundwater table or into the stream (cf. Directive 2009/128/EC of the European Parliament and of the Council of 21st October 2009). The herbicides are also non-specific, and depending on the method of application can result in loss of other vegetation. This can cause destabilisation of the ground, for example, along streams and rivers (Green 2003).

Restoring invaded habitats by stimulating successional processes through direct seeding and/or by transplanting native species can also be a solution for both the conservation of native communities and the control of invasive species (Sheley and Smith 2012). Such alternative strategies have already been successfully tested against various herbaceous invasive plants including Asian knotweeds. In their experimental tests, Dommanget et al. (2015) planted cuttings of fast-growing willow species on previously mowed knotweed patches in order to stimulate the regeneration of a competitive canopy. After two or three years with repeated cuts, Asian knotweeds were dominated by willows and their biomass had significantly decreased. Similarly, Delbart et al. (2012) showed that mowing associated with native trees transplanting was the most efficient mechanical control method. However, these techniques require a repeated and long-term application (Barták et al. 2010).

Asian knotweeds are very persistent, and effective control measures require thorough monitoring and follow-up treatments. It is also important to note that these measures are often very expensive; in Great Britain, the annual cost of infestation (including costs of research; costs to control knotweed along rivers, railways and roads; costs to control knotweed on development sites; devaluation of housing; and costs to local authorities for dealing with infestations) by Japanese knotweed was estimated to be about €230 million (Williams et al. 2010). In the whole of Europe, the total annual economic cost of Japanese knotweed infestations was estimated to be about €2.3 billion (Kettunen et al. 2008).

Asian knotweed invasions of forests is driven by forest disturbances, climate change and the effective dispersal by seeds of hybrids.

The presence of Asian knotweeds in the forests is a growing concern for many forest managers; the French National Forest Office, for instance, is concerned about Asian knotweed infestations developing along forest edges because of the risk they represent if a clearing or a disturbance occurs thus reducing competitive pressure.

Although knotweeds are considered to be pioneers with a broad environmental range (Figure 53), it is generally recognised that some habitats are more susceptible to invasion than others; this may be attributed to differences in propagule pressure, climatic constraints and intrinsic biotic resistance (Chytrý et al. 2008). Concerning forest ecosystems, the most susceptible to invasion by Asian knotweed are frequently disturbed forests, riparian woodlands and deciduous forests (e.g. poplar plantations). Coniferous mountain forests and shrublands are not as susceptible to invasion.

Many examples of forests invaded by Asian knotweeds can be found in the literature (e.g. Beerling et al. 1994, Schnitzler and Muller 1998, Bímová et al. 2004, Dommanget et al. 2013, Gerber and Schaffner 2014). However, it is important to note that mature forests are rarely invaded by knotweeds except along their margins (Beerling et al. 1994). In a study carried out in southern Poland, Asian knotweeds were reported to be less common in forests, than in gardens, railways, wetlands or wasteland (Chmura et al. 2013).

Asian knotweeds affect the growth and germination of ground vegetation and tree species. This can cause changes in composition of plant communities, which can consequently impact forest management and timber production. At sites in Massachussets (USA), Aguilera et al. (2010), for instance, found that natural regeneration of tree species – including sugar maple (*Acer saccharum* Marsh.), silver maple (*Acer saccharinum* L.), and hickory (*Carya ovata* (Mill.) K.Koch) – was lower in stands that had been invaded by Asian knotweeds. Similarly, Siemens et al. (2007) reported that growth of silver maple saplings was significantly reduced under hybrid knotweed, mainly due to the reduced light level.

Figure 53. Asian knotweeds thrive in a broad range of environments: (a) along rivers; (b) in urban areas; (c) along forest edges; and (d) in wild garden waste (photos: F. Dommanget).

Dommanget et al. (2014) demonstrated that the growth of three species with potential for restoration – e.g. black poplar (*Populus nigra* L.), grey willow (*Salix atrocinerea* Brot.) and osier (*Salix viminalis* L.) – was noticeably reduced when watered with leachates from soil in which Japanese knotweed was growing.

In forests, observation and prevention are the most efficient management method for Asian knotweed.

Removal of Asian knotweeds helps the spontaneous re-establishment of native species. Following local application of herbicides, coniferous species such as western red cedar (*Thuja plicata* Donn), Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and broadleaved trees such as red alder (*Alnus rubra* Bong.) or black cottonwood (*Populus trichocarpa* Torr. & A.Gray ex.Hook.) were able to recolonise the areas that had been invaded by Asian knotweeds in Washington State (USA) (Urgenson et al. 2014). Cutting back Asian knotweed also benefitted the establishment and growth of planted oak (*Quecus* spp.) saplings along the Bronx River in New York City (Haight et al. 2014) as well as common ash (*Fraxinus excelsior* L.) and sycamore (*Acer pseudoplatanus* L.) saplings in the Czech Republic (Barták et al. 2010). Barták et al. (2010) report that there was frequent re-sprouting of Asian knotweeds in forest stands in spite of the application of herbicides. The plants were however, relatively small and weak. It is preferable to prevent establishment of Asian knotweeds rather than rely on post-establishment control and eradication (Simberloff et al. 2013).

On sites infested by Asian knotweeds, a frequent and repeated effort to control knotweeds should be maintained in order to allow native species to successfully re-establish until canopy closure occurs (Dommanget et al. 2015). Regular and selective cuttings for at least four consecutive years help the cover and the diversity of native species to increase in invaded patches (Gerber et al. 2010). The active restoration of a native plant community can also be used as a control tool against Asian knotweeds but knotweed shoots must be mowed specifically for a minimum of two or three years depending on the site and on native species growth (Dommanget et al. 2015). Attention must be then paid to forest clearings in close proximity to sites infested by Asian knotweeds; it is important to minimise disturbance within kilometres around infestations of Asian knotweed. Following cutting or pulling, knotweed remnants such as stems, rhizomes or seedlings should be removed from the site and disposed of safely (Miller et al. 2015). Similarly, forest managers should be aware of the dispersion risk through the use of machinery along the trails. Having been used in infested areas (i.e. for wood harvesting, knotweed management, etc.), all machinery should be carefully cleaned to remove knotweed fragments and prevent infestation of new sites (Cottet et al. 2015). Child and Wade (2000) provide suggestions for increasing public awareness and provision of information about good practice for knotweed management and prevention of its spread into unaffected areas.

Some habitats are more susceptible to invasion than others mainly due to differences in propagule pressure, climatic constraints and intrinsic biotic resistance.

Recent research shows that hybrid knotweed seems to disperse efficiently by seed in Europe (Buhk and Thielsch 2015), which is especially promoted by the presence of forest clearings and favourable light conditions in freshly disturbed sites. Sexual reproduction also represents opportunities to adapt to changing environmental conditions. As seedling establishment can be reduced by summer drought and late frost (Funkenberg et al. 2012), the predicted climate change scenarios may favour the establishment of hybrid knotweed in forests, which might provide some respite from the hottest of the summer temperatures. The effects of climate warming have already been observed within the northern part of its distribution in North America, with the further northward spread of viable seeds (Groeneveld et al. 2014). Even if warmer summer temperatures could limit seedling survival (Funkenberg et al. 2012), climatic changes are likely to reduce late-spring frosts and favour extreme wind events (Christensen et al. 2007), which could provide favourable conditions for knotweeds to colonise forests.

It is important to understand the risk presented by Asian knotweeds in order to prevent their further expansion. Control of knotweed is expensive and better results are achieved when the invasion risks are considered prior to the possible invasion or, at least, as early as possible once an infestation has been identified (Child and Wade 2000).

Competition is an effective way to control Asian knotweed infestations and to prevent their spread into neighbouring areas. In infested areas, forestry practices should be adapted to minimise the disturbance in areas adjacent to knotweed infestations and to reduce light availability for the knotweeds on the forest floor. In disturbed areas close to Asian knotweed infestations, knotweed growth should be kept under control (in non-riparian forest areas this could involve application of herbicides, in riparian areas other methods should be considered), until natural regeneration of desired species has become established. The spread of Asian knotweed should be kept under careful observation.

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Disturbed forest in southern Switzerland after a fire in 2006. Paulownia and Ailanthus trees invade the burned area from the edges (photo: F. Krumm).

4 Key aspects of introduced and invasive tree species

The fourth section of the book presents some of the key aspects of introduced and invasive tree species where various factors affecting introduced and invasive tree species are discussed. The section is initiated with economic aspects of introduced tree species, followed by discussion of the importance of species competition and migration limitation of tree distributions during global change. The pathogens of introduced tree species and the interaction between introduced tree species and arthropod communities are discussed in the following chapters. The final chapters address the implications of introduced species on biodiversity and on natural disturbances.

Text Boxes

4.1 Economic aspects of introduced tree species – opportunities and risks

Marc Hanewinkel and Jorie Knook

> ▶ *Economic aspects were often a driver to introduce new tree species – the perception of these species has changed over time.*

In the long history of tree species that have been moved from their original growing ranges into other areas, economics has often been the main driver of the introduction of tree species to large areas where they did not occur before (Essl et al. 2010). While single trees have mostly been introduced for ornamental reasons in urban or peri-urban areas such as parks (Dickie et al. 2014), new forest stands sometimes covering large parts of landscapes have been established with clear expectations towards an increased economic productivity, or – to speak with the terminology of the Millennium Ecosystem Assessment (MEA 2005) – with the goal of an improved delivery of ecosystem services, be it provisioning services (e.g. timber-based raw material, non-timber forest products) or regulating services (e.g. erosion control). Thus, when these species were first introduced, it was usually the economic potential or other expected benefits that was the dominant factor in the perception of decision makers (Richardson 1998). A good example therefore is the introduction of Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco var. *menziesii*) in south-western Germany at the end of the 19th century. This perception has – at least since the end of the 20th century – changed. The associated trade-offs and risks such as the potential loss of biodiversity, a change of the risk regime, the replacement of native species and related biodiversity leading to potentially high management costs of the introduced species that are often looked upon as invasive, have to a large degree, changed the attitude towards these species and has created conflicts between different stakeholder groups.

This chapter analyses the economic background of the opportunities and risks of planting introduced species. This analysis is based on a literature review in the Web of Science (March 2016) with the main key words ‘economics’ – ‘invasive tree species’, ‘introduced tree species’ and variations. From the original set of around 170 references that were found, only about two dozen that are included in the reference list of this chapter were useful, showing that the scientific background for this question is small.

> ▶ *There are opportunities and risks of introduced species from an economic point of view.*

The introduction of ‘non-native species’ in an area has manifold economic implications, but is also related to an array of potential conflicts and trade-offs. Dickie et al. (2014) give an overview of the multitude of goods and services that introduced species may deliver to societies ranging from cultural (e.g. amenity), provisioning (e.g. timber, honey, medicinal), supporting (e.g. biodiversity, N-fixation) to regulating (e.g. erosion control) services. It is clear from this analysis that when discussing economic implications of introduced species, we have to take into account all potential ecosystem goods and services delivered by the introduced species to different users. However, this study also highlights the trade-offs and conflicts related to these species and lists three major areas of conflicts: (i) trees in urban or near-urban areas, (ii) trees delivering direct economic benefits, and (iii) invasive trees replacing natural species as a source of habitat or food for rare species. Here, Dickie et al. (2014) refer to a dichotomous view on introduced species in which one group focuses on the risks – the potential costs of management of the species (and in the extreme case – the cost of eradication) and other potential negative effects; while others focus on the potential opportunities presented by introduced species.

The costs of managing invasive species can be important – so can be the benefits of these species.

The costs of managing introduced invasive species can indeed be very high. Davis et al. (2011) report an amount of about US$80 million granted by the US Congress to support ongoing control and eradication of tamarisk (*Tamarix* spp.) in US riverbank environments for a period of only five years. Pejchar and Mooney (2009) cite figures for the management of invasive species in the range of US$14.45 billion for China and US$128 billion yearly for the US, but criticise the lack of systematic empirical methods of estimating costs and that the studies usually do not consider benefits. The benefits of well-integrated species with a long history of management can indeed be important. In Germany, Douglas fir is one of the most productive tree species in terms of growth, economic output and consequently also for carbon sequestration. Heidingsfelder and Knoke (2004) show that the financial return of Douglas fir may be more than 100 % greater than that of the second most productive species in Germany, i.e. Norway spruce (*Picea abies* L. Karst). Red oak (*Quercus rubra* L.) is more productive than indigenous oaks under similar growth conditions and therefore has value as an economic species (Woziwoda et al. 2014) that has over the last decades also developed a market for higher valued products of the timber beyond fire or pulpwood.

Managing invasive species means comprehensive risk management.

Dealing with introduced species requires a classical approach of risk management (Haimes 2004) that should take into account not only potential impacts and the likelihood that they occur (risk assessment and evaluation), but also potential trade-offs of measures within the risk handling part that consider potential benefits and especially the attitude towards risk of different stakeholder groups and their views towards introduced species. These views strongly depend on: the environment of the stakeholders (urban vs. rural); the wealth of the involved societies (rich vs. poor) (Kull et al. 2011); the state of knowledge (lay public vs. experts) (Fischer et al. 2014); and particular interests (e.g. production of specific providing services such as honey or essential oils form introduced species) that these groups may have in the management – or indeed the non-management–of the species. Differing interests inevitably lead to conflicts that may occur within a process of managing introduced species and may lead to economically inefficient solutions if, for example, costly management programs are stopped before completion due to the resistance of interest groups (Dickie et al. 2014)

▶ *Even invasive species causing high management costs may provide ecosystem services.*

The question of whether a species is looked upon as 'invasive' and may have negative impacts or even necessitate management is controversial in many parts of the world. Schlaepfer et al. (2011) present examples where introduced species may provide habitat or even deliver food sources for rare species. Even tree of heaven (*Ailanthus altissima* (Mill.) Swingle), which is considered to be one of the most invasive species in Europe and strongly suppresses native tree species, contains a multitude of medically active substances in the leaves and the bark that may be used for a variety of medical purposes, e.g. some substances have shown inhibition of cancer cells (Sladonja et al. 2015). Turnbull (1999) reports that eucalypts (*Eucalyptus* spp.) delivers not only raw material for timber and pulp production, but also essential oils and honey that are used by rural communities in southern Europe. Even Australian acacias (*Acacia* spp.), looked upon as one of the most invasive group of tree species worldwide (Rejmánek and Richardson 2013), were deliberately introduced in Portugal to stabilise sand dunes (Marchante et al. 2010).

▶ *The risks related to invasive species can be considerable – the decision if and how to handle these risks needs careful investigation.*

On the other hand, the introduction of new species can be subject to significant risks that may in the end lead to high costs of management, and in the most extreme case, the necessity to eradicate the species (Pejchar and Mooney 2009). Gaertner et al. (2014) observed that introduced species may change the fire regime of native ecosystems. Both, fire frequency and severity can be higher in forests of newly introduced pine and acacia species, which may negatively affect ecosystem feedbacks (Le Maitre et al. 2011). Tree invasion in shrublands may increase the fire frequency, and invasion of grass into stands of non-native tree species may also change the fire regime and lead to increased fire frequencies and altered fire intensities compared with native plant communities (Gaertner et al. 2014). Invasive species such as acacias may build up massive seedbanks and thus suppress native plants, mainly after disturbances (Le Maitre et al. 2011). The biodiversity in red oak dominated forests in terms of abundance and diversity of plants was found to be lower than in native oak forests (Woziwoda et al. 2014). All these negative effects may lead to the decision that management of these species is necessary. The cost of this type of management has to be seen as an investment and requires the analysis of economic aspects such as the use of appropriate interest rates that take into account the preferences of future generations (Dickie et al. 2014). The decision concerning whether or not to manage an introduced species requires careful investigation. Types of invasive tree species based on their relative degree of impact on the environment and the benefits associated with their cultivation and utilisation that can be used as a guideline to management activities are defined by van Wilgen and Richardson (2014). Caplat et al. (2013) highlight the advantages of developing spatially explicit models for prioritising and allocating management efforts for invasive species, while Kaplan et al. (2013) propose a protocol for developing risk maps at national, landscape, and local scales to improve detection rates of invasive plant species.

There may be manifold beneficiaries of invasive species – these are often in rural or even poor communities.

An important aspect in the evaluation of introduced species is consideration of the beneficiaries from the ecosystem services of the trees, and of who would consequently suffer from management strategies aiming at reducing the occurrence of those species. Kull et al. (2011) use the example of Australian acacias to illustrate that it is often poor communities that take advantage of the acacia resource (either present in their landscape via plantation or invasion), and it is those communities that may be negatively affected by policies to eradicate acacia. Turnbull (1999) hypothesises that the conflicts that occur, for example, about the benefits and disadvantages of eucalypt plantations in India, are often between 'the poor and the very poor'. In Europe, these aspects may not be as pronounced as in developing countries; however, we have to acknowledge that in some parts of Europe, it is mostly rural communities that may benefit from introduced species and may not be willing to accept a reduction of the species area on a large scale.

Introduced species may offer an opportunity to mitigate the economic impacts of climate change.

A new aspect in the discussion of introduced species emerges when these species are analysed with the background of climate change. Hanewinkel et al. (2013) have shown that climate change may cause severe economic loss to European forestry due to the fact that currently productive but drought- and heat susceptible species like Norway spruce that is currently the most important species for the timber industry in large parts of central and northern Europe will be replaced by less productive species such as Mediterranean oaks (e.g. *Quercus pubescens* Wild. or *Quercus ilex* L.). They discuss the possibilities of mitigating this impact by using introduced species. Interestingly, in the United States there is, at least in parts of the scientific community dealing with economics, a completely different view on the aspect of climate change regarding potentially invasive species (Sohngen and Mendelsohn 1998, Shugart et al. 2003). In the United States, climate change is seen as an opportunity to introduce fast growing species that are adapted to warmer and drier conditions and suffer at the moment from cold temperatures and short vegetation times. The focus is mostly on fast growing pine species (see Table 20, column III).

The selection of new species to replace native species under climate change is a complex process that needs careful investigation considering their potential invasiveness.

In order to enhance the adaptation of European forests to climate change, tree species more suited to the expected new climate could indeed be introduced. Bolte et al. (2009) discuss the establishment of 'neo-native' forest species, including the use and intermixing of native and non-native tree species as well as non-local tree provenances in order to adapt forests better to future climate conditions. For some areas of southern Germany a pragmatic method to select introduced species against the background of climate change has been developed (Schmiedinger et al. 2009). Based on this investigation Schmiedinger et al. (2009) proposed a catalogue of prospective tree species recommended for growth tests under changing climatic conditions together with a list of tree species with an existing record of experiences for growing under drier and warmer conditions in Bavaria (southern Germany). Bolte et al. (2009) list non-native species that have proven to grow well under the more continental and drier climatic conditions in northeastern Germany and add a series of species that may be suitable if these conditions further change. Table 20 lists some of these introduced species. Long-term experience in planting and growing most of them in Europe is still limited. Some of the species, especially those of the category I, may be an alternative to the native species under changing climatic conditions in larger parts of western and central Europe. The species of category III may be future alternatives under climate change.

This approach is similar to the notion of managed relocation (Richardson et al. 2009) and, in order to be considered as an option, would have to be subjected to careful risk assessment concerning whether the species has the potential to become invasive. At least two of the species in Table 20 e.g. black cherry (*Prunus serotina* Ehrh.), black locust (*Robinia pseudoacacia* L.) are already known to be invasive outside their natural range.

Table 20: Non-native or potentially new species under climate change in Germany according to (a) Schmiedinger et al. (2009) in Bavaria (southern Germany) and (b) Bolte et al. (2009) in northeastern Germany.

I: Adapted species with well-investigated growth according to (a) and (b)	II: Not yet adapted species with some information on growth following (b)	III: New species recommended for growth tests following (a)
Abies grandis (a)	*Abies nordmanniana**	*Abies borisii-regis*
*Abies nordmanniana**	*Abies procera*	*Abies bornmuelleriana* [*A. nordmanniana* subsp. *equi-trojani*]
Acer saccharum (a)	*Chamaecyparis pisifera*	*Abies cephalonica*
Castanea sativa (a)	*Juglans nigra*	*Carya glabra*
Pseudotsuga menziesii (a,b)	*Picea sitchensis*	*Fagus orientalis*
Quercus rubra (a,b)	*Prunus serotina*	*Pinus echinata*
Robinia pseudoacacia (b)	*Tsuga heterophylla*	*Pinus peuce*
Thuja plicata (b)		*Pinus ponderosa*
		Pinus tabuliformis
		Pinus virginiana
		Quercus mongolica
		Tilia tomentosa

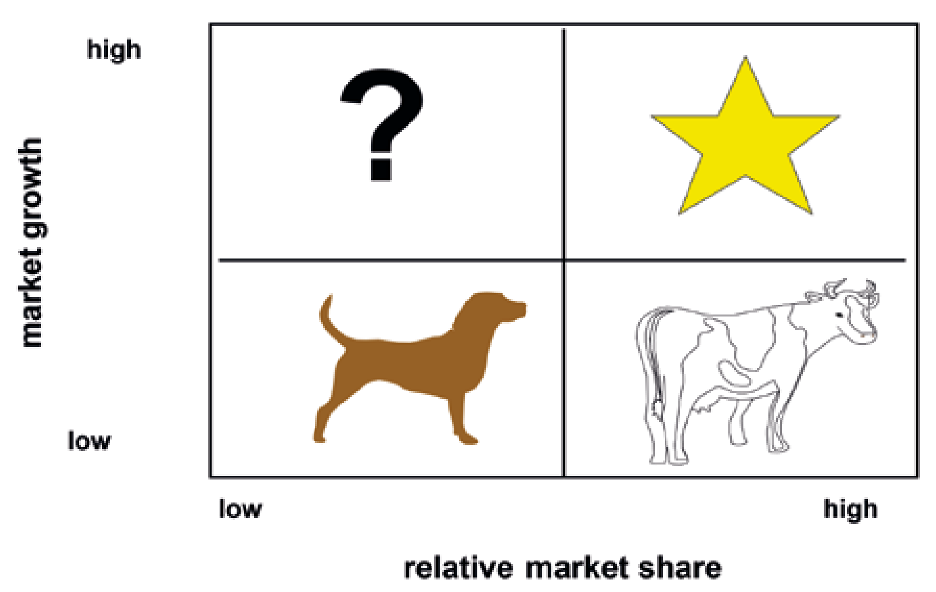
* *Abies nordmanniana* was placed in category I by Schmiedinger et al. (2009) and category II by Bolte et al. (2009)

In other European countries, the use of drought adapted species that have been imported from other countries may be a chance to adapt forests to future climatic conditions. After Morocco and Algeria, the country with the largest area of Atlantic cedar (*Cedrus atlantica* (Endl.) Manetti ex Carrière) forests is France with 20 000 ha (Bariteau et al. 2007). This species is particularly well adapted to dry and warm Mediterranean conditions and may, therefore, be a future option for other European countries expecting similar climatic conditions.

One distinct difference to the situation in the United States is that in Europe there are very few fast growing softwoods in southern areas, whereas in the United States the southern pines are a group of native fast growing softwoods (Sohngen 2009) that might become suitable for planting farther to the North of the continent under warming temperatures and changing precipitation regimes. The southern pines include loblolly pine (*P. taeda* L.), longleaf pine (*P. palustris* Mill.), shortleaf pine (*P. echinata* Mill.) and slash pine (*P. elliottii* Engelm.). The lack of fast growing softwood species in Europe is likely due to the Ice Age legacy with the Mediterranean Sea acting as a barrier that caused massive extinctions of the tertiary tree flora. In order to compensate for potential economics losses, new coniferous species that could replace the highly productive, but climate-sensitive, Norway spruce and silver fir (*Abies alba* Mill.) to balance negative effects on the timber markets would be needed, but are difficult to find even on a global scale.

> ▶ *Portfolio analysis is a way to analyse the potential of introduced tree species under changing environmental conditions from an economic point of view.*

Box 19: Example of a portfolio analysis – the product-market portfolio to derive norm-strategies for product placement and investment – from the Boston Consulting Group (after Oesten and Roeder 2012).



Portfolio analysis is a strategic management tool used to identify strategically important key factors. These factors are displayed in a two-dimensional matrix, one dimension being influenced by the business itself (in this diagram 'relative market share'), while the other dimension is determined by the environment ('market growth'). The different products of the business are then placed within the different sectors of the matrix that have specific denominations linked to norm-strategies. In this hypothetical example (the product-market portfolio of the Boston Consulting Group) products with a low market share and growth ('*dirty dogs*') are linked to a disinvestment-strategy aiming at actively reducing market shares, while those with high market share and growth ('*stars*') are actively promoted to increase the share. Products with high market shares in low growth conditions ('*cash cows*') will be treated along a strategy of maintaining the market share without big investments, while those in a specifically uncertain environment (potentially high growth with low market shares '*question marks*') will be handled as increasing investments with careful market observation.

Portfolio analysis needs to take into account the economic potential as well as potential conflicts related to invasive species.

Managing introduced new species under changing environmental conditions is an example of complex, long-term decision making under high uncertainty that should be treated within strategic management. In business economics, one approach that is often applied in this domain is – beside scenario development – the portfolio analysis (for a brief explanation see Box 19). The two dimensions used in the matrix when conducting a portfolio analysis of introduced species (Figure 53) are on the one hand, the potential negative impacts (van Wilgen and Richardson 2014), but at the same time the conflict potential that is related to the perception of different stakeholder groups. These impacts and conflict potentials (y-axis) should not only look at the possible management costs of reducing invasive species, but also the reduced benefits that may be linked to such a reduction. On the x-axis of Figure 53, the economic potential of the introduced species has to be taken into account. Assessment of the economic potential should include all ecosystem goods and services delivered by introduced species and should refer to all stakeholder groups having an interest in these services.

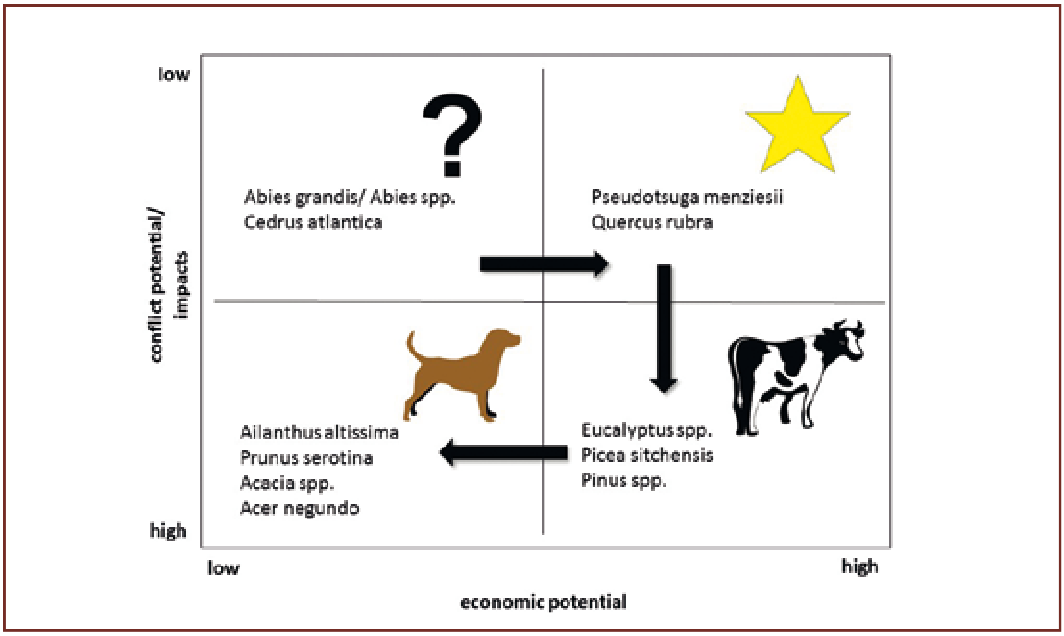


Figure 53. Portfolio analysis of introduced tree species considering their economic potential (x-axis), and the conflict potential/negative economic impacts (e.g. necessity for costly management interventions y-axis) under changing climatic conditions here, mostly from a central European perspective. Tree species in the different sections of the graph (for the meaning of those see Box 19, related norm strategies are discussed in the text) are meant as examples from different parts of Europe and are not exhaustive. Arrows in the graph point at the potential development of the different species over time: Sitka spruce (*Picea sitchensis* (Bong.) Carr.) may lose economic potential while cedars (*Cedrus* spp.) may be more important under dryer and warmer conditions and the conflict potential of red oak may increase with increasing influence of nature conservation groups.

> *The portfolio analysis of invasive species has to look into the future and take into account regional conditions when developing norm strategies how to deal with the species.*

The portfolio analysis has to be dynamic (depicted by the arrows in Figure 53) i.e. it has to reflect changing environmental as well as societal framework conditions and has to be designed according to regional circumstances (e.g. the bioclimatic conditions) in the different forest areas in Europe. It is of course impossible to conduct a single portfolio analysis for the whole of Europe. The tree species that are shown in Figure 53 are only examples from a specific perspective (in this case mostly a central European one) and from different areas in Europe. They are not exhaustive and can significantly vary across Europe. The norm-strategies that can be assigned to the different sectors of Figure 53 have to be explicitly adapted to these regional circumstances. The sector with high conflict potential/impact and low economic potential of the introduced species (lower left sector in Figure 53 '*dirty dogs*' Box 19) is where management activities reduce or even eradicate the species. The species that is mostly named in many areas in Europe is the tree of heaven, but black cherry, ash-leaved maple (*Acer negundo* L.) (Vor et al. 2015), and in southern Europe, Australian acacias have a large invasive potential. The lower right sector of Figure 23 ('*cash cows*') is probably the one with the highest conflict potential. Here we find highly productive species such as Sitka spruce (*Picea sitchensis* (Bong.) Carr) in the British Isles, eucalypts (*Eucalyptus* spp.) in Portugal and Spain, and productive pines (*Pinus* spp.) (Table 20) that have partly been introduced in the Mediterranean, though not to the same extent as, for example, Monterey pine (*Pinus radiata* D. Don) in New Zealand and South America. Essl et al. (2010) have shown that these non-native conifers are more likely to escape from cultivation, become naturalised and turn into invasive weeds on the continents of the Southern Hemisphere. These species have mainly been planted to produce timber and fibre and contribute to a large degree to the economic output of private and public forest enterprises. A significant reduction of the area of these species would therefore cause considerable economic losses. On the other hand, an increase of the area of these species to other areas in Europe would for many stakeholder groups not be acceptable, especially in an environment where a multifunctional, integrative forest management approach is the guideline. Therefore, a strategy for these species would be not to expand the area on a large scale but to manage them on the existing area and – in the long term – to adapt the management of these species to accepted silvicultural schemes or to integrate native species. There has been an increase in interest in transforming uniform even-aged plantations into irregular, uneven-aged forests; examples of such transformations were discussed at a IUFRO conference in 1999 (Cameron et al. 2001). On the other hand, a drier and warmer regime will not favour tree species, such as Sitka spruce, that have evolved and are adapted to very humid conditions.

> *There highest uncertainties within the portfolio analysis are related to the most productive species and to those with the highest conflict potential.*

The highest uncertainty in the portfolio matrix is related to the upper left section '*question marks*'. Many of the tree species listed in Table 20 (e.g. *Abies* spp. would be classified here) but also *Cedrus* spp. belong to this category. This is also the part where we have the greatest regional differences in Europe. For example, a species like Douglas fir that has a long tradition and is widely planted in central Europe is still a '*question mark*' in many other parts of Europe (e.g. in Scandinavia). The economic importance of these '*question marks*' may increase in the future. A strategy for these species would be to intensify research in the form of long-term species trials including a variety of provenances to reduce the uncertainty related to growth and vulnerability.

Finally, there are species in the upper right section of the portfolio ('*stars*') that are linked to high hopes when it comes to adaptation to climate change and economic performance. Douglas fir is certainly a species that would fall into that category in some areas in Europe, though there is a conflict potential related to the species mostly regarding biodiversity (Schmid et al. 2013). Red oak may be another example but with an even greater conflict potential that may increase in the future due to the observed negative impacts on biodiversity and the dominance in the regeneration compared to e.g. native oaks (Woziwoda et al. 2014). A strategy for these species could be to integrate them in mixtures with native species and to manage them in a long-term, uneven-aged silvicultural system to simultaneously reduce their assumed negative impacts and benefit from their economic performance. A successful example for Douglas fir is discussed by Schütz and Pommerening (2013). Under these conditions, an expansion of the area of these species (a typical strategy for '*stars*' in a standard portfolio analysis) taking into account the given limits of existing certification schemes is justifiable.

Conclusions – economic aspects of invasive species as a complex problem

When looking at introduced species from an economic point of view, we have to take into account the perceptions and values of all ecosystem goods and services through the eyes of different user-groups. A decision to manage any species with the goal of reducing its area – or perhaps even to eradicate it – can incur very high costs. Such a decision has to be very carefully evaluated and has to take into account all involved stakeholder groups and the potential benefits that the different stakeholders actually have or expect from these species. Failing to do so may lead to an economically inefficient solution, e.g. when expensive programs to control introduced invasive have to be stopped before completion. In some areas in Europe, the introduction of new species may be seen as an opportunity to compensate for the economic impacts of climate change. Here, productive species – such as Norway spruce – that are particularly suffering from climate change may be replaced by new species such as Douglas fir. As a general framework to evaluate introduced species from an economic point of view under changing environmental conditions we propose a portfolio analysis considering the potential impacts and conflicts on one hand, and the economic impact including all ecosystem services, on the other hand. Such a portfolio analysis has to take into account potential future developments regarding the different species, the perception of stakeholders and the related uncertainties.

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4.2 Importance of species competition and migration limitation for tree distributions during global change

Eliane S. Meier and Niklaus E. Zimmermann

Ongoing climate change, land use change, and biological invasion may dramatically alter large-scale species distributions in the near future; understanding interactions of these key impacts is of major importance when predicting the potential distribution of species under global change.

Geographical ranges of plant species may change more noticeably only over longer time periods; this is mainly due to plant species being stationary during their whole life cycle with their dispersion being bound to reproduction, although wind, water, animals or humans may enhance their dispersal (Nathan and Muller-Landau 2000). Consequently, the current ranges of species with long life cycles have emerged over long periods of time. For instance, the ranges of most European trees started to take shape after the late glacial maximum when the climate in the northern hemisphere began to warm up and deglaciation was initiated (e.g. Tinner and Lotter 2006; see chapter 1.1). Because the climate during the Holocene was relatively stable, it is expected that current ranges are a result of the adaptation of species to the present environment, despite potentially low migration rates (Kullman and Kjallgren 2000).

Today, global change is assumed to rapidly alter large-scale plant species distributions (e.g. Parmesan and Yohe 2003) and many species have to adjust their ranges at a rate equal to the shifting climate in order to track suitable environmental conditions (Parmesan et al. 1999). However, if a species is highly limited in its ability to migrate, then it must either rapidly adapt to the new environmental conditions in their current habitat (Pearman et al. 2008), or it will go locally extinct (Channell and Lomolino 2000). On the other hand, and as a side effect of increased international trade during globalisation, humans introduced species into areas they would otherwise have been unlikely to have reached by natural dispersal alone. Following such intentional introductions, species often start spreading (Mack et al. 2000). Thus, research on the key drivers of species distributions at large spatial scales is not only useful in enhancing our understanding of ecological concepts, but it is also important for improving species management strategies, especially in light of rapid global change.

Drivers of species distributions may operate at different spatial scales.

In order to better understand how quickly species can migrate to certain areas during global change, we have to broaden our understanding of the most important drivers of species distributions. Based on our current understanding, the known drivers operate at different spatial scales and with different magnitudes, although they may, in some cases, act in an interrelated fashion. At the continental scale, gradual trends in macroclimate are hypothesised to be the key factors shaping species ranges, while at regional scales, topography and climatic extremes may play a key role for species distributions. At local scales, biotic interactions, soil or land use may be among the most important factors explaining species distributions (Pearson and Dawson 2003).

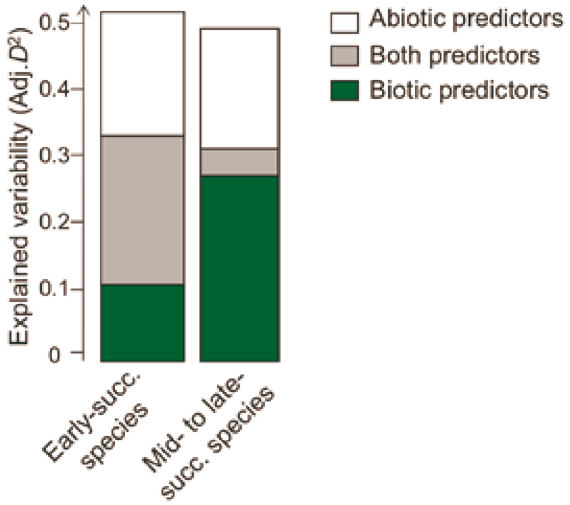

Figure 54. Partial explained variability (adj.D2) by the biotic predictors, the abiotic predictors and both predictors for early and mid- to late successional species.

During Holocene, species range shifts of up to 100 km per century were observed (e.g. Cheddadi et al. 2013); range shifts of similar magnitude are also anticipated under current climate change scenarios (Prentice et al. 1992). However, such range shift projections are expected to be flawed because additional drivers have emerged, and the known drivers that act on different hierarchical levels may be interrelated to some degree. First, compared to Holocene, current forest fragmentation and human interventions may impair natural migration. Second, for instance, biotic interactions like interspecific competition among tree species may limit species ranges if macro-climatic conditions are less severe (Maestre et al. 2009). Further, the importance of these different drivers may be specific to the ecology of individual tree species, i.e. the relative importance of drivers may depend on the physiological tolerances, competitive ability or dispersal ability of particular species. As a consequence, key drivers may be similar for species that are characterised by similar traits (Lavorel and Garnier 2002).

▶ *Species interactions and environmental factors are both important for large-scale species distributions.*

Analogous to the high level of invasiveness experienced by some introduced tree species after being released from natural enemies in their introduced environments (Stohlgren and Schnase 2006), the abundance of native tree species also depends on the importance of biotic interactions. The scale at which biotic interactions become important determinants of large-scale species distributions and the variability in the importance of these biotic interactions for large-scale species distributions was for a long time largely unclear (Araújo and Guisan 2006).

Yet, it was revealed, that biotic variables, which are often said to only affect local species distributions, also affect large-scale species ranges by adding important local information on biotic interactions and other small-scale processes (Meier et al. 2010). Among 11 investigated tree species in Switzerland, biotic variables (i.e. relative abundance, relative abundance of large individuals and total shading by larger individuals of co-occurring species) and abiotic variables (i.e. degree-days with a 5.56 °C temperature threshold, summer frost frequency, moisture index from March to August, precipitation days, potential yearly global radiation, topographic position and slope) contributed equally and mostly independently from each other torward explaining spatial range patterns (Figure 54). When addressing groups of species with similar traits, it was shown that biotic predictors helped to explain the distribution of mid- to late-successional tree species more than of early-successional tree species (Figure 54). Mid- to late-successional species, by definition, replace early successional species, which do not grow well when there is competition.

These results indicate that the implicit inclusion of biotic interactions is insufficient when using species occurrence data to predict large-scale species patterns with the help of empirical species distribution models (SDMs; Guisan and Zimmermann 2000), although such data inherently depict the realised niche (i.e. the area where species can be observed in nature as a result of abiotic factors and biotic interactions; Hutchinson 1957). In order to depict the realised niche more accurately, it is essential to include biotic predictors, such as the relative abundance of the most important competitor species into SDMs. However, it should be noted that the general extent of pan-European ranges of trees did not dramatically change when including biotic predictors (see Meier et al. 2011). Most variation explained by biotic predictors occurred at smaller spatial scales by modifying predictions within species ranges. In any case, models developed to include both biotic and abiotic predictors were more accurate and showed somewhat constrained spatial domains, implying that the inclusion of biotic predictors also affected range shapes.

▶ *The strength of biotic interactions increases towards favourable growing conditions, which leads to strong effects on species distributions in the south of Europe and at low elevations.*

According to the stress-gradient hypothesis, stronger competitive replacement of species is expected under physiologically favourable conditions than under physiologically stressful conditions (e.g. Bertness and Callaway 1994) (Figure 55). Until now, empirical quantifications of the variation in the strength of interspecific competition along large-scale climate gradients has been largely missing (Gaston 2009). The same is true for the potential effect of this variation on current and future species ranges, for both native as well as introduced species.

Meier et al. (2011) demonstrated that the strength of biotic interactions not only varies between species of differing traits (Meier et al. 2010), but also along environmental gradients. In line with the stress-gradient hypothesis, the abundance of European beech (*Fagus sylvatica* L.) in Europe was strongly linked to the abundance of its three major competitor species, i.e. Norway spruce (*Picea abies* (L.) H. Karst.), Scots pine (*Pinus sylvestris* L.) and pedunculate oak (*Quercus robur* L.), under abiotically favourable growing conditions (i.e. moderately warm and moist climate). However, this link became weaker towards conditions of high physiological stress (i.e. cold and/or dry climate). In geographical terms, this led to the strongest biotic interactions occurring at low elevations and in southern parts of central Europe, and thus to strong reductions in the predicted spatial distribution of European beech when biotic predictors (i.e. the relative abundance of the three competitor species) were explicitly included in SDMs. We conclude that the explicit inclusion of biotic predictors assists reducing the uncertainties when projecting large-scale SDMs to current or future climate, especially under favourable growing conditions. Moreover, knowledge on climatic conditions under which competition is strong may improve species management strategies; e.g. one can reduce competitors in order to enhance the occurrence of endangered species.

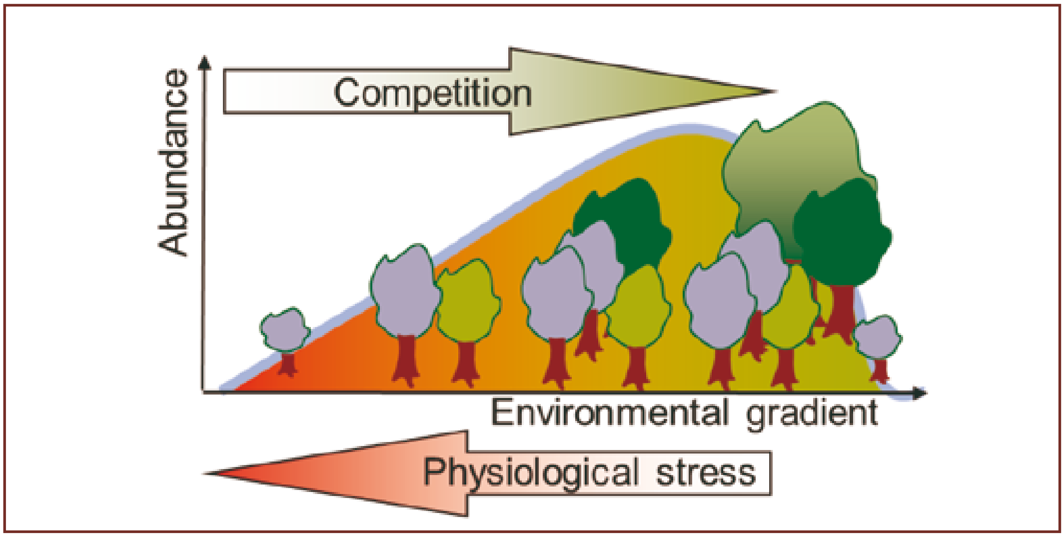

Figure 55. Under adverse climate conditions, species abundances are mainly limited by climate, i.e. for trees in Europe cold and dry conditions, while under favourable climate conditions, competition limits species distributions (abundance of an exemplary species along an environmental gradient is coloured in lilac).

However, the above mentioned findings also have certain limitations. First, it is hard to distinguish between cause and effect when using observational data alone and thus to determine which tree species outcompetes or facilitates other species. This means that the direction of biotic effects cannot easily be retrieved from observational presence/absence data alone. Second, we assumed shifts of species distributions to be unlimited under future climate when projecting future species patterns under the inclusion of biotic interactions. Meier et al. (2012) demonstrated that this is only a realistic scenario for early successional species, and not for mid- and late-successional species. Early successional species are by definition good colonisers of new environments, and therefore many invasive species are early successional species. To improve the resolution of these issues, it may be important to test the competitive abilities of individual tree species under different climate conditions as well as the implementation of more realistic migration rates for range shift projections.

Migration characteristics will determine the ability of species to track suitable habitats during climate and land-use change.

The importance of dispersal limitation for a species' distribution becomes apparent when focusing on species that are introduced by humans into areas that they never would have reached by natural dispersal alone, but from where they consequently start spreading rapidly (Welk 2004), such as the invasive tree of heaven (*Ailanthus altissima* (Mill.) Swingle), see chapter 5.7 and 5.10 for details). Dispersal limitations that impede such invasion of (temporally) non-colonised and suitable habitats may depend on the following:

- *The magnitude of a historical event* causing disequilibria is defined by the degree and frequency of the disturbance (Delcourt and Delcourt 1988); since spatially and temporally small-scale disturbances (e.g. fire) and spatially and temporally large-scale disturbances (e.g. climate change) may generate different legacies. Severe historical incidents, coupled with current occurrences, such as habitat fragmentation due to unsuitable land-use types, might be responsible for the currently debated range filling limitations of European plants (e.g. Svenning and Skov 2004).
- *Species traits* such as dispersal agents (e.g. wind, water, animals, humans, or none at all) or traits that help to differentiate between early- and mid- to late-successional species, may also determine the degree of migration limitation and, hence, the degree to which species distributions are not in equilibrium with their environment (Buckley 2008). For instance, early-successional species show longer seed dispersal distances than mid- to late- successional species. Thereby, mid-to late successional species may be more migration limited by habitat fragmentation, which is a growing issue in the highly managed European landscapes. Early-successional tree species, including most of the invasive species, may be less migration limited by habitat fragmentation, and thereby, may colonise many vacant habitats during climate and land-use change. Later in the successional sequence, the competitive ability of early successional species is generally lower.
- According to the stress-gradient hypothesis, biotic constraints such as out-competition vary as a function of environmental gradients (Bertness and Callaway 1994) and thus, depending on the *degree of species' interactions* and on the abiotic severity of the habitats through which species migrate, species may be more or less constrained in tracking the fluctuations in environmental conditions according to the traits they have.
- *Spatial patterns of suitable habitats* may also impede species from tracking a changing climate. According to the percolation theory (Turner 1989, Stauffer and Aharony 1994), patches of different sizes, shape and connectivity may impede plant migration through the landscape with different intensities until a percolation value (i.e. percolation threshold) is reached and species are no longer able to migrate. Furthermore, the spatial arrangement of populations may also influence the spread of a species; core populations may be the principal sources of propagules (Hulme 2003) and, hence, largely contributing to long distance dispersal, while small outlying populations have a large edge to area ratio. Therefore, this may contribute to their increased expansion within certain habitats (e.g. Moody and Mack 1988).

> *Early-successional tree species migrate substantially faster than mid- and late-successional species due to early-successional species having rapid growth rates, producing large amounts of seed able to travel longer distances; many invasive tree species possess such traits.*

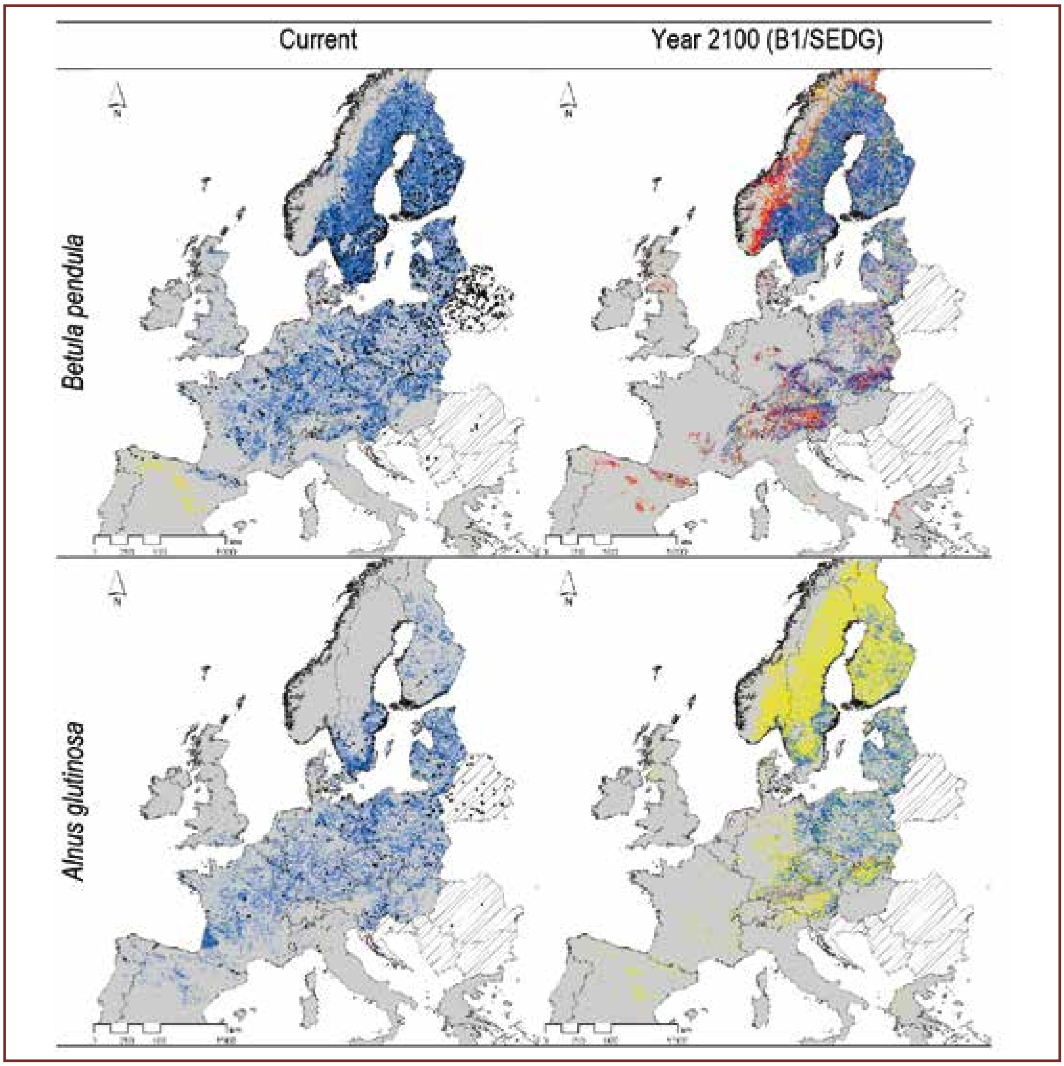

Figure 56. Predicted distributions of an example early- (silver birch, *Betula pendula* Roth) and late-successional (common alder, *Alnus glutinosa* (L.) Gaertn.) species for current climate and 2100 (B1/SEDG climate and land-use scenarios) for a no migration scenario (top layer, blue), a realistic migration scenario (middle layer, red) and an unlimited migration scenario (bottom layer, yellow). Current observations from ICP Forest Level 1 are represented by black dots. To generate maps that most accurately represent the current range of the tree species, the predictions of current species distributions (yellow) were constricted to species occurrences within the 50 x 50 km^2 quadrats from the Atlas Flora Europaeae (Jalas and Suominen, 1972–1996) (blue). The no-migration scenarios of 2100 are the overlap between the predicted current and future distributions.

Projecting the adjustment of species ranges to (more) realistic changing environmental conditions requires the implementation of migration processes at large scales, for which no standard approach currently exists. Therefore, dispersal limitation is one of the main sources of uncertainty when projecting species distributions under a changing climate (Araújo and Guisan 2006). Meier et al. (2012) developed a framework, which can be used to analyse the migration limitations for the most important tree species across Europe. It was showed that interspecific competition, which is higher under favourable growing conditions for a given species (Meier et al. 2011), reduced the range shift speed more in comparison to the unfavourable macro-climatic conditions (i.e. very cold or dry climate). Additionally, the results clearly indicated that habitat fragmentation slows down migration rates due to the presence of unsuitable land-use types. When applying these relationships to geographic space, early-successional tree species migrated about ten times faster than mid- to late-successional species. This is because early-successional species are generally characterised by rapid growth rates, and produce large amounts of seed that can be dispersed over longer distances compared to mid- and late-successional species. This causes mid- and late-successional species to migrate predominantly into previously colonised forest habitats where interspecific competition is higher. Their higher shade tolerance does not offset this disadvantage, resulting in their already lower migration rates to decrease yet further. Thus, under future scenarios of a changing climate, the early-successional species may have fewer constraints to migration and thus no time lags in the re-adjustment of ranges under climate and land-use change, while the mid- and late-successional species may disappear from areas that become unsuitable and largely fail to track suitable climates and will not be in equilibrium with their environment (Figure 56). For example, under a realistic migration scenario, common alder is expected to disappear from many parts of its native range (Figure 56).

The results from Meier et al. (2012) may help to improve the interpretation of range shift maps from SDMs (i.e. to assign a more realistic migration assumption for a given species), to better estimate extinction risks, to design reserve networks, and to plan assisted migration of ecologically or economically important species with strong migration limitations.

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Disturbed forest in the Carpathian mountains, south-western Poland. Wind-throw, bark-beetle attacks and fires are frequent disturbance types in mountain forest ecosystems. Such disturbance sequence inrease in number and severity due to climatic changes (photo: F. Krumm).

4.3 Introduced or native tree species to maintain forest ecosystem services in a hotter and drier future?

Andreas Rigling, Arthur Gessler, Linda Feichtinger, Valentin Queloz and Thomas Wohlgemuth

Climate change might profoundly alter patterns and processes in forest ecosystems that have consequences on the biogeochemical cycling, biodiversity and productivity (e.g. Lindner et al. 2014). Temperature- and drought-related changes have been identified as important triggers of forest decline and vegetation shifts worldwide (Allen et al. 2010). In Europe, several native tree species such as Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* (L.) H. Karst.) and European beech (*Fagus sylvatica* L.) are showing increased sensitivities to recent increases in temperature and extreme droughts resulting in growth reduction or increased mortality rates (Temperli et al. 2012, Rigling et al. 2013, Lebourgeois et al. 2010). It is predicted that there will be increases in the frequency and intensity of extreme precipitation events as well as in the occurrence of drought periods in the upcoming decades (IPCC 2014). In combination with increasing temperatures, so-called 'hotter droughts' are to be expected (Allen et al. 2015), which might play a key role in driving future forest dynamics by directly increasing drought-induced mortality or indirectly by reducing tree growth and vigour, impairing seedling establishment and increasing the susceptibility of trees to pests and diseases (Anderegg et al. 2015).

Such changes will challenge sustainable forest management practices that aim to provide the variety of ecosystem services in the future. An essential element of forest management is the selection of suitable tree species mixtures. On one hand, biodiversity (i.e. selection and complementarity effects, Loreau and Hector 2001) might improve the drought resistance of trees in more diverse forests (e.g. Van der Plas et al. 2016). On the other hand, future forest management and an adapted tree species portfolio should consider the future climatic conditions. As native tree species might suffer from a hotter and drier future climate in certain regions, the native species composition might be complemented by drought tolerant tree species of non-native origin (Lindner et al. 2014).

Introduced tree species have been planted and promoted in Europe since the late 19th century. They were originally selected and planted in the introduced range on the basis of their timber quality and productivity. In the future, however, introduced tree species with a potentially higher drought tolerance might become more relevant in terms of their ability to cope with the future climate change (Lindner et al. 2014).

An overview on the potential and limitations of 15 introduced tree species relevant for central Europe was recently published by Vor et al. (2015). In this chapter we focus on two of the introduced tree species mentioned in this publication, i.e. Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and black pine (*Pinus nigra* Arnold), which is non-native in most areas in western Europe (San-Miguel-Ayanz et al. 2016). Although climate change predictions for future performance of Douglas fir in western North America suggest significant drought-induced range shifts until 2090 (Weiskittel et al. 2012), Douglas fir and black pine are often discussed as potential non-native alternatives to the native, and economically and ecologically important, Norway spruce and Scots pine (Spellmann 2011, Kownatzki et al. 2011, Jansen et al. 2013, Lévesque et al. 2013; Moser et al. 2016). In addition, and not further included in this chapter, the following drought-tolerant species may be of considerable interest; e.g.:

- Eucalypts (*Eucalyptus* spp.) that are mainly planted in Spain and Portugal (Chapter 5.5);
- Black locust (*Robinia pseudoacacia* L.), which is planted as a pioneer species to improve soil fertility (Chapter 5.1);
- Tree of heaven (*Ailanthus altissima* (Mill.) Swingle) that starts invading some European forests originating from gardens and public green areas (Chapter 5.7);
- Other pines (*Pinus* spp.) (Chapter 5.8) and cypresses (*Cupressus* spp.).

> *The vulnerability of trees to drought varies amongst species due to intrinsic traits and shifts between life stages, in particular between the establishment and the old growth phase.*

Sensitivity against biotic and abiotic stress can considerably vary during a tree's life (e.g. Oliver and Larson 1996). Hence, when discussing the impacts of drought on forest ecosystems and defining species that can potentially substitute native species in our forests in future, it is crucial to distinguish amongst different age phases. However, how can we quantify the drought tolerance of tree species?

Many studies focus on the key processes such as mortality, growth limitations and regeneration success along time, tree age and various environmental gradients (e.g. Lévesque et al. 2014a). In particular, comparative measurements on drought tolerance in provenance trials (e.g. Eilmann et al. 2013) or multiple tree species experiments stands (e.g. Eilmann and Rigling 2012) are best suited to interpret the relative drought tolerance of species or provenances. Analyses should ideally combine different time windows such as decadal trend analysis with single and extreme year reactions (e.g. Lévesque et al. 2014a) and intra-annual responses (e.g. Lewis et al. 2001). In order to gain further understanding of the mechanisms behind observed growth reactions, a combined analysis of growth and physiological measurements, e.g. stable isotope analysis, water-use efficiency or cavitation are particularly valuable (e.g. Lévesque et al. 2014b). It is also important to try extrapolating the results from tree to stand and landscape scales and to cross-validate the experimental findings; in such cases, process-based modelling approaches are useful (e.g. Temperli et al. 2012).

Douglas fir seedlings can be vulnerable to dry conditions (Hermann and Lavender 2004), which may include factors such as frost droughts during winter (Anekonda et al. 2002, Kownatzki et al. 2011). In a pot experiment, the native Scots pine was found to be more drought-tolerant in its initial seedling growth phase than Douglas fir whose seedlings have slower root growth into deeper soil layers (Moser et al. 2016). Due to this slow lateral root growth, Douglas fir seedlings are delayed in reaching deeper water resources that do not tend to get depleted during droughts. Similar results were obtained in an experiment where saplings of eight different tree species were planted at three xeric sites in the Swiss Rhone Valley (Rigling et al. unpublished). The mortality highly varied among the different tree species, with Douglas fir showing the highest mortality rates from all tree species considered (Figure 57). In another experiment, introduced black pine seedlings from a Mediterranean seed source were found to be more drought tolerant in comparison to the native Scots pine seedlings from the central Alps; the black pine seedlings had a higher root-to-shoot ratio allowing a better exploitation of soil water resources (Richter et al. 2012).

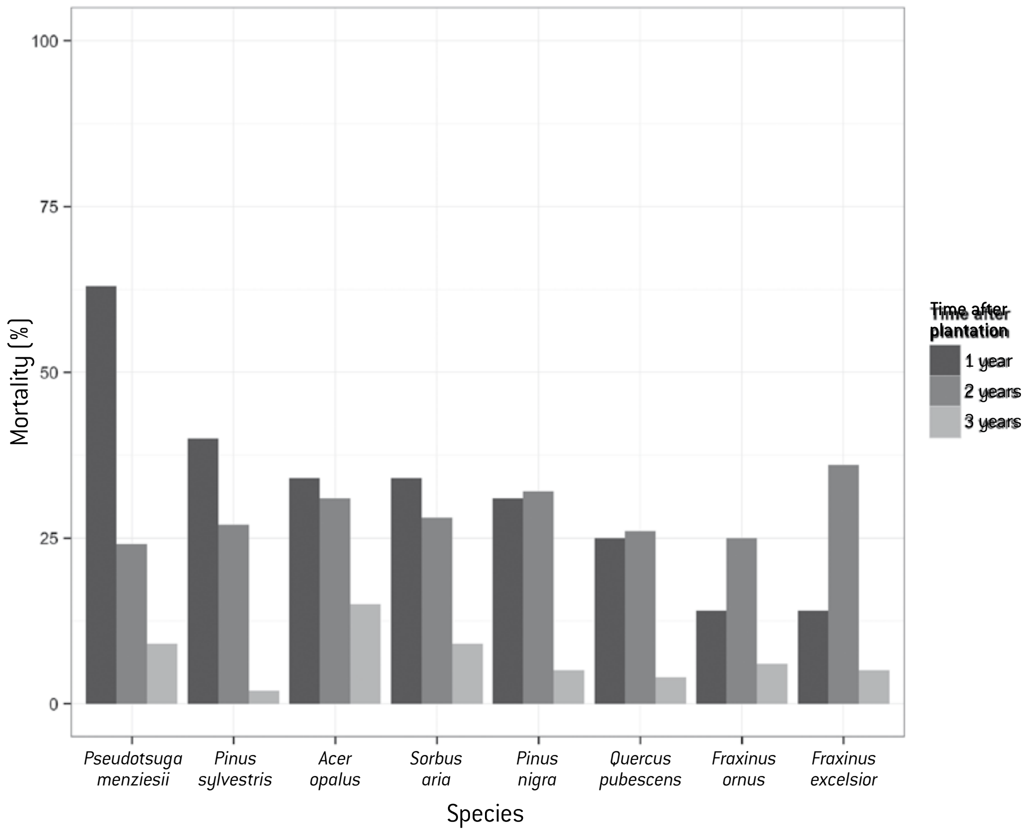

Figure 57. Tree species-specific survival and mortality considered at different temporal scales; i.e. one, two and three years after planting]. Mortality rates are mean percentages of the species planted at three different sites in the dry inner-Alpine Swiss Rhone valley.

Management aiming at increasing drought resistance of future forests needs to carefully consider tree species identity but also provenances.

There is also considerable variation between provenances within a species with regard to their drought tolerance. Introduced provenances originating from areas with dry summers and cool winters tend to be best adapted to warm and dry conditions in Europe, which was demonstrated, for instance, in a climate chamber experiment where Douglas fir seedlings from interior regions have been found to be best adapted to extended heat and drought periods (Jansen et al. 2014). Therefore, such provenances might be suitable for forestry in central Europe bearing in mind predicted warmer and drier conditions for the region. However, it should be kept in mind that Douglas fir interior provenances are more susceptible to certain fungal diseases (e.g. Rhabdocline needlecast – *Rhabdocline pseudotsugae* Syd. and Swiss needlecast – *Phaeocryptopus gaeumannii* (T. Rohde) Petr.) as opposed to coastal provenances from wetter regions (Hartmann et al. 2007). This trade-off illustrates the importance of provenance selection combined with careful site assessments.

High tree mortality rates were reported for many tree species and regions throughout Europe in the years that followed the extremely hot and dry year of 2003 (Carnicer et al. 2011), which, in the case of Douglas fir, resulted in a range of responses. In several regions in France, including the highly productive Bourgogne and Midi-Pyrénées, the growth of Douglas fir declined and greater tree mortality was observed; this was attributed to an extreme soil water deficit. The recovery after recurrent drought episodes was aggravated by soil nutrient deficiency (Sergent et al. 2014).

In addition, partial or complete needle necrosis during and after the heat wave in 2003 were observed in the area around the Massif Central in France (Martinez-Meier et al. 2008). Although surviving Douglas fir had significantly higher wood density in their stems and branches indicating a lower risk for cavitation than the dying trees, a high variability in wood properties and subsequent increased occurrence of cavitation amongst the different provenances and site conditions were observed. Hence, Dalla-Salda et al. (2009) concluded that Douglas fir seemed to be able to adjust to the extreme droughts and to recover during the following year, indicating a high adaptive potential of Douglas fir.

Douglas fir is highly sensitive to drought in the germination and the establishment phase but once installed this species is able to adjust to extreme drought events.

This is consistent with a study from a xeric environment on a steep south-facing slope with shallow soils in the inner-Alpine Swiss Rhone valley (Eilmann and Rigling 2012; Figure 58) where four different coniferous species – Scots pine, European larch (*Larix decidua* Mill.), black pine and Douglas fir – were planted in 1970. In order to enable seedling establishment in this very dry environment, the trees were irrigated during the first years after periods without rainfall. The analysis focused on the growth response during the four extremely dry years (including that of 2003) as well as during the recovery period that followed. Douglas fir and black pine showed no mortality, high growth rates and a plastic response to the extremely dry years. On the other hand, lower growth rates, a slow recovery after drought was observed for Scots pine and European larch. Mortality increased in Scots pine, and European larch experienced crown dieback. Such findings were confirmed by Lévesque et al. (2014a) who studied the tree growth responses of five conifer species in relation to past climatic variations and severe droughts across several climatic gradients of four biogeographic regions in central Europe, i.e. the northern Swiss Alps, the Swiss Plateau (Figure 59), the foothills of the Jura Mountains, and the dry central Alps (Figure 60). The radial growth of black pine and Douglas fir was less affected by climatic variability and drought than that of native Norway spruce, European larch and Scots pine. black pine and Douglas fir were able to maintain high radial increments and only few tree ring chronologies responded significantly to temperature, precipitation and soil moisture along the gradient. Black pine and Douglas fir follow a drought avoidance strategy and maintain effective stomatal control to reduce transpirational water loss during drought, which helps them maximise their carbon uptake when soil moisture conditions are favourable (Lassoie and Salo 1981, Lebourgeois et al. 1998). Hence, mature black pine and Douglas fir are able to maintain a positive carbon balance under dry conditions making them less sensitive to drought. Growth reductions in black pine and Douglas fir during extremely dry years were rare and occurred only at the driest sites located in the valleys in the central Alps (Figure 60). However, both species were able to recover to or even exceed their pre-drought growth levels in the year following the events, indicating their high ability to offset drought-induced growth declines (Lévesque et al. 2013).

Figure 58. Afforestation experiment summarised by Eilmann and Rigling (2012) where Scots pine, European larch, black pine and Douglas fir were planted in a dry environment near Gampel in the dry inner-Alpine Swiss Rhone valley (photo: A. Rigling).

These results agree with those of a modelling study from the Black Forest in Germany where a process-based model (LandClim) was applied to simulate forest dynamics and the provision of ecosystem services under a range of climate change and management scenarios (Temperli et al. 2012). Among them, the introduction of Douglas fir was tested as an applied management scenarios. Results indicated a high future risk of drought-induced dieback in Norway spruce forests, which is why large-scale conversions to more drought-adapted forest types, where Douglas fir is admixed, were recommended.

There are, however, differences between Douglas fir provenances with regard to sensitivity to extreme droughts and a trade-off between long-term growth performance under 'average' conditions and the response of a given provenance to extreme events (Jansen et al. 2013). Nonetheless, the promotion of Douglas fir has been discussed as an option for achieving high timber yields under hotter and drier climate conditions.

Figure 59. High productive mixed stand with Douglas fir and European beech in the Swiss lowlands near Stein am Rhein where the average height of Douglas fir is 40 m (photo: A. Rigling).

> *When substituting native with introduced tree species, large-scale monocultures should be avoided and mixed as well as uneven-aged stands that are less sensitive to pests and diseases should be promoted.*

Introduced tree species can certainly be considered as interesting alternatives when native tree species show high vulnerability to drought. However, due to the persisting uncertainties with regards to the effects that introduced tree species may have in new environments and ecosystems, the first choice should always be to use native tree species. On the other hand, recent experience with introduced diseases and pests such as the ash die-back (caused by *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz & Hosoya) or the emerald ash borer (*Agrilus planipennis* Fairmaire) demonstrate that native, well adapted tree species, may face sudden existential problems (Orlova-Bienkowskajy 2014, Gross et al. 2014; see Text Box 20 on ash dieback). When we conclude substituting native tree species, large-scale monocultures should be avoided and mixed and uneven-aged stands that are less sensitive to pests and diseases should be promoted.

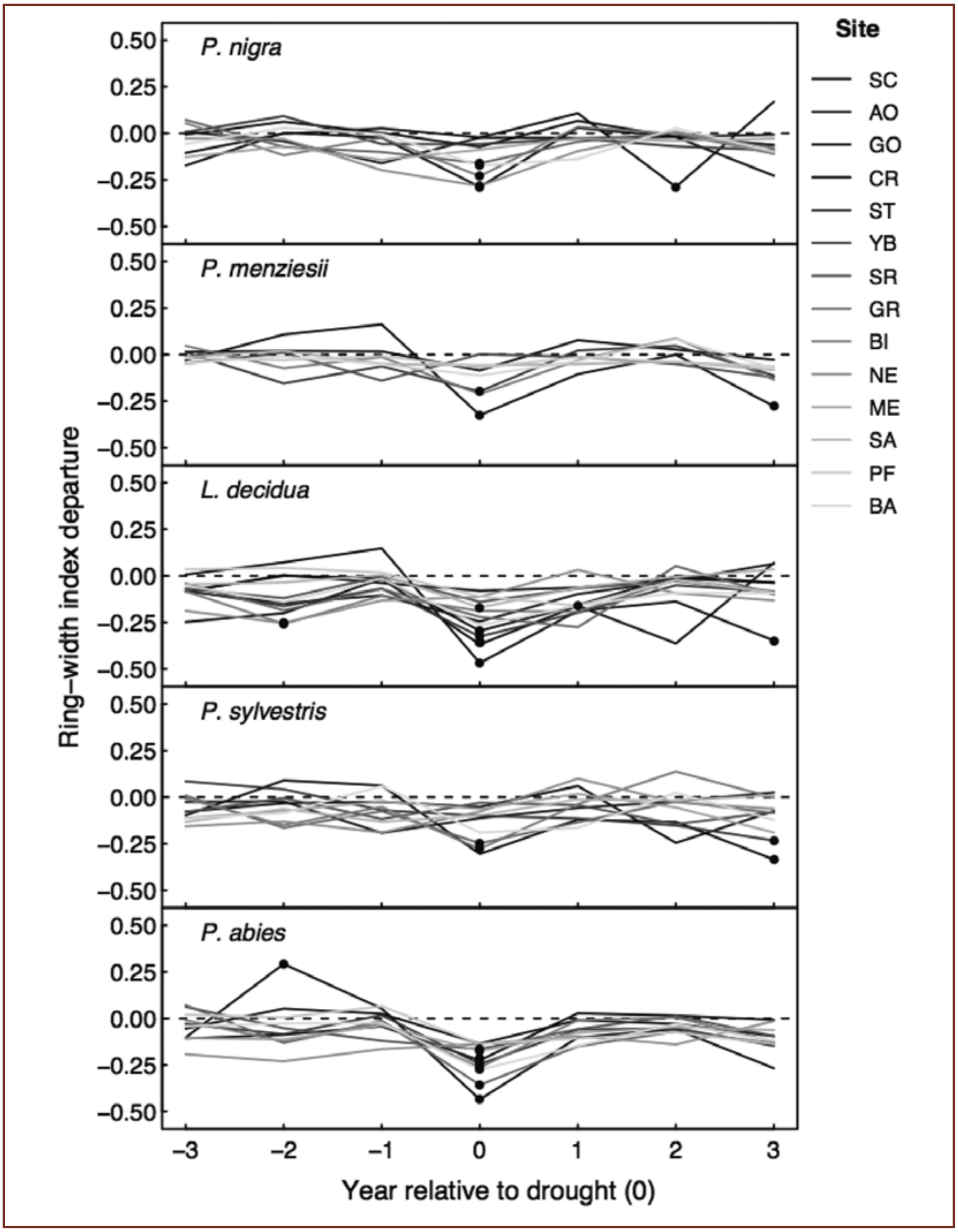

Figure 60. Superposed Epoch Analysis showing negative and positive tree growth departures (standard chronologies with autocorrelation retained) for the drought year (0) and 3 years before and after the drought year. Black dots indicate significant ($P \leq 0.05$) growth departures from 1000 random simulations. Extreme dry years correspond to the three driest years with the lowest soil moisture and the extreme drought year 2003 (Lévesque et al. 2014a, adapted).

▶ *In order to prepare current forests to future hotter and drier conditions, trade-offs between lowered productivity but increased drought resistance need to be considered.*

Another important aspect to be considered are the trade-offs between productivity and drought resistance; Montwé et al. (2015) for instance concluded that selecting drought-resilient provenances as an adaptation strategy for climate change could compromise timber productivity. This philosophy has already been practiced in some protection forests where the forest stands are managed to retain or enhance their stability with productivity being a secondary aim. Nevertheless, if such ideas are to be applied to forests where timber production is the primary management aim, optimising forest management towards improved drought resistance (and less so for timber production) would therefore be a complete change of priorities.

It is important to focus on alternative species that are drought-resistant in order to facilitate the adaptation of our forests to predicted future climatic changes. However, it is crucial to note that both direct as well as indirect effects of heat and drought stress on tree performance are to be considered; biotic stresses and their interactions with abiotic constraints as well as the overall sensitivity of tree species to pests and diseases also need to be born in mind (San-Miguel-Ayanz et al. 2016). The aim in such cases should thus be to minimise ecosystem vulnerability and to optimise the provision of all ecosystem services (Lindner et al. 2014).

▶ *New pests or diseases have the potential to rapidly and fundamentally alter the performance of any tree species, be the tree species native or introduced.*

Box 20. Ash dieback – an example of a new fast spreading pathogen putting a native tree species at risk.

Ash (*Fraxinus* spp.) trees in Europe are threatened by a new fungal disease. This phenomenon is called 'ash die-back' and caused by the pathogen *Hymenoscyphus fraxineus*. The first declining ash trees were reported in north-east Poland in 1992. After that the disease spread rapidly through airborne spores; by 2016, after only two decades, the pathogen had been recorded in much of the range of common ash (*Fraxinus excelsior* L.) – this demonstrates the susceptibility of tree species to new pests or diseases, be the tree species native or introduced. However, the pathogen threatens not only common ash but also other European ash species (e.g. narrow-leaved ash – *F. angustifolia* Vahl; manna ash – *F. ornus* L.) and North American ash species (e.g. green ash – *F. pennsylvanica* Marshall; black ash – *F. nigra* Marshall). In contrast, Asian ash species like Manchurian ash (*F. mandshurica* Rupr.) and Chinese ash (*F. chinensis* Roxb.) are resistant to the disease confirming the origin of the pathogen in east Asia. More than 90 % of common ash trees in Europe suffer from ash dieback while 10 % of the trees seem to be tolerant or resistant. However, the emerald ash borer (*Agrilus planipennis*) has been spreading around Moscow recently and also threatens common ash (Orlova-Bienkovskaja 2014). Asian ash species seem to be quite tolerant to this pest and could be a potential replacement species for common ash in Europe.

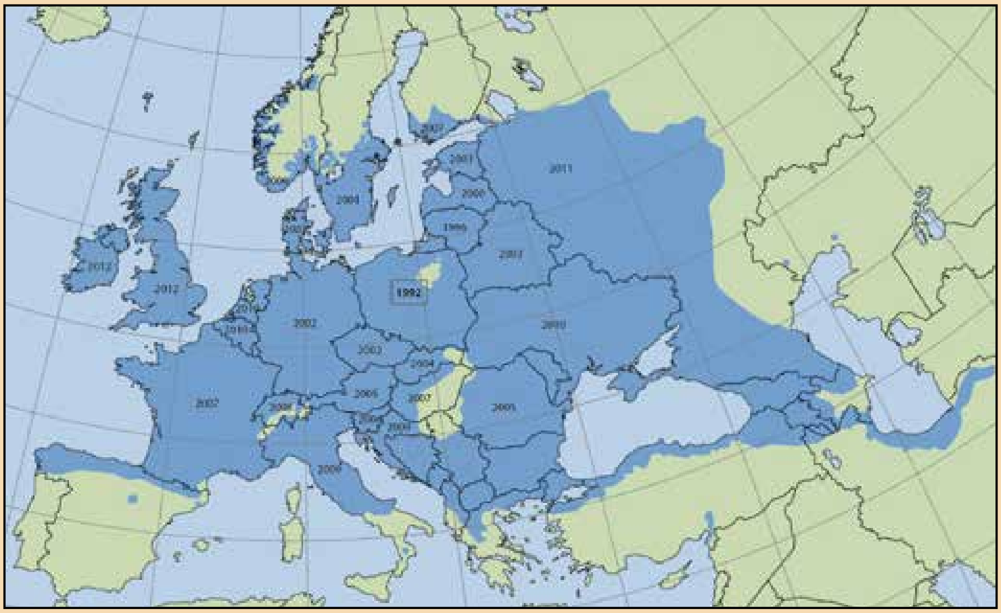

Figure 61. Map representing the natural range of common ash (blue) and the first record of ash dieback in the different European countries. Modified from EUFORGEN (2009) and Gross et al. (2014).

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4.4 Pathogens of introduced trees: prospects for biological control

Steve Woodward, Alberto Santini and Tuğba Doğmuş

Diseases affecting invasive tree species are widespread and some are well-known. To date, however, pathogens have been little used in attempts to control spread of these trees. In this short review, a list of selected introduced tree species is used to demonstrate the pathogens that attack these plants both within and outside their native ranges. The focus is on tree species that are of introduced origin and are invasive in certain parts of Europe, including ash-leaved maple (*Acer negundo* L.), tree of heaven (*Ailanthus altimissima* (Mill.) Swingle), eucalypts (*Eucalyptus* spp.), black cherry (*Prunus serotina* Ehrh.), red oak (*Quercus rubra* L.), Siberian elm (*Ulmus pumila* L.), Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.). A range of specific and non-specific diseases for each species is reviewed with a view to assessing the use of these organisms in control and management of problematic tree species. Caution must be applied, however, as many pathogens are not host specific; moreover, predicting the behaviour of pathogens introduced from the native areas where the trees evolved is very difficult.

Humans have moved plants from their centres of origin to other regions in the world during migrations at least since the dawn of agriculture, some 12 000 to 15 000 years ago. In the majority of instances, the tree species which survived these translocations became valued components in the new environments to which they were added. In a minority of cases, however, introduced trees were so well adapted to conditions in the new environments they reproduced freely, and became problems in themselves. In the last 500 years, humans have decreased journey times markedly, with a consequence that the rate at which plants can be moved, even intercontinentally, allows survival of more plant species (or plant propagules). Many introduced tree species are now grown widely, and some of them have become problematic and invasive.

An important factor in the success of many invasive plants (and other organisms), is that escape into the wider environment in a region where the organism has not existed to date releases it from the biotic constraints which may have impacted on vigour, survival and reproduction in the region where the organism evolved. These checks and balances to growth are due to the presence in the native ranges of invasive trees of pests, pathogens and other competitors that reduce vigour.

> *Pathogens can limit the ability of a tree to grow and reproduce. Where pathogen constraints are removed, the tree may become invasive.*

Trees are subjected to a wide range of biotic problems that can reduce vigour and reproduction and, in some instances, kill the affected hosts. Some disease-causing agents may result in mortality of the infected hosts; most, however, are debilitating to some extent, but do not lead directly to tree death.

Diseases have rarely been used to control and manage introduced and invasive plants (Van Driesche et al. 2009). Clearly, the ideal candidate pathogens for controlling an invasive tree species would be those, which are highly specific to that plant species do not affect any other plants within the invaded area where the control is desired, and significantly reduces fecundity or kills the plant before reproduction. In preference, a pathogen that is native to the region where the tree is causing problems should be used. These requirements are generally very difficult to achieve in full, although some diseases are recognised that attain these needs for herbaceous plant species.

The use of pathogens or pests organisms (bioherbicides) in the management and control of trees and other woody species is not a new idea. For example, invasive persimmon (*Diospyros* spp.) can be controlled by applying a suspension of the wilt pathogen, *Cephalosporium diospyri* Crand. to stumps of felled trees, which is a method that has been used in, for example, the pastures of Arkansas since the 1960s (Wilson 1965).

Figure 62. *Neonectria ditissima* canker on maple. Note the characteristic red pustules in the lesion (photo: S. Woodward).

Acer negundo L., commonly known as **ash-leaved maple**, is usually a medium sized fast growing tree in its local and introduced range. Apart from non-specific root diseases and decays, maple species are typically susceptible to mildews, cankers and *Verticillium* wilt. Several species of Ascomycota (Erysiphaceae) are responsible for mildews on maples in general. Ash-leaved maple is prone to attack by *Sawadea* spp., though the disease does not usually seriously affect host vigour. Cankers on maples can be caused by a number of different pathogens. On individuals of low vigour, coral spot, caused by *Nectria cinnabarina* (Tode) Fr., may result in dieback of younger shoots. This weak pathogen is not usually a problem on vigorous trees, however, another pathogen, *Neonectria ditissima* (Tul. & C.Tul.) Samuels & Rossman (formerly *Nectria galligena*), has a very wide host range on angiosperm trees (Figure 62) and may also attack ash-leaved maple. *Eutypella parasitica* (R.W. Davidson & R.C. Lorenz), a pathogen native to North America but recently established in Europe, causes cankers on maples (Cech et al. 2016), including ash-leaved maple. Infection can reduce strength in twigs, branches and main stems, but is rarely lethal.

Verticillium wilt can prove lethal to maples in many instances, particularly on ornamental varieties used in parks and gardens (Pegg and Brady 2001). *Verticillium albo-atrum* Reinke & Berthold or *Verticillium dahliae* Kleb., therefore, could prove suitable pathogens for testing as biological control agents against ash-leaved maple. A recent report suggested that two species of wilt inducing *Fusarium, Fusarium solani* (Mart.) Sacc. and *Fusarium oxysporum* Schltdl., were responsible for extensive mortality of ash-leaved maple in South Kazakhstan (Turaliyev et al. 2015). Details of this problem, however, are lacking currently.

▶ *Maples are susceptible to a wide range of pathogens, the most destructive of which are probably root pathogens and* Verticillium *wilt.*

Tree of heaven (*Ailanthus altissima* (Mill.) Swingle) is a fast growing invasive tree species introduced from China into Europe in mid-18th century. A potential pathogen for biological control of tree of heaven is under development in the USA (Snyder et al. 2013). Based on reports of mortality of this invasive tree in Pennsylvania, first noted in 2002 (Schall and Davis 2009), *Verticillium nonalfalfae* Inderb., H.W. Platt, Bostock, R.M. Davis & K.V. Subbarao was demonstrated to be highly virulent on tree of heaven, with the first isolate obtained causing 100 % mortality in inoculated young plants within nine weeks of treatment and the same rate of mortality in mature trees in the field within three months (O'Neal and Davis 2014). This same pathogen was reported recently from tree of heaven growing in two provinces in Austria with severe symptoms of wilting (Maschek and Halmschlager 2016). The occurrence of virulent strains of *V. nonalfalfae* in Austria suggests that this pathogen could be further developed for the management of *A. altissima* in Europe, depending on whether the pathogen is native in the region.

▶ *Tree of heaven produces copious quantities of seed, enabling it rapidly to invade disturbed areas.*

Apart from *V. nonalfalfae*, several other potentially useful pathogens of tree of heaven are known, including *Fusarium oxysporum* f.sp. *perniciosum* (Hepting) Toole and the rust fungi *Aecidium ailanthi* J. Y. Zhuan and *Coleosporium* sp. are known from this host tree, both in the native range in China and in North America (Ding et al. 2006). Various *Coleosporium* spp. are present in Europe, though none has been reported on tree of heaven. Stringent and wide-ranging specificity tests on these pathogens would be required however, before introduction into any European regions. Rust pathogens often have complex life cycles involving at least two genera of host plants, and predicting the wider implications of introducing such a pathogen is extremely difficult.

Eucalypts (*Eucalyptus* spp.) are now widely grown in Mediterranean countries of Europe and in all similar ecosystems world-wide for pulp and fibre production. Wherever trees of this genus are grown, however, numerous diseases have been recorded, of varying threat to the hosts themselves. A range of *Mycosphaerella* species cause leaf spot diseases of varying intensities (Figure 63). Some trees can be seriously defoliated by these pathogens under conditions conducive to infection and disease development (Park and Keane 1982). *Mycosphaerella* spp., causing serious leaf spots and defoliation, for example, have been limiting factors in establishing eucalypt plantations in Australia (Jackson et al. 2008). Other pathogens, including *Phaeoseptoria eucalypti* Hansf. and *Aulographina eucalypti* Cooke & Massee) Arx & E. Müll. can cause serious foliage diseases on eucalypts in many parts of the world. *Mycosphaerella* spp., including *Mycosphaerella eucalypti* (Wakef.) Hansf., *Mycosphaerella nubilosa* (Cooke) Hansford, *Mycosphaerella aurantia* A. Maxwell, *Mycosphaerella madeirae* Crous & Denman, *Mycosphaerella marksii* Carnegie & Keane are present in Europe and, under environmental conditions suitable for disease development, can cause suppression of growth in plantations (Aguin et al. 2013).

Figure 63. *Mycosphaerella* causes leaf spot on *Eucalyptus* and can be particularly damaging in plantations (photo: S. Woodward).

Species in the Myrtaceae, including eucalypts, are under great threat from the invasive rust pathogen *Puccinia psidii* G. Winter (Glen et al. 2007); this pathogen, native to South America, is considered the greatest threat to eucalypt plantations globally, and has proved a major obstacle to the establishment of rose gum (*Eucalyptus grandis* Hill ex Maiden) plantations in Brazil. Being autoecious (requiring only a single host plant species), the rust can establish in all parts of the world where susceptible Myrtaceae grow. The pathogen has, to date, not been recorded in Europe. However, despite the apparent wide host range, it is clear that numerous biotypes of the pathogen exist (Coelho et al. 2001); for example, isolates of the pathogen from guava failed to cause infections of eucalypts and vice versa (Ferreira 1983). Although it may be possible to select for rust biotypes that infect only eucalypt species without damaging native European Myrtaceae, based on a great deal of previous experience of pathogen introductions globally, and the comment made about *Aecidium ailanthi* above, this potential use of *P. psidii* is highly unlikely.

Rust (caused by Puccinia psidii*) poses an enormous risk to the future of eucalypt plantations in many regions of the world.*

Eucalypts are subject to several seriously damaging canker diseases. Amongst these, probably the best known is *Chrysoporthe cubensis* (Bruner) Gryzen. & M.J.Wing. (syn. *Cryphonectria cubensis*), which has been long known as a major cankering agent on *Eucalyptus* spp. (Gryzenhout 2013). In severe cases, infected trees die, although there is considerable variation in susceptibility within species. A further complication is the discovery of cryptic species within the *C. cubensis* complex, i.e. different species within the complex that are essentially morphologically identical (Vanhellemont et al. 2010). However, the disease is not known to occur in Europe.

Ceratocystis fimbriata Ellis & Halsted causes a troublesome wilt disease of eucalypts in South and Central America, and is particularly damaging in some of the plantations established in Brazil (Harrington 2013). First reported as recently as 1997 in Bahia Province, Brazil, the disease has become more widespread with time. It is likely that the pathogen has spread to South Africa, where several reports of killing in eucalypt plantations were attributed to *C. fimbriata* (Roux et al. 2000). The wide host range bacterium *Ralstonia solanacearum* has also been associated with severe wilt in eucalypt trees in South America, China and Taiwan, Australia and South Africa (Coutinho et al. 2000). A strain of *R. solanacearum* tolerant of cool conditions has been reported in Europe through (European and Mediterranean Plant Protection Organisation) EPPO, although it has not established widely to date.

Phytophthora species are well known pathogens on eucalypt species, with several major outbreak regions in the World (Figure 64). Arguably the most severe damage is caused by *Phytophthora cinnamomi* Rands. and *Phytophthora elongata* A. Rea, M. Stukely & T. Jung to natural and replanted jarrah (*Eucalyptus marginata* Don ex Sm.) in western Australia (Shearer et al. 2009, Rea et al. 2010). High levels of mortality occur in these forests, and susceptible plants include many of the more minor woody plants also present in these ecosystems. Similar problems occur in Victoria State, Australia, where the forests are reduced to a scrub of very poor quality trees (Davison 2015). Severe losses in *Eucalyptus* plantations due to *P. cinnamomi* infection also occur in parts of South Africa (Meyer et al. 2016). Many species of *Phytophthora*, including *P. cinnamomi*, are present in Europe; their use in controlling an invasive plant, however, is impossible to recommend, due to the very wide host range of this species, and usually within the genus as a whole.

Many species of Phytophthora *have wide host ranges; for example,* Phytophthora cinnamomi *can attack and kill over 900 species of woody plants.*

Figure 64. Death of eucalypts infected by *Phytophthora cinnamomi* (photo: S. Woodward).

Black cherry (*Prunus serotina* Ehrh.) is a widespread species in many parts of Europe. Work carried out within the native range of black cherry in North America clearly demonstrated the role pathogens can play in the natural distribution of this species during growth and maturation of seedlings of the plant. Where a build-up in root-infecting *Pythium* species (*Pythium attrantheridium* Allain-Boule & Levesque, *Pythium macrosporum* Vaartaja & Plaats- Niterink, *Pythium intermedium* de Bary, *Pythium heterothallicum* W.A. Campb. & F.F. Hendrix and others) occurs, growth of the same species underneath the mature tree is prevented (Packer and Clay 2000). It was postulated that the absence of many of these *Pythium* spp. in Europe is at least partially responsible for the invasive nature of black cherry in Europe (Reinhart et al. 2010).

Research in the native range of black cherry, in North America, suggests that the root pathogens which build up around the trees as they mature are absent in Europe, possibly leading to the invasive nature of this tree.

Prunus spp. are susceptible to leaf spot and canker caused by *Pseudomonas syringae* pv. *morsprunorum*. The bacterial pathogen has a winter phase, in which cankering is caused on twigs and branches, and a late spring/summer phase, in which a leaf spot, with typical shot-hole symptoms, occurs (Freigoun and Crosse 1975). Although many *Prunus* spp. can be severely damaged or killed following infection, when the main stem is girdled by *P. syringae*, black cherry is not particularly badly damaged by this pathogen.

Work undertaken in the Netherlands, where black cherry successfully invades sandy soils (Vanhellemont et al. 2010) demonstrated that the wound-colonising hymenomycete pathogen *Chondrostereum purpureum* (Pers. ex. Fr.) Pouzar can control the production of coppice shoots and re-sprouting, following cutting of black cherry and other hardwood trees (De Jong 2000). Although *C. purpureum* causes the serious disease known as silver leaf on stone fruits, risk analyses suggest that its use in control of re-sprouting of potentially invasive woody plants is justified (De Jong 2000). The mycoherbicide formulation based on *C. purpureum* can kill living stumps of several other hardwood species apart from black cherry, including *Populus euramericana* Dode Guinier, and various species of *Alnus* and *Betula* (De Jong 2000).

Red oak (*Quercus rubra* L.) is a North American species, widely planted in northern Europe since its introduction in the 18th century. Under suitable conditions, it can seed profusely, resulting in numerous seedlings colonising forests and parks. Considerable damage to red oak timber yields can result from infection by *P. cinnamomi* (Marçais et al. 1993), although infections caused only basal cankers and did not kill inoculated trees. It is highly likely that many other *Phytophthora* spp. can severely debilitate or kill red oak, although these pathogens could never be recommended for deliberate treatments due to wide susceptibility amongst woody plants.

A major disease that can kill red oak in North America is wilt caused by *Ceratocystis fagacearum* (Bretz) J. Hunt (Juzwik et al. 2011). This pathogen does not occur in Europe; however, it is on the EPPO's A1 list of pathogens for which all measures must be taken to prevent entry. Although causing rapid dieback and death of *Quercus* spp. in the red oak section (*Lobatae*; syn. *Erythrobalanus*), the pathogen can also affect oaks in other sections, including the white oaks (*Lepidobalanus*; syn. *Leucobalanus*), *Mesobalanus* and *Cerris*, which include the oak species native to various parts of Europe (MacDonald et al. 2001).

Bacterial scorch of oak foliage is another disease which affects oak species in North America (Janse and Obradovic 2010) and is caused by a strain of *Xylella fastidiosa* not known to be present in Europe. It is important to note that determining a specific pathogen that could result in suppression of the red oak population is difficult because most diseases to which it is subject in Europe also affect native oaks on the continent.

Ulmus pumila L., the **Siberian elm**, is an introduced tree species in Europe, which is native to northern Asia. Many European and American species of *Ulmus* were decimated by the Ascomycota, *Ophiostoma ulmi* (Buisman) Nannf. and *O. novo-ulmi*, in the 20th century (Brasier 1988, 1991). While European and North American species of elms were very susceptible to Dutch elm disease (DED), with infected trees dying within 1 – 2 years (Smalley and Guries 1993), several Eurasian species exhibited varying degrees of tolerance to DED (Smalley and Guries 1993). In response to the two DED pandemics, Siberian elm was planted to replace the native elms in several countries, including Italy, Spain and the USA. To date, widespread hybridisation has been documented between the introduced Siberian elm and introduced field elm (*Ulmus minor* L.) in Spain (Cogolludo-Agustin et al. 2000) and between Siberian elm and the native red elm (*Ulmus rubra* Muhl.) in the Midwestern USA (Zalapa et al. 2010).

These hybrids are considered a threat for the conservation of the genetic diversity of the native elms in both the USA (Zalapa et al. 2010) and in Spain (Cogolludo-Agustin et al. 2000). The hybridisations between Siberian elm and field elm and between Siberian elm and red elm have increased genetic diversity and, at least in the Midwestern USA, affected the genetic structure of Siberian elm populations (Zalapa et al. 2010), contributing to increased habitat range for Siberian elm compared to its native range (Zalapa et al. 2010). Moreover, hybridisation may help explain the fact that Siberian elm has become an invasive in 41 states (USDA, NRCS 2002).

Few diseases are reported for Siberian elm; *Nectria cinnabarina* (Tode) Fr., for instance, may cause dieback in the crown (Went 1940). *Mycosphaerella ulmi* Kleb. and *Erysiphe clandestina* Biv. are powdery mildew pathogens which can occasionally damage elms. Elm yellows, caused by phytoplasma 'Candidatus *Phytoplasma ulmi*', is an increasing cause of elm dieback and death in Europe. First reported in Europe at the end of the last century (Mittempergher 2000), elm yellows was found to be widespread in Italy on field elm and Siberian elm trees (Carraro et al. 2004). Symptoms of infection include epinasty, yellowing, dwarfing and premature leaf fall, witches' brooms at the tips of twigs and branches and precocious opening of vegetative buds. In some cases, elm yellows can kill young plants.

Sitka spruce (*Picea sitchensis* (Bong.) Carr.) was introduced into Britain almost 190 years ago, where it forms a considerable proportion the forest cover, yet it has remained remarkably free of serious pests and diseases in that time. Moreover, the tree has few serious pathogens in its native range in the Pacific North West, where the main problems on Sitka spruce are root and stem rot diseases attacking old trees. In European situations, pathogens attacking the native Norway spruce (*Picea abies* L. Karst.) also attack Sitka spruce, though with the exceptions of root pathogens, none have to date caused significant damage on the non-native host tree.

> *Despite having been introduced into Europe over 190 years ago, Sitka spruce has proved remarkably resilient against pests and pathogens.*

Arguably, the most serious diseases are caused by the root-infecting pathogens *Armillaria ostoyae* (Romangn.) Herink and *Heterobasidion annosum* Fr. Bref. sensu lato (Gregory and Redfern 1987). *A. ostoyae* is the most common species of *Armillaria* that attacks gymnosperm trees. In the majority of situations, *H. annosum* causes severe decay of the stem in *Picea* spp. (Figure 65), and it is only on sites where the inoculum potential is high and soil conditions conducive to disease development (old agricultural soils, high pH) that Sitka spruce is killed by *H. annosum* (Bodles et al. 2005). Sitka spruce also suffered serious but localised mortality from infections of the ascomycete root pathogen *Rhizina undulata* Fr., though the problem was greatly reduced in the 1950s by banning the lighting of fires during thinning and felling operations (Gregory and Redfern 1987).

The shoot pathogen *Sirococcus strobilinus* Preuss has been found causing defoliation and dieback of Sitka spruce, although serious outbreaks are almost entirely confined to nursery situations. Both *Chrysomyxa abietis* (Wallr.) Unger and *Chrysomyxa rhododendri* de Bary occur occasionally on needles of Sitka spruce, but neither species does serious damage (Crane 2000).

Figure 65. A large conk of *Heterobasidion annosum* at the base of a Sitka spruce killed by the infection (photo: S. Woodward).

Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) may be considered invasive in certain situations, where natural regeneration occurs prolifically in suitable environmental and edaphic conditions. It must, however, be remembered that it is also a desirable timber-producing tree, and great care must be taken when considering control of the species using pathogenic microorganisms.

By far the most significant disease impacting on the vigour of Douglas fir is Swiss needle cast, caused by *Rhabdocline pseudotsugae* Syd. This pathogen is specific to Douglas fir, and was probably introduced into Europe in the early 20th century. The disease can cause massive reductions in vigour to Douglas fir plantations in the Pacific North West, where the pathogen and host are native, but rarely results in significant losses in native forests. In Europe, particular varieties of Douglas fir vary in response to *R. pseudotsugae*, with *P. menziesii viridis* being more commonly planted than the *caesia* and *glauca* forms, due to lower susceptibility (Bednářová et al. 2013). Severe losses of current year needles can occur when conditions are conducive to infection; such conditions include high humidity conditions in the spring.

> *Swiss needle cast can cause massive reductions in vigour to Douglas fir plantations in the Pacific North West of North America, but rarely results in significant losses in native forests.*

A similar, though usually less damaging needle pathogen of Douglas fir is *Phaeocryptopus gäumannii* (T. Rohde) Petr., which was also first introduced into Europe in the early 20th century. Needles are lost from infected trees two to three years after infection (Bednářová et al. 2013).

A shoot disease of Douglas fir is caused by *Phacidiopycnis pseudotsugae* (M. Wilson) G.G. Hahn (*Phaciopycnis pseudotsugae*, *Phomopsis pseudotsugae*), a pathogen with a wide host range, infections of which can result in dieback of young shoots following girdling of growth (Phillips and Burdekin 1992). The disease is principally a problem in nurseries and on younger trees and is present throughout western Europe.

Diplodia sapinea (Fr.) Fuckel is a well-known latent pathogen of various Pinaceae with a worldwide distribution, mainly located in warm temperate environments, but now spreading northward (Oliva et al. 2013). *D. sapinea* is known to attack also Douglas fir, but the rate of infection has so far proved limited by the absence of an efficient vector to spread the pathogen from pines. Recently, Luchi and co-workers (Luchi et al. 2012) demonstrated that the introduced cone bug *Leptoglossus occidentalis* is a reliable vector, able to spread *D. sapinea* from pines to different conifer species that are hosts to both, such as Douglas fir.

Douglas fir can be attacked by root decaying fungi, such as *Armillaria* spp. and *Heterobasidion* spp., although in general, the tree is not badly damaged. For example, *Heterobasidion* species may decay roots, but the fungus rarely grows into the lower stem of Douglas fir.

Concluding comments

Requirements for pathogens for use in the biological control of invasive plants have been outlined in this chapter, along with the potential undesirable side effects of this approach. Although most of the tree species used as examples here are subject to attacks by numerous diseases, both in their native environments and in the introduced regions, the success of potentially invasive trees is partly dependent on the absence of highly destructive pests and pathogens. With two possible exceptions, the application of *Chondrostereum purpureum* in controlling resprouting of black cherry and the use of *Verticillium nonalfalfae* in management of tree of heaven, using pathogens to control invasive trees is a highly contentious and problematic area of research and development. Many of the trees are considered useful in some manner, at least in parts of the invaded ranges; some are specifically planted for timber production and, arguably, require protection against pathogen attacks. Increasing populations of potentially damaging pathogens in invaded regions may lead to unforeseen consequences in terms of collateral damage to other non-target plants. Moreover, our increasing knowledge of cryptic speciation within apparent pathogen species complexes adds further complication to the use of pathogens as biological control agents against invasive plants. Although it may initially seem desirable to introduce a pathogen from the native range of the problematic tree species into an invaded region, taking into consideration the possible complications arising from such actions, most learnt from multiple environmental disasters observed in parallel work (e.g. the cane toad in Australia) have taught us to be very cautious.

> ▶ *Increasing populations of potentially damaging pathogens in regions invaded by trees may lead to unforeseen consequences in terms of collateral damage to other non-target plants.*

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TEXT BOX IV: Interactions between introduced game fauna and flora

Alexander Held and Frank Krumm

For centuries, hunting has been one of the most important pathways for the introductions of birds and mammals. A major cause for deliberate introductions in European forests was the enrichment of the palette of huntable animals, e.g. muntjac (*Muntiacus* spp.), mouflon (*Ovis aries* Linnaeus, 1758), fallow deer (*Dama dama* Linnaeus, 1758), and sika deer (*Cervus nippon* Temminck, 1838) among other species. Hulme et al. (2008) stated that the introduction for the purpose of food and hunting were the primary introduction pathways for birds (61 species) and mammals (31 species). Unintentional introductions of predators (i.e. escapes due to animal-aided hunting techniques such as falconry or ferreting) have also occurred, and these have had important ecological consequences, for instance for ground nesting birds. Results from the DAISIE (Delivering Alien Invasive Species Inventories for Europe) project have shown that hunting has been an important pathway for introduction of animal species in Europe; hunting accounts for 25 % of introductions of bird species (Kark et al. 2009), and 21 % of introductions of mammal species in Europe (Genovesi et al. 2009). Nevertheless, in recent decades, intentional introduction for hunting purposes has become much less common. This is primarily as a consequence of an increase of natural populations of game species, but also because of changes in the regulatory framework, and also changes in the approach and attitudes of hunters towards wildlife management.

> *Introductions of tree species have a long tradition and so have the introductions of animal species for different purposes.*

Regardless of such developments, several introduced animal species have reached great importance as game in Europe (Tapper 1999). As is the case for introduced species in general, only a few game species have become established in the wild; however, where they have established, these species have caused a range of negative effects on native species and native ecosystems. It is important to note that most of these species were kept in game parks from which they escaped and naturalised in the wild. In Germany, during the Second World War and during the following occupation by the allied forces, many enclosures and game parks were abandoned and animals escaped into the wild. In some cases, the population densities of these animals became so high that they caused serious damage to the forests due to selective browsing, bark stripping and fraying. Sika deer, for instance, has been introduced from Asia to many European regions in order to enrich the hunting bag with alternative trophies.

> *Sika deer and Sitka spruce in Ireland – an example of interactions of introduced species.*

A case worth elaborating in more detail is that of sika deer, Sitka spruce (*Picea sitchensis* (Bong.) Carrière) and rhododendron (*Rhododendron ponticum* L.) in Ireland. Sika was first introduced to Ireland in about 1860 and subsequently also to Germany (1893), Austria, Belarus, Czech Republic (1891), Denmark (1900-1910), France (1890), Hungary, Poland (1895–1911), Switzerland (1939), Ukraine (1909) and the UK (1898) (CABI 2016). Since sika deer populations reached high to very high densities in many Irish counties, nature conservation, forestry and agriculture organisations have become increasingly aware of the negative deer impact and effects caused by sika deer. Since the deer management is not harmonised with the land management objectives in Ireland, it is only recently that an Irish deer management policy has come into force (2015/2016). Sika deer quickly adapted to the habitats within its introduced range and its population densities became rather difficult to control by traditional hunting methods like stalking due to sika's high fecundity and elusive behaviour. It is important to note that the spread of this species has been immense in certain areas such as the Wicklow Mountains. The high browsing pressure posed by sika deer recently resulted in suppression of some of the native tree species, especially ecologically valuable species such as oaks (*Quercus* spp.) and ash (*Fraxinus excelsior* L.). In addition, sika deer have caused damage to herbaceous ground vegetation that has a high value in terms of biodiversity. On the other hand, rhododendron, which has also been introduced to Ireland, is not attractive by deer and has become highly invasive. Sika deer and rhododendron have formed an unexpected and unwanted synergy and have quickly and completely changed an ecosystem.

As a result of the above, sika deer is the most influential factor determining which tree species are used for afforestation (and natural regeneration of course) in a number of regions across Ireland. Sitka spruce is not browsed by sika deer, whereas most other suitable tree species, and especially the native tree species, will never grow beyond browsing height, unless sika deer are excluded by a game fence or seedlings are protected by tree guards. The combination of sika and rhododendron plays a role in the fact that another introduced species, Sitka spruce, is the most widespread tree species in Ireland – Sitka spruce accounts for 52 % of the forest area in Ireland (see chapter 5.4). Of course, the current forestry grant system which supports Sitka spruce plantations is also a factor, but the field conditions with sika deer are indeed a limiting factor. The consequences and associated risks of developing forests with only one tree species is obvious and needs no discussion.

Figure 66: Abundant natural regeneration inside deer fence with an obvious lack of it outside the fence due to heavy browsing (photo: M. Scholz).

Sika deer also cause substantial problems in southern Germany, Switzerland and the Czech Republic where it seriously affects regeneration of the forest, and therefore has serious implications for forest management and forest specific biodiversity.

Figure 67. A massive herd of sika deer in central Bohemia, Czech Republic (photo: J. Peterka).

> *The slow, but cumulative effects of high deer populations on forests are an example of a Creeping Environmental Problem (CEP).*

Generally, selective browsing of small trees by wildlife is considered as one of the most severe challenges in forest management across Europe. The effects of wildlife on natural regeneration are generally rather slow and often go unnoticed; however, the effects accumulate towards a tipping point and can have drastic consequences for an ecosystem (e.g. Oliver and Larson 1996). The phenomenon can be described as a Creeping Environmental Problem (CEP) and accounts for millions of Euros of damage per year. Unlike for fires or storms, the effects are not immediately visible. The changes in tree species composition and related biodiversity happen so slowly that in day-to-day life we do not notice the effects. We do not see the missing oak, sycamore (*Acer pseudoplatanus* L.) and silver fir (*Abies alba* Mill.) seedlings and the new situation becomes "normal". As selective browsers, ungulates have a strong impact on the vegetation cover. They reduce growth and height of the trees and they influence the vertical plant layer and the plant species composition in a forest area, which has then an effect on the fauna (Gill and Beardall 2001). In some cases, the local extinction of certain vulnerable species is possible (Martin and Daufresne 1999) However, managing forest systems towards resilient and stable, diverse forest for climate change scenarios need a high level of forest biodiversity as a prerequisite for that resilience.

Example: mouflon and wolf in Germany

The mouflon is a species of wild sheep that was introduced to several regions in Germany around the 1900s as an addition to the game fauna. It rapidly spread as there was no natural predator. Mouflon was and is seen very critical in the forestry and nature conservation context, but was naturalised by the authorities due to its long presence. Active eradication of mouflon as well as protecting mouflon gene pools were postulated over the years. However, the unexpected re-colonisation of wolves a hundred years later (*Canis lupus* Linnaeus, 1758) started to dramatically change the situation resulting in mouflon going locally extinct over a very short period. In order for mouflon to co-exist with wolves, its needs extensive areas of rocks and cliffs to be able to escape the wolves. In Germany, the areas colonised by mouflon after the 1900s were not sufficiently rocky to provide mouflon with sufficient refuge areas, and therefore it has disappeared as wolves have reappeared.

Natural control mechanisms are likely to develop over time, at least for some species, if allowed by man and not hindered by well-intentioned reactive management. This example of mouflon and wolves may serve to emphasise a calm and more relaxed in certain cases, science based management approach for management of introduced species, allowing for more time for observation and analysis before taking action, based on the best available knowledge. In this particular case nature created a new balance; it only took one hundred years. Looking at the consequences of a particular introduced species in isolation, does not provide a better understanding of current ecosystem processes, as there are many factors that need to be taken into consideration. The impacts that introduced game species have on native ecosystems are a good example of the complexity of the situation. The case of mouflon emphasises the need to allow for some time and observation, over time, nature can achieve some new balance. Where there have been introductions of new species, there is a need for assessment of the potential of the new species to cause damage, and an observation of its effects on ecosystems. In most cases, a more relaxed approach to introductions is called for as the introductions will have rather limited economic and ecological effects.

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4.5 Introduced tree species in central Europe – consequences for arthropod communities and species interactions

Martin M. Gossner

The forest landscapes in central Europe are characterised by a comparatively low diversity of native tree species as result of postglacial dispersal limitations (Normand et al. 2011, Svenning and Skov 2007). Since prehistoric times, these forests have largely been shaped by human activities (Konold and Beck 1996). As well as changes in land use, e.g. conversion to agriculture (Hansen et al. 2013), fast-growing tree species native to Europe, in particular Norway spruce (*Picea abies* (L.) H.Karst.), have extensively been planted outside their natural distributional ranges (Schelhaas et al. 2003). Large-scale losses in these artificial stands after wind-throws and bark beetle attacks, which are expected to increase due to climate change, have hastened the need for the discussion about suitable alternative tree species that have lower risk and guarantee high yield (Bolte et al. 2009).

Since the late 1980s, the suitability of introduced tree species for forestry has increasingly been tested in cultivation trials, in order to increase the availability of tree species in forests of central Europe (e.g. Ganghofer 1884, Otto 1993). While high timber yield and stability were the main focus of these early experiments, the complexity of potential effects on ecosystems has increasingly been recognised and is now considered in the evaluation of cultivation suitability (Otto 1993, Vor et al. 2015). Nevertheless, the discussion on the cultivation of introduced tree species between forestry, nature conservation and society is still emotional rather than evidence-based. This is not least because our knowledge on the ecological consequences of planting introduced tree species, i.e. for biodiversity and species interactions is still limited due to the complexity of potential interactions, unpredictable species adaptations and unpredictable responses to climate change. Some introduced or co-introduced species might become invasive, meaning that they rapidly spread and cause damage to the environment, human economy or human health.

Generally, effects of introduced tree species on native arthropod communities can arise from:

1. non-native insect species introduced together with or following the introduction of the tree species;
2. missing adaptations to the plant compounds of the introduced tree species as it is expected that host specific herbivores are most severely affected with the effects possibly cascading up to higher trophic levels;
3. tree structural differences to native tree species, which might either increase or decrease structural heterogeneity and therefore alter the availability of niches; and
4. alterations of the physical environment of forests, which may have additional far reaching consequences for a large range of organisms.

The aim of this chapter is to stimulate an evidence-based discussion of the consequences of planting introduced tree species in forests of central Europe on arthropod communities and related species interactions. Based on evidence from recent scientific studies, I would like to evaluate the consequences of introduced tree species for nature conservation and forest protection.

> *Current knowledge suggests negative as well as positive effects of co-introduced animals on native plant and animal communities. The specific direction and trajectories of effects highly depend on species specific traits, number of introduction events and phylogenetic distance to native species.*

There are plenty of examples of non-native animals introduced together with its hosts. Among them are several specialised herbivores, feeding only on one plant genus, but also generalists, using a broader range of host plants (Table 22).

Specialised herbivores introduced with non-native trees might have negative effects on its host also in the region to which they were introduced and thus reduce plant fitness (see examples in Vor et al. 2015). However, there are also indications of effects on native animal species. Douglas fir wooly adelgid (*Gilletteella cooleyi* (Gillette 1907); *G. coweni* (Gillette 1907)) is fed on by native aphidophagous species and is assumed to even promote population sizes of these species which in turn might have positive effects on aphid pest control on native tree species (Gossner et al. 2005). In contrast, ant abundance is expected to be negatively affected by Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco). This is due to non-suitability of Douglas fir wooly adelgids for ants, e.g. of the genus *Formica*, as honey-dew resource and the lack of other honey-dew producing aphid species (Lachnidae) on Douglas fir (Gossner 2004). Other introduced insect species are parasitised by native insects. Kasch and Nicolai (2002) showed that 10 % of the mining larvae on black locust (*Robinia pseudoacacia* L.) were parasitised by native Chalcidid wasps (Chalcididae), indicating either plasticity of native species or adaptations to the new introduced host.

Table 21. Examples of insect species that were co-introduced with tree species to Europe. Specialist means that a particular species feeds on only one plant genus.

Species	Order	Family	Feeding specialisation	Introduced tree species	First detected in Europe	Switch to native hosts	Remark	Reference
Gilletteella cooleyi	Hemiptera	Adelgidae	specialist	*P. menziesii*	1910	No	Complex generation and host change; galls on *Picea sitchensis*	Postner (1955), Steffan (1970), Wimmer (1935)
Gilletteella coweni	Hemiptera	Adelgidae	specialist	*P. menziesii*	1910	No	No host change	
Nematus tibialis	Hymenoptera	Tenthredinidae	specialist	*R. pseudoacacia*	1825	No		Kruel (1952), Kulfan (2012), Rasplus et al. (2010), Tóth et al. (2011), Vor et al. (2015)
Parectopa robiniella	Lepidoptera	Gracillariidae	specialist	*R. pseudoacacia*	1970	No		
Phyllonorycter robiniella	Lepidoptera	Gracillariidae	specialist	*R. pseudoacacia*	1983	No		
Etiella zinckenella	Lepidoptera	Pyralidae	generalist	*R. pseudoacacia*	1989	Yes		
Megastigmus spermotrophus	Hymenoptera	Torymidae	specialist	*P. menziesii*	1893	No	Competing with introduced Leptoglossus occidentalis	Auger-Rozenberg and Roques (2012), Lessmann (1974)
M. pinsapinis	Hymenoptera	Torymidae	specialist	*C. atlantica*	1947	No	Competing with *M. schimitscheki.* Probably introduced much earlier than the date reported.	Auger-Rozenberg and Roques (2012), Ros et al. (1993)
M. schimitscheki	Hymenoptera	Torymidae	specialist	*C. libani, C. brevifolia*	1994	No	competing with *M. pinsapinis*	
M. specularis	Hymenoptera	Torymidae	specialist	*Abies spp.*	1945	Yes	tend to displace native chalcids	
M. rafni	Hymenoptera	Torymidae	specialist	*Abies spp.*	1952	Yes		
M. milleri	Hymenoptera	Torymidae	specialist	*Abies spp.*	1952	Yes		
M. pinus	Hymenoptera	Torymidae	specialist	*Abies spp.*	1931	Yes		
M. atedius	Hymenoptera	Torymidae	specialist	*Picea spp.*	1954	Yes		
M. transvaalensis	Hymenoptera	Torymidae	specialist	*S. terebinthifolia*	1962	No		
M. nigrovariegatus	Hymenoptera	Torymidae	specialist	*Rosa spp.*	1987	Yes		
Dreyfusia nordmannianae	Hemiptera	Adelgidae	specialist	*A. nordmanniana*	1840	Yes	Compete with native *Dreyfusia piceae* on *Abies alba*	Nierhaus-Wunderwald and Forster (1999)
Dasineura gleditchiae	Diptera	Cecidomyiidae	specialist	*G. triacanthos*	1975	No	Negative effects on plant fitness	EPPO (2008)

Figure 68. Examples of species that were introduced to Europe with their host plants: A) *Gilletteella* spp. on Douglas fir; B) *Phyllonorycter robiniella* (Clemens 1859) on black locust or other vectors such as C) *Leptoglossus occidentalis* (Heidemann, 1910), a seed predator on conifers, introduced from western North America in 1999 (photos: A.B. Wermelinger and C. Gossner).

Introduced seed wasps illustrate different consequences on species interactions. The seed wasp *Megastigmus spermotrophus* Wachtl, 1893, introduced with Douglas fir in 1893 and now widely distributed in Europe is a specialised herbivore that has not switched over to native tree species and occupied the whole seed cone niche in Douglas fir before the western conifer seed bug (*Leptoglossus occidentalis* Heidemann, 1910) arrived in 1999 (Auger-Rozenberg and Roques 2012). Other introduced cone wasps, however, switched to native trees and either displaced native cone wasps on native firs (*Abies* spp.) or increased the cone damage with negative effects on regeneration of native roses (*Rosa* spp.). Therefore, introduced species compete with native insects for food resources (Fabre et al. 2004). Another specialist introduced insect species that caused severe damage on silver fir (*Abies alba* Mill.) in central Europe is the conifer woolly adelgid (*Dreyfusia nordmannianae* Eckst., 1890) that was introduced from the Caucasus with Caucasian fir (*Abies nordmanniana* (Stev.) Spach). As Auger-Rozenberg and Roques (2012) suggests for chalcids, no general invasive pattern exists and different biological traits might explain invasive success of introduced species.

Introduced generalist herbivores are more likely to negatively affect native species because they can grow and survive on many different plant species. The western conifer seed bug, which was first introduced from North America to northern Italy in 1999 (Taylor et al. 2001) and expanded over whole Europe in the last years (Fent and Kment 2011) is an illustrative example. It affects not only seeds of introduced Douglas fir, but also native pines (*Pinus* spp.) and thus can limit natural regeneration of native species and reduce their fitness by dispersing pathogens (Lesieur et al. 2014, Tamburin et al. 2012). Among moths, the introduced fall webworm (*Hyphantria cunea* Drury, 1773) that caused defoliation on introduced e.g. ash-leaved maple (*Acer negundo* L.), tree of heaven (*Ailanthus altissima* (Mill.) Swingle) as well as native hosts in Europe (Krehan and Steyrer 2009), and the Ailanthus silkmoth (*Samia cynthia* Drury, 1773) that feeds on a broad range of native woody plants as well as the introduced tree of heaven (Vor et al. 2015).

The most prominent cases among beetles are the Asian long-horned beetle (*Anoplophora glabripennis* Motschulsky, 1853) which causes severe damage on deciduous trees in North America and Europe (Hu et al. 2009, Meng et al. 2015) and the emerald ash borer (*Agrilus planipennis* Fairmaire, 1888) that is already invasive in Russia and severe consequences for introduced and native ash species (*Fraxinus* spp.) are also expected to occur in central Europe (Orlova-Bienkowskaja 2014).

The probability of an introduced tree species to be colonised by native insects depends on many different factors such as tree-specific physical, chemical and phenological traits as well as phylogenetic isolation of the introduced species, its abundance in the introduced range, the time since introduction and surrounding tree species effects.

It is assumed that insects feeding on plant tissue (herbivores), in particular host specialists are most strongly affected by introduced tree species due to missing adaptations, e.g. to 'novel' plant compounds ('taxonomic isolation', Connor et al. 1980). Accordingly, introduced tree species with closer native relatives in the new area should share more herbivores due to phylogenetic conservatism (Branco et al. 2015, Roques et al. 2006). This is caused by co-evolution between insects and plants and the conservation of functional plant traits and has been shown to be an important mechanism explaining the herbivore communities in the canopy of mature introduced Douglas fir and red oak (*Quercus rubra* L.) (Gossner et al. 2009). However, depending on the interplay of the biology and evolutionary history of the herbivore taxon, local abundance of native tree species and phylogenetic scale and other assembly mechanisms might increase in importance. Among those, geographic contingency predicts that plant lineages can evolve different biotic and abiotic traits in different parts of the world, which results in different co-evolutionary processes (Thompson 1999). Mass effects, the immigration from locally abundant plant species (Shmida and Wilson 1985) has shown to be an important mechanism in introduced Douglas fir (Gossner et al. 2009); an immigration from surrounding European beech (*Fagus sylvatica* L.) trees was observed in mixed Douglas fir-beech stands.

It can be assumed that the number of arthropod species colonising introduced trees will increase with the time since their introduction (Frenzel et al. 2000, Gossner 2004). Moreover, they may increase with increasing distribution of an introduced tree species, as shown for woody species in Great Britain (Kennedy and Southwood 1984). This is because adaptations become more likely with time and probability to coincide. In general, the degree of host genus specialisation in plant feeders (phytophages) of central European conifers is low, at least at lowland sites (Gossner 2004, Roques et al. 2006; Tahvanainen and Niemelä 1987). Thus, the expansion of the host spectrum of native insects on introduced conifers such as Douglas fir might be more likely than on broadleaved trees such as red oak leading to a lower difference in diversity between introduced and most closely related native conifer tree species (Gossner 2004). Although many oak specialists are not able to use introduced red oak (Gossner 2004, Wehrmaker 1990), some may even reach higher abundance on the introduced tree due to competitor avoidance as long as they manage to cope with the physical and chemical traits of the new host (Gossner 2008). Ongoing adaptation to different nutrient and secondary plant compounds might be observed in species developing in acorns (Gossner and Gruppe 2004). While weevils that are specialised on one plant genus (monophagous) did not successfully develop in acorns of red oak, tortricids that use different plant genera (polyphagous) successfully emerged from red oak acorns, but still in significantly lower numbers than from native oak acorns (Gossner and Simon 2005). Also a few galls of the Diptera family Cecidomyidae and the Hymenoptera family Cynipidae were already observed on red oak (Ruff 2008), indicating adaptations to the new host, although the switch from the group of white oaks (all native European oaks) to red oaks should be less likely (Osten-Sacken rule, Osten-Sacken 1865). Other specialists have also successfully switched from native to introduced woody plants, such as the European birch aphid (*Euceraphis punctipennis* Zetterstedt 1828) that switched from birches (*Betula* spp.) to plane trees (*Platanus* spp.) (Olthoff 1986), the fruit fly (*Rhagoletis meigenii* Loew, 1844) from common barberry (*Berberis vulgaris* L.) to Oregon-grape (*Mahonia aquifolium* (Pursh) Nutt.) (Soldaat and Auge 1998) and native seed wasps from native to introduced spruces (*Picea* spp.) (Ros et al. 1993). As well as phylogenetic relatedness also phenology, i.e. the matching in flowering time between introduced and native hosts, played an important role for these host switches.

Wood feeding species (xylophagous) also show some degree of host specificity, at least during the early wood decomposition stages (Gossner et al. 2016) and might therefore negatively respond to introduced tree species. Diversity in deadwood harvested in the crowns of introduced Douglas fir and red oak (Gossner 2004) as well as in large trunk parts of Douglas fir during the first three years of decomposition (Gossner et al. 2016) has been shown to be significantly lower than in native spruces or oaks. This might be partly a result of different wood properties independent of tree origin (Kahl et al., pers. com.). Nevertheless, a total of 158 saproxylic species emerging from a total of 60 Douglas fir logs exposed in three regions of Germany during the first three years of decomposition were found. This equals to at least 37 % of all species emerging from logs of a total of 13 tree species and 75 % of all species emerging from native Norway spruce. The suitability of introduced tree species for saproxylic species changes along deadwood decomposition need to be clarified by future studies and experiments. Möller (1998) gives some indications that suitability might greatly vary among introduced tree species, decreasing from black cherry (*Prunus serotina* Ehrh.) to red oak to black locust. This might be due to an increasing phylogenetic distance to the next native tree species (black cherry: 9.5 Mio a, red oak: 17, black locust: 97.5; Durka and Michalski 2012). Most likely similar mechanisms operate in xylophagous and phytophagous species.

Introduced tree species might also affect food webs, which are assumed to have severe consequences for the inter-relationships in biocoenoses (Pimm et al. 1991). When herbivores develop faster on introduced than on native trees, they might escape their natural enemies and thus cause outbreaks. This has, for example, been shown for pine processionary (*Thaumatopoea pityocampa* Denis & Schiffermüller, 1775) on introduced Monterey pine (*Pinus radiata* D.Don) and native maritime pine (*Pinus pinaster* Aiton) in Italy (Buxton 1990). The earlier pupation on Monterey pine reduced the exposure time to the parasitoid tachinid *Phryxe caudata* (Rondani, 1859) which in turn may have caused the mass occurrence of the caterpillars on this pine.

Plant architecture and structure and therefore the abundance and diversity of different niches has been found to be an important factor driving arthropod diversity on trees (Lawton 1983). Besides deadwood, also other structures of introduced trees may support diversity by providing additional niches. One example is bark structure (Nicolai 1986). Coarse and fissured bark where organic matter can accumulate might favour insect diversity by providing shelter and resources. Examples are the highly structured bark of sycamore (Klausnitzer 1988, Olthoff 1986) supporting many overwintering species. Douglas fir also has a very thick and coarse bark structure protecting the tree from frequently occurring fire in its natural distributional range (Starker 1934). Surprisingly, this does not favour diversity compared to Norway spruce, most likely due to reduced food availability for species groups that depend on structure such as spiders (Gossner 2004, Gossner and Ammer 2006). This is because the coarse structure of the bark seems to be less suitable for species changing strata during their life cycle among those many herbivores (Gossner and Ammer 2006). Crown structure also greatly differs among tree species and this might affect taxa, such as spiders, which have been shown to be limited by habitat structure, i.e. twig and needle structure (Halaj et al. 2000). Blick and Gossner (2006), for example, found differences in the composition of prey capture guilds between spruce and introduced Douglas fir. While net-building spiders were much more important in the canopy of spruce compared to Douglas fir (55.2 % vs. 23.8 %), running spiders showed a contrasting pattern (37.0 % vs. 67.3 %). Additionally, crown structure affects microclimatic conditions, being for example more open and more exposed (overtopping surrounding trees of same age) in Douglas fir compared to native tree species and thus favouring thermophilous species in summer (Gossner and Ammer 2006), but reducing insect abundance in winter (Gossner and Utschick 2004).

Higher resource abundance (‘More Individual Hypotheses’; Srivastava and Lawton 1998) as well as higher resource diversity (‘Resource Heterogeneity Hypothesis’; Hutchinson 1959) have been shown to affect the diversity of higher trophic levels. A reduced suitability of introduced tree species for native herbivores and a lower insect abundance due to reduced structural microhabitat availability might thus cascade-up to higher trophic levels (see Box 21). Such cascading effects have been shown for red oak as well as Douglas fir (Gossner 2004, Gossner and Ammer 2006). Reduced food resources on introduced trees might be even more severe for tertiary consumers such as birds. Negative effects of reduced arthropod abundance in winter on birds have, for example, been shown in Douglas fir crowns (Gossner and Utschick 2004). However, this is not necessarily the case, e.g. when co-occurring introduced insect species attracts native predators, herbivores reach high abundance due to reduced competition (e.g. on red oak, see above), high attractive flowers for pollinators (e.g. butterfly bush *Budlleja davidii* Franch.; Owen and Whiteway 1980) or a high diversity of microhabitats increasing niche availability and therefore insect diversity (Crooks 2002). These potentially positive effects due to high attractiveness might, however, also have negative consequences when introduced species act as ecological trap. An ecological trap occurs when the attractiveness of a habitat increases disproportionately in relation to its value for survival and reproduction. A reduced fitness of native insects on introduced trees has been demonstrated for some herbivorous species such as the nun moth (*Lymantria monacha* Linnaeus, 1758) (Gruppe and Gossner 2006) and garden white butterflies (*Pieris* spp.) (Rodman and Chew 1980).

Box 21. Trophic cascades

The trophic cascade is an ecological concept, which goes back to Aldo Leopold who first described this mechanism based on his observations of overgrazing of mountain slopes by deer after human extermination of wolves (Leopold 1949). It stimulated new research in many areas of ecology. The concept generally assumes that food webs are organised in different distinct trophic levels, such as plants, insect herbivores and their predators. One could imagine of top-down and bottom-up cascades.

In the top-down cascade, the food chain is disrupted by the removal of a consumer. Regarding introduced tree species this could arise when herbivores, but not their predators, are co-introduced with the tree species (assuming that predators reduce herbivore prey abundance in its natural range) or when the introduced tree species are released from the main herbivore. This could cascade to the primary producer level by either decreased (no herbivores present) or increased (reduced predation pressure on herbivores) herbivory pressure, and therefore influence plant fitness and competitive ability.

In the bottom-up cascade, the co-introduction of herbivores along with an introduced tree species in the new area might cascade up the trophic chain by reducing population sizes of higher trophic levels such as invertebrate (secondary) and vertebrate (tertiary) consumers. This is because the new introduction reduces food availability.

▶ *Stand level effects highly depend on introduced tree species identity and different aspects of forest management, e.g. tree species mixture and thinning, which affect biotic (plant and litter composition) as well as abiotic stand conditions (light, temperature, air humidity).*

Introduced tree species might alter litter input, tree specific rooting and shading and release allelopathic substances (biochemicals that influence the germination, growth, survival, and reproduction of other organisms). By this the physical and chemical properties of forest stands including forest soils are changed, which, in turn, might affect arthropod communities (e.g. Prescott and Grayston 2013). Several studies have shown negative effects of introduced tree species on the diversity of ground dwelling predators and decomposers regarding Douglas fir (Schmid et al. 2014), but the effect of tree species might depend on season, age and forest management (Ziesche and Roth 2008).

The influence of introduced tree species also highly depends on the tree species composition, e.g. whether introduced tree species are planted in monocultures or admixed as single trees in native forest stands (e.g. Oxbrough et al. 2016). Engel (2001), for example, found a decreasing abundance of large decomposing arthropods (macrofauna, > 2 mm) from Douglas fir to mixed Douglas fir-spruce to pure spruce stands. However, the abundance in pure Douglas fir stands was still much lower than in beech stands. Species living on or in the bark of Douglas fir showed a lower diversity (all species and conifer specialists) in spruce and beech-dominated stands but not in Douglas fir dominated stands when compared to spruce. In the canopy, a higher diversity (all species and conifer specialists) was found on Douglas fir compared to spruce in spruce- and Douglas fir-dominated stands, while contrasting effects were observed in beech-dominated stands (Gossner and

Ammer 2006). In the canopy of broadleaved stands, the diversity of true bugs (Hemiptera) decreased with increasing proportion of introduced red oak while the dominance of single species increased (Gossner 2008).

A change in community composition of arthropods by the introduction of tree species leads to a change in trophic interactions and consequently to an alteration of ecosystem processes, such as herbivory, leaf and wood decomposition, nutrient cycling and pest control, in the canopy and on the ground.

By changing arthropod species composition, either directly or indirectly, by altering the physical and chemical stand properties through the introduction of tree species, many processes where arthropods are involved, such as herbivory, pollination, predation, decomposition and nutrient cycling may be highly affected.

Most studies on decomposition and nutrient cycling focused on riparian systems (Ferreira et al. 2016) with many studies on introduced tree species in European managed forests being inconclusive. Litter decomposition of Douglas fir needles might be enhanced compared to other conifers such as spruce and thus reduced soil acidification (Knoerzer et al. 1995, Pontegnie et al. 2005). However, in a decomposition experiment in southern Germany using containers of different mesh sizes, decomposition rates of the macro (species > 2 mm) and mesofauna (0.1–2 mm) were similar to native silver fir and Norway spruce in the first year (Engel 2001). Also results from north-west Germany do not show differences in leaf decomposition between Douglas fir, Norway spruce, Scots pine (*Pinus sylvestris* L.) and European beech forest stands (Mindrup et al. 2001). These results question the improvement of soil quality by Douglas fir. Moreover, deeper soil layers may face acidification and destabilise soil humus constituents with Douglas fir (Hüttl and Schaaf 1995, Marques and Ranger 1997). The decomposition of introduced red oak was much higher than those of conifers in the study of Engel (2001), but similar to native pedunculate oak (*Quercus robur* L.). For black cherry, the proposed soil improvement could not be confirmed in pine forests of north Germany (Rode et al. 2002). In contrast, due to a favourable C/N ratio, litter of introduced black locust is rapidly decomposed and promotes biological activity in the soil (Gemeinhardt 1959). Wood decomposition might be slower in introduced compared to native trees because native insects are not adapted to the physical and chemical wood properties. Corresponding with a relatively low diversity of deadwood dependent (saproxylic) beetles emerging from experimentally exposed Douglas fir logs (Gossner et al. 2016), decay rate of Douglas fir was lowest compared to 12 native tree species in a large-scale deadwood experiment (Kahl et al., pers. com.). More decomposition experiments involving a larger number of introduced tree species are necessary for a more comprehensive evaluation of the consequences of introduced tree species for decomposition.

Species feeding on plant tissue might be most strongly affected by introduced tree species (see above). Therefore, lower herbivory rates on introduced compared to native tree species are expected, which is supported by several studies (Agrawal and Kotanen 2003, Dietz et al. 2004). As well as its effects on nutrient cycling, this might lead to a competitive advantage over native trees (Box 22). The effects of reductions in herbivore populations as a result of invasions by introduced trees might cascade up the trophic chain and this may reduce predation potential due to reduced population sizes of predators. However, successful switches of native herbivores to the new host or co-introductions of non-native herbivores might increase damage on introduced trees due to a lack of control by native antagonists (biotic resistance hypothesis; see e.g. Maron and Vilà 2001). These antagonists might adapt to herbivores on the new host given enough time. This is possibly due to interrupted chemical communications, as attraction of antagonists induced by herbivore damage has been shown to be an important mechanism in forests (Gossner et al. 2014). A decoupling of trophic interactions might significantly increase in importance with climate change in future. Such trophic decoupling has been shown in pollinator systems due to changing phenology (Rahmstorf et al. 2013), but it may also occur between herbivores and predators and parasitoids and this could lead to unpredictable consequences for forest protection.

Box 22. Enemy Release Hypothesis

Within a native community, a plant species is exposed to a broad range of natural enemies (specialist and generalist). The strength of interaction depends on the plant species itself and on abiotic and biotic factors. This leads to complex indirect effects on the plant performance and abundance. The lack of natural enemies, i.e. herbivores, on an introduced species in the introduced range is assumed to be a competitive advantage over native species. It is considered as important mechanism of biological invasions and referred to as 'Enemy Release Hypothesis, ERH' (Keane and Crawley 2002, Liu and Stiling 2006). The ERH states that non-native plants introduced in a new region are less regulated by herbivores and other natural enemies and thus increase rapidly in distribution and abundance. In introduced tree species, this most likely, occurs when regeneration is increased due to reduced seed predation or when reduced herbivory increases competitive ability over native tree species. The ERH predicts that: (1) specialist enemies will be absent from the new region; (2) host switching by specialist enemies of native congeners will be rare; and (3) native generalist enemies will have a greater impact on the native competitors (Keane and Crawley 2002).

While some support for ERH has been found in experimental studies excluding potential herbivores by using insecticide (DeWalt et al. 2004), other studies have shown contradictory results (Siemann and Rogers 2003). The importance of ERH for tree species introduced to Europe is not well studied. Reduced seed predation (Gossner and Simon 2005) and reduced herbivory (Ruff 2008) on introduced red oak compared to indigenous pedunculate oak, in particular in specialised herbivores could be confirmed. The massive regeneration and high invasive potential of red oak in Europe (Adamowski 2004) may be an indication for 'enemy release'. However, due to overall high seed production of native species, the competitive advantage of red oak over native species remains unclear. In contrast, for introduced black cherry, a high infestation and seed predation was observed in a study in Belgium, but due to the high seed production of black cherry, effects on the invasiveness are suggested to be low (Vanhellemont et al. 2014).

Leaf herbivory is known to be generally higher in seedlings than in mature trees. Herbivory caused increased mortality of seedlings (Linit et al. 1986). Hence, reduced herbivory of seedlings could lead to a competitive advantage of introduced trees in Europe. The potential advantage of 'enemy release' for introduced trees should decrease with time due to adaptations of native insect species to the introduced trees.

Effects of introduced tree species on organismic communities and related processes are multifaceted and shaped by species adaptations, species plasticity and global change. This warrants a cautious use of introduced tree species from a nature conservation as well as from an economic point of view.

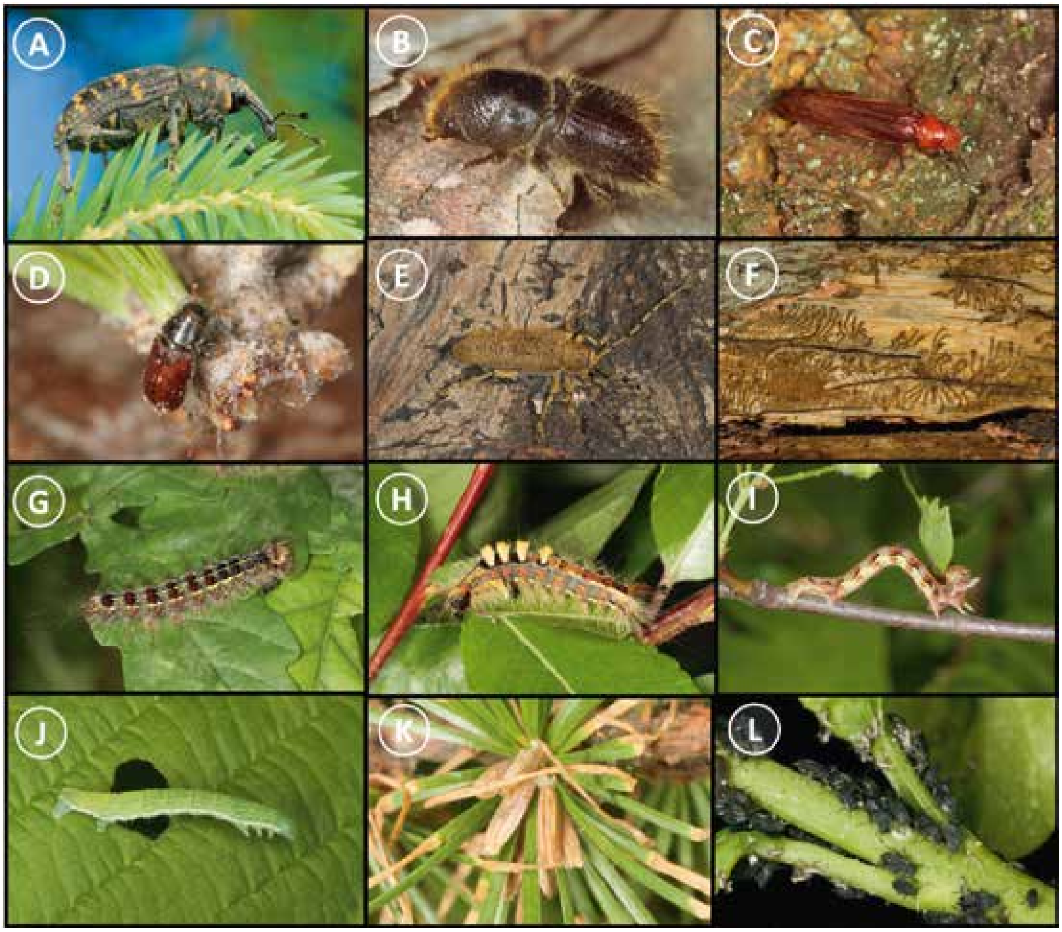

Figure 69. Examples of potential pests on introduced tree species in Europe: A) native Hylobius abietis (Linnaeus 1758) affecting young plantations of Douglas fir and grand fir. B) native spruce bark beetle (*Ips typographus* Linnaeus, 1758) and C) introduced ship-timber beetle (*Hylecoetus dermestoides* Linnaeus, 1761) attacks Douglas fir. D) native lesser pine shoot beetle (*Tomicus minor* Hartig, 1834) attacks black pine, (E) the native longhorn beetle (*Saperda carcharias* Linnaeus, 1758) attacks hybrid poplar and (F) the native large larch bark beetle (*Ips cembrae* Heer, 1836) attacks Douglas fir and Japanese larch. Among native moths, gypsy moth (*Lymantria dispar* Linnaeus, 1758) (G) feeds on Douglas fir and red oak, with the Rusty Tussock Moth (*Orgyia antiqua* Linnaeus, 1758) (H) feeding on Douglas fir. The mottled umber (*Erannis defoliaria* Clerck, 1759) (I) and the winter moth (*Operophtera brumata* Linnaeus, 1758) (J) feed on red oak, and the western larch case-bearer (*Coleophora laricella* Hübner, 1817) (K) feeds on Douglas fir and Japanese larch. The black bean aphid (*Aphis fabae* Scopoli, 1763) (L) causes damage on black locust (photos: A) WSL, Birmensdorf, B-I) B. Wermelinger).

Although most studies have found a reduced insect diversity on introduced compared to native trees (Ashbourne and Putman 1987, Gossner 2004, Kennedy and Southwood 1984, Peterken 2001), these studies also showed that many native insects already accepted introduced trees as hosts or habitats. Mostly all guilds are already represented on introduced trees, showing similarity in resource use between related native and introduced trees as well as between introduced trees in the natural and introduced distributional range (Ashbourne and Putman 1987, Gossner 2004). Thus, introduced tree species provide habitat for certain species and such conditions do not necessarily need to lead to a lower number of insect species, but rather to a different species composition than in the case of native tree species. Due to ongoing adaptations the insect diversity on introduced trees will further increase in the future. Although ecological consequences of trees most relevant to forestry, such as Douglas fir, are estimated to be less severe (Schmid et al. 2014, Vor et al. 2015), plantations of introduced trees will cause changes in community compositions, which will most likely affect ecosystem processes and services. Moreover, 'enemy release' might result in a competitive advantage for introduced tree species and may, combined with high recruitment (e.g. Douglas fir, red oak, black locust), cause problems in priority areas for nature conservation such as nature reserves (e.g. Knoerzer 2002). Therefore, a cautious use of introduced tree species in forestry is recommended.

Most introduced species in Europe have a large number of potential pest species within their natural distributional range. Douglas fir, as one of the most important introduced tree species in Europe, is known as the tree species with the greatest spectrum of pest species among tree species in North America and Canada (Altenkirch et al. 2002). In Europe, many introduced tree species already harbour a high number of insect species, which has partly already reached population densities that cause an amount of damage that is of forestry concern (Table 22).

Table 22. Examples of native and introduced insect species that caused severe damage to introduced tree species in Europe or are proposed to increase in importance as pests, in particular with climate change (*). Although species marked with § is considered as specialist of another tree genus, it switched to introduced Douglas fir.

Insect species	Insect order	Insect family	Feeding guild	Feeding specialisation	Affected introduced tree species	Remark	Reference
Hylobius abietis	Coleoptera	Curculionidae	phytophagous	polyphagous	*P. menziesii, Abies grandis*	Young plantations	Baier and Thiel (2009), (Möller and Heydeck 2009)
Strophosoma melanogrammum	Coleoptera	Curculionidae	phytophagous	polyphagous	*P. menziesii*	Young plantations	
Lymantria dispar	Lepidoptera	Noctuidae	phytophagous	polyphagous	*P. menziesii, Quercus rubra*	Stand level oak Lepidoptera complex	Lemme (2009), Möller and Heydeck (2009), Csóka and Szabóky (2005)
Orgyia antiqua	Lepidoptera	Noctuidae	phytophagous	polyphagous	*P. menziesii*	Stand level	
*Hyphantria cunea‡**	Lepidoptera	Noctuidae	phytophagous	polyphagous	*A. negundo, A. altissima*		Krehan and Steyrer (2009), Vor et al. (2015)
*Samia cynthia**	Lepidoptera	Saturniidae	phytophagous	polyphagous	*A. altissima*		Vor et al. (2015)
*Lymantria monacha**	Lepidoptera	Noctuidae	phytophagous	polyphagous	*P. menziesii, L. kaempferi*		
*Dendrolimus pini**	Lepidoptera	Lasiocampidae	phytophagous	Pine specialist	*P. menziesii*		
*Bupalus piniaria**	Lepidoptera	Geometridae	phytophagous	Pine specialist	*P. menziesii*		
*Panolis flammea**	Lepidoptera	Noctuidae	phytophagous	Pine specialist	*P. menziesii*		
*Coleophora laricella**	Lepidoptera	Coleophoridae	phytophagous	Larch specialist§	*P. menziesii, L. kaempferi*		
Cephalcia lariciphila	Hymenoptera	Pamphiliidae	phytophagous	Larch specialist	*L. kaempferi*		
Diprion pini	Hymenoptera	Diprionidae	phytophagous	Pine specialist	*P. nigra*		
Aphis fabae	Hemiptera	Aphididae	phytophagous	polyphagous	*R. pseudoacacia*		Rédei et al. (2012)

Operophtera brumata	Lepidoptera	Geometridae	phytophagous	polyphagous	*Q. rubra*	Oak Lepidoptera complex	Csóka and Szabóky (2005), Heydeck and Majunke (2002), Turčáni et al. (2009)
Erannis defoliaria	Lepidoptera	Geometridae	phytophagous	polyphagous	*Q. rubra*	Oak Lepidoptera complex	
Thaumetopoea processionea	Lepidoptera	Notodontidae	phytophagous	Oak specialist	*Q. rubra*	Oak Lepidoptera complex	
*Cryphalus abietis**	Coleoptera	Curculionidae	xylophagous	polyphagous	*P. menziesii*		Blaschke et al. (2008); Lemme (2009); Möller and Heydeck (2009); Vor et al. (2015)
*Pityophthorus pityographus**	Coleoptera	Curculionidae	xylophagous	polyphagous	*P. menziesii*		
*Pityogenes chalcographus**	Coleoptera	Curculionidae	xylophagous	polyphagous	*P. menziesii*		
*Pityogenes bidentatus**	Coleoptera	Curculionidae	xylophagous	Pine specialist	*P. menziesii*		
*Pityogenes quadridens**	Coleoptera	Curculionidae	xylophagous	?	*P. menziesii*		
*Ips acuminatus**	Coleoptera	Curculionidae	xylophagous	Pine specialist§	*P. menziesii,* *P. nigra,* *P. leucodermis,* *P. peuce*		
*Ips typographus**	Coleoptera	Curculionidae	xylophagous	polyphagous	*P. menziesii*		
*Ips cembrae**	Coleoptera	Curculionidae	xylophagous	polyphagous	*P. menziesii,* *L. kaempferi*		
*Hylecoetus dermestoides**	Coleoptera	Curculionidae	xylophagous	polyphagous	*P. menziesii*	Wood-damaging pest	
*Xyloterus lineatus**	Coleoptera	Curculionidae	xylophagous	polyphagous	*P. menziesii*	Wood-damaging pest	
Xylosandrus germanus‡*	Coleoptera	Curculionidae	xylophagous	polyphagous	*P. menziesii*	Wood-damaging pest	
Gnathotrichus materiarius‡*	Coleoptera	Curculionidae	xylophagous	polyphagous	*P. menziesii*	Wood-damaging pest	
Tomicus piniperda	Coleoptera	Curculionidae	xylophagous	Pine specialist	*P. nigra*		Vor et al. (2015)
Tomicus minor	Coleoptera	Curculionidae	xylophagous	Pine specialist	*P. nigra*		
Saperda carcharias	Coleoptera	Cerambycidae	xylophagous	polyphagous	*P. x canadensis*		Vor et al. (2015)
Gonioctena quinquepunctata	Coleoptera	Chrysomelidae	phytophagous	polyphagous	*P. serotina*		Klaiber (1999)

Weevils caused severe damage in young plantations of Douglas fir; many non-specialised Lepidoptera species are classified as potential serious pests of Douglas fir at stand level. Several other moths (among them also tree specialists), sawflies and aphids have caused severe damage to introduced tree species or are proposed to increase in importance as pests in future, in particular with climate change (Table 22). Although species that are feeding specialists on oaks are only rarely observed on red oak (Gossner 2004, Gossner and Simon 2005, Sammler et al. 2011, Wehrmaker 1990). Several species of the oak Lepidoptera complex frequently and severely damage red oak, at least under outbreak situations (Table 22). Bark beetles also increase in importance on introduced tree species. Several species breed already successfully in Douglas fir and may increasingly attack vital tree species in future, whereas other native and introduced bark beetles might increase in importance as pests that damage wood.

With increasing plantation area and time since introduction, adaptations of native pests to the new host or spill-over mass effects from dominant surrounding tree species become more likely, and thus the risk of economically relevant damage will increase. Thus a very cautious use of introduced tree species in forestry is required not only from a conservation but also from an economic point of view. Especially in the combination with climate change (increasing temperature, drought, wind throws etc.) unpredictable consequences for forest protection, e.g. by increasing plant stress, the number of insect pest generations and decoupling of herbivore-antagonist interactions (e.g. reduced pest control by antagonists) may arise. More studies are needed to better estimated climate change effects on the pest-antagonist complex of introduced tree species for a more reliable evaluation of potential risks to forestry.

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TEXT BOX V: Research gaps for a reliable assessment of the effects of Douglas fir on forest biodiversity

Kurt Bollmann and Rolf Holderegger

Forestry in central Europe is promoting the increased cultivation of introduced Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) under climate change, as Douglas fir is more drought-resistant than the native Norway spruce (*Picea abies* L. H. Karst). This trend creates a demand for more evidence of the impact of Douglas fir on non-timber forest functions such as the conservation of biodiversity. Major concerns about an intensified cultivation are the potentially uncontrolled spread of Douglas fir, competition with and threat of native species or the outbreak of new pests and plant diseases. Hence, we reviewed the available publications (scientific publications, grey literature, reports) on Douglas fir from six countries (Austria, Belgium, France, Germany, Switzerland, the Netherlands) with regard to impacts on soil conditions, on the native flora and fauna, on fungi, and for natural regeneration. In total, we reviewed 93 publications and reports (from 1948 to 2014), of which 74 % originated from Germany (Tschopp et al. 2014).

Overall, the results of single studies are heterogeneous, sometimes contradictory, and distinct tendencies are not obvious. In general, Douglas fir stands provide habitat for numerous plant, animal and fungal species. However, many studies showed a shift in species composition, richness and diversity with a tendency to less complex interspecific interactions compared to stands with native trees. This characteristic is considered to make stands with Douglas fir more vulnerable to diseases. Species composition of the herb layer varies considerably among studies and is strongly influenced by the type of management. The impact of Douglas fir on arthropod and bird species communities is age dependent. In particular, young stands are inhabited by fewer species due to the smoother bark of Douglas fir, which offers fewer microhabitats. Stands with older trees provide habitat for equal numbers or even more species than stands with native trees. Natural regeneration of Douglas fir has been observed in many study areas, in particular on dry, acid and rather nutrient-poor sites. There, Douglas fir is competitive and may displace other tree species. Douglas fir fructifies early, and its seeds are dispersed up to 200 m (but in some cases up to several kilometres). Hence, many conservationists call for site-specific regulations of the tree mixture proportion as well as for an abandonment of the cultivation of Douglas fir in and around nature reserves.

The above listed findings are not sufficient to reliably assess the overall and long-term impact of Douglas fir cultivation on native forest biodiversity in central Europe and for the derivation of sound management recommendations. There is a particular need for projects that account for the site-specific national regeneration and dispersal potential of Douglas fir as well as the impact of various mixture proportions on forest biodiversity in general, and threatened and rare species in particular. Holderegger et al. (in press) have set up an agenda of the most urgent research questions with respect to: (1) the potential invasiveness of Douglas fir; (2) the sustainable mixture proportion of Douglas fir with other tree species; (3) Douglas fir as an eventual host and introduction pathway for new diseases.

(1) Potential invasiveness. In order to estimate how invasive could Douglas fir become with intensified cultivation, three questions must be answered: (i) What is the dispersal range of Douglas fir seeds? (ii) Where does Douglas fir establish? (iii) How competitive is Douglas fir rejuvenation at those sites? According to literature, maximum dispersal distances of Douglas fir are approximately 200 m in central Europe (Tschopp et al. 2014, 2015). However, genetic studies of wind-dispersed tree species report distances of more than one kilometer to several kilometers (Kremer et al 2012). Aiming to assess the long-distance dispersal and seed establishment of Douglas fir in central Europe, we propose a well designed genetic study with kinship analysis or assignment tests.

(2) Sustainable mixture proportions. The crucial question is at what mixture proportions of Douglas fir with other native tree species – in central Europe mainly European beech – do negative quantitative (number of species, species abundance and richness) and qualitative (effect on forest species of conservation concern, national priority species, Red List species) impacts on biodiversity occur. In particular, the qualitative assessment of the impact of Douglas fir on forest biodiversity has been neglected so far (Tschopp et al. 2014, 2015). In essence, several stands with Douglas fir in different mixture proportions and stocking on similar site conditions have to be compared. This is not easy to achieve because several replicates per case are needed to produce statistically robust results. We estimate that around 20 Douglas fir stands with different mixture proportions would be needed.

(3) Potential host and introduction pathway for diseases. Some authors consider the introduction of new pests as the greatest threat of an intensified cultivation of Douglas fir (Schmid et al. 2014). The introduction of new pests with seed or seedlings from abroad or the sudden shift of a pest from a known to a new host cannot be excluded entirely. However, there are reasons to assume that Douglas fir does not represent a high risk in that respect as long as the trade with seeds and plants is regulated according to national plant protection ordinances and international import restrictions. Douglas fir has been cultivated in central Europe for more than a century. Currently, no obvious symptoms of damage are documented. Only the Douglas fir wooly adelgid (*Gilletteella cooleyi* Gillette) has established in Europe, but is confined almost exclusively to Douglas fir itself and has not caused economically or ecologically relevant damages in central European forests. We therefore do not consider the introduction of new pests as a major research gap compared to questions (1) and (2).

Conclusions. The above research questions regarding the potential invasiveness of the Douglas fir and its impacts on biodiversity are not easy to answer and their investigation are rather expensive. Without scientific evidence, however, we will not have a sound basis for the forthcoming debate and decisions with regard to an appropriate and ecologically sustainable management of Douglas fir in central Europe.

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4.6 Introducing tree species in forests and the implications for biodiversity

Yann Dumas

> *Since the agricultural settlement of Europe in the mid-Holocene, native forests have been extensively cleared and transformed; however, afforestation efforts can support the reduction of biodiversity loss and to approach to the original ecological situation.*

Depending on the intensity of deforestation in different regions, there are potential positive effects of afforestation (using native tree species) on biodiversity. Such effects are related to the actual proportion of forest in the given landscape; the afforestation tends to be low in areas where the forest cover is high. However, it is usually high in areas with a high proportion of intensive agriculture or in heavily urbanised areas. Forests have been heavily exploited and transformed due to their economic value. Uncultivated areas such as moors, bogs and grasslands became particularly rare due to human activity. Although such habitats were considered to be of a lesser economic value, they host high value for biodiversity. When such habitats are afforested, strong negative effects on specific biodiversity can be observed. The implication of afforestation is hence two-fold: on the one hand, afforestation can have significantly positive effect on forest species by offering them the opportunity to colonise new areas. Afforested areas further provide temporary refuge areas for some non-forest species such as grassland butterflies (Villemey et al. 2015). On the other hand, at the landscape level, it may, in some cases, have a negative effect on gamma biodiversity, especially when afforestation occurs at the expense of native habitat damage; in such case, it may lead to the decline of rare species population (Bastos et al. 2012).

These effects are usually observed regardless of the origin of species used for the afforestation. However, the magnitude of such effects may be related to the characteristics of the specific tree species used. Therefore, it is important to focus on the reasons why some tree species are associated with a lower biodiversity than other tree species and what is the role of introduced tree species with invasive character.

> *Each species, regardless of being native or introduced, acts as an ecological filter for biodiversity due to its morphological, chemical, ecological and historical traits.*

The dominant tree species determines the microclimate of a specific site (Barbier et al. 2009) and litter acidity (Barbier et al. 2008). In turn, these factors influence the community of associated species (Figure 70).

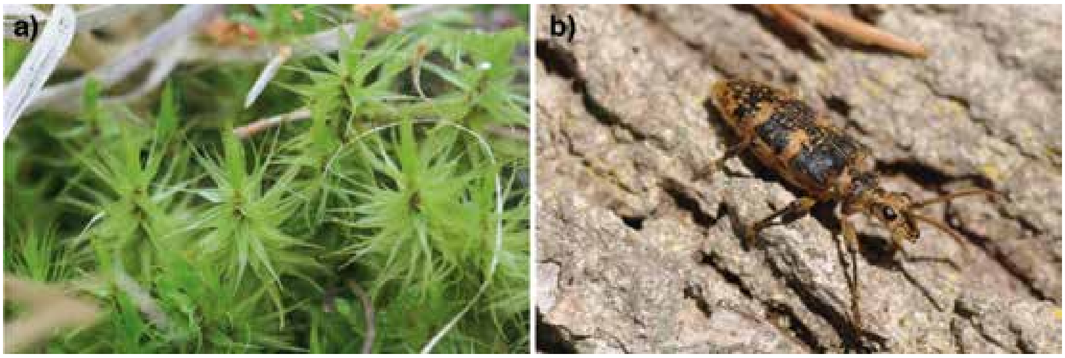

Figure 70. a) Rugose fork moss (*Dicranum polysetum*), a rare bryophytes species favoured by Scots pine plantation in lowland area, Montereau, OPTMix experimental site, France (photo: Y. Dumas) and b) *Rhagium* (*Megarhagium*) *sycophanta* – an insect species associated with oak deadwood (photo: B. Nusillard).

For example, a tree whose bark exfoliates regularly (e.g. *Pinus sylvestris* L.) will not be favourable by a rich community of epiphytic mosses, or a tree species (e.g. *Carpinus betulus* L.) that forms a dense canopy intercepting a lot of light thus prevents the development of diverse ground vegetation. This demonstrates that each tree species favours a different group of organisms to varying extent.

The soil and climate of the area where a particular species is distributed also acts as a filter and can lead to a co-evolution phenomenon over the long term. The tree species with a large native distribution and/or a greater ecological variation, usually results in the species being associated with greatest biodiversity. When a tree species is introduced into a new geographical area, most of the links with the other living organisms in its native range are lost. Therefore, a new period of co-evolution over the long term is necessary for new inter-relations between native organisms and the introduced tree species to develop and reach a certain level of biodiversity supported by native tree species.

This must be viewed as an average effect and does not mean that an introduced tree species may never accommodate for more species than the native ones for a particular group of organisms. However, there are several examples where introduced tree species can accommodate for greater biodiversity than native species. For example, the diversity of bryophytes and fungi was reported to be greater under Norway spruce (*Picea abies* (L.) H. Karst.), species introduced to Great Britain, in comparison to the native Scots pine (Quine and Humphrey 2010). Another such example may be found in Sweden where the floristic diversity is found to be greater under European larch (*Larix decidua* Mill.), which is an introduced tree species to Sweden in comparison to the native Norway spruce (Felton et al. 2013).

▶ *Replacing native tree species with introduced ones generally results in a decline of native biodiversity.*

Sessile oak (*Quercus petraea* (Matt.) Liebl.) and pedunculate oak (*Quercus robur* L.) colonised northern Europe at the end of the last Ice Age (about 10 000 years ago). For thousands of years, the plasticity of oak species and associated co-evolution processes allowed oaks to develop the greatest insect biodiversity in comparison to any tree species in Great Britain (Kennedy and Southwood 1984; Figure 70b).

The study from Great Britain by Kennedy and Southwood (1984) reported over 400 species of insect associated with sessile and pedunculated oaks, in contrast to only two and nine insect species associated with black locust (*Robinia pseudoacacia* L.) and horse chestnut (*Aesculus hippocastanum* L.), respectively, which are tree species introduced to Great Britain about 400 years ago. Unfortunately, studies of this type are very rare not allowing us to draw a comprehensive picture of the biodiversity associated with each tree species and it is consequently difficult to assess the impact of their replacement.

An introduced invasive tree species may strongly interfere with other species.

Due to the strong competitive traits, some invasive species may cause a significant reduction of local diversity, e.g. on plantation sites, which is linked to the competition for water, minerals or light, but also to mulching effects or allelopathy. For example, the tree of heaven (*Ailanthus altissima* (Mill.) Swingle) produces a natural herbicide ailanthone and causes the loss of vascular plants species richness from the sites invaded by this tree by 15 to 30 % (Motard et al. 2011). This, however, depends on the ecological context (Figure 71a). In many cases, invasive tree species show a greater density than native tree species (Delmas et al. 2011); among invasive plants growth forms, trees have a greater impact on species richness than for instance grasses and herbaceous plants (Gaertner et al. 2009). As the ground flora represents the basis in the food chain, cascading effects on other parts of biodiversity are likely to occur (Haddad et al. 2000).

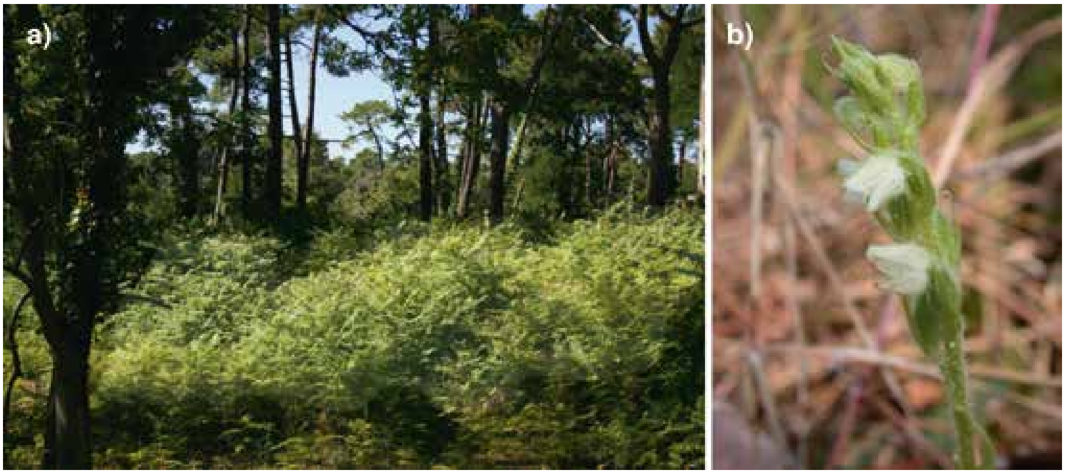

Figure 71. a) Forest site invaded by the tree of heaven that causes floristic diversity loss by 15 to 30 %; Charente-Maritime, France (photo: Y. Dumas) and b) creeping lady's-tresses in Nogent-sur-Vernisson, Domaine des Barres, France – a species favoured by the introduced Scots pine in lowland forest (photo: L. Léquivard).

Invasive species have a strong ability to quickly colonise sites outside the area of their original introduction. Sites that have a high conservation value providing habitat for rare species that are located in a close proximity to plantations comprising of introduced species are likely to be affected by the consequent colonisation of the plated species. At the landscape level, the disappearance of rare species contributes to the reduction and homogenisation of the overall diversity. Open habitats such as sand dunes or grasslands are particularly susceptible to invasion by, for instance, the tree of heaven (Kowarik and Säumel, 2007) or black locust (Kleinbauer et al. 2010). Riparian forests are also susceptible to the invasion and ash-leaved maple (*Acer negundo* L.) may be an example of tree species commonly found invading this valuable habitat (Schnitzler et al. 2007; Chapter 5.10).

When conservation of natural habitats is a priority, planting tree species such as ash-leaved maple, tree of heaven, eastern white pine (*Pinus strobus* L.), black cherry (*Prunus serotina* L.) or black locust that can be highly invasive under certain conditions should be avoided (Weber and Gut 2004). If such species need to be planted, sensitive natural areas that are likely to be negatively affected should be avoided (Stupak et al. 2011) and a buffer zone around the planted area should be designated to prevent the spread of the species. In order to prevent the natural spread of such species, planting native tree species with dense foliage, typical of late-successional communities, may be the most efficient control method (Calviño-Cancela and Neumann 2015).

It is often assumed that undisturbed natural forests are resistant to plant invasions. However, even dense forests with low light levels are potentially susceptible to invasion by shade-tolerant introduced tree species (*Prunus serotina* Ehrh.). Martin et al. (2009) identified nine temperate shade-tolerant tree species that were considered to be potentially invasive (for forests in the United States). Furthermore, ornamental plantings of species in parks and gardens are also considered an important source of propagules (Dyderski et al. 2015). The forests around urban areas are particularly susceptible to invasion, not only by introduced tree species, but also by a large number of introduced species of other life forms.

▶ *Unintentional introduction of species associated with the deliberately introduced species may also happen.*

Additional species may be unintentionally introduced along with the target species; such species may be adapted to their new environment and may be able to naturalise and enrich the local – sometimes poor – community. The creeping lady's tresses (*Goodyera repens* (L.) R.Br.) may be considered as such example as it was unintentionally introduced into the French lowland forests in 19th century (Figure 71b). The seeds of this small mountain orchid were introduced into the area along with Scots pine seeds used to afforest this area as the seeds may adhere to Scots pine cones when harvested for their seed. The orchid's seeds may subsequently mix with Scots pine's seeds during transport or extraction from cones (Larchevêque 1898). The Cooley spruce gall adelgid (*Adelges cooleyi* Gillette), which is a source of food for native insect predators in Europe, was introduced along with Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Gossner and Ammer 2006) (Chapter 4.5). It may be considered as another case of unintentional introduction. If unintentionally introduced species do not show invasive behaviour, the situation may be viewed positively, as it corresponds to an increase in species richness.

However, there are many cases when unintentional introductions of organisms associated with planted introduced tree species are less favourable for biodiversity. These include mycorrhizal fungi capable of promoting the development and establishment of the tree species, which in turn, may become invasive (Chapter 2.5). Ten species of fungi associated with Australian eucalypts (*Eucalyptus camaldulensis* Dehnh. and *Eucalyptus globulus* Labill.) that could become invasive and affect biodiversity were identified in Spain (Diez 2005). Bacteria (*Bradyrhizobium* spp.) associated with the western Australian golden wattle (*Acacia saligna* (Labill.) H.L.Wendl.) were for instance found in Portugal (Crisóstomo et al. 2013).

Introducing closely related tree species may cause uncontrolled gene flow into the wild populations.

In Sweden, the populations of native species of aspen (*Populus tremula* L.) may be at risk due to the uncontrolled gene flow from the stands of planted hybrid aspen (*Populus tremula* L. x *P. tremuloides* Michx.) (Felton et al. 2013). This is also the case for black poplar (*Populus nigra* L.) that can be found in some of Europe's riparian forests, which is a habitat that is relatively scarce in Europe. Uncontrolled gene flow through hybridisation with ornamental varieties of poplar or plantations of hybrid poplar are also common as reported by e.g. Pautasso (2009). Hybridisation could induce lower adaptation of this species to the natural ecosystem and its disappearance. However, apart from specific genetic variations, some species may also adapt very quickly to newly introduced tree species, which is particularly the case of the species that use plantations as surrogate habitat regardless of the tree species' origin. For example, eucalypt stands can be used as a shelter for the endangered Iberian Lynx (*Lynx pardinus* Temm.) when moving between patches of their preferred habitat (i.e. Mediterranean scrubland) in central Spain (Ferreras 2001).

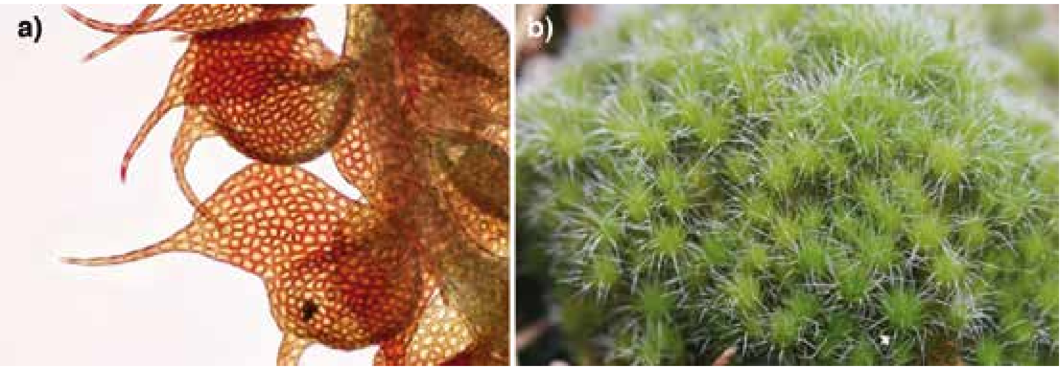

Figure 72. a) rustwort (*Nowellia curvifolia*) – Saint-Martin-d'abbat – Forest of Orléans, France (photo: Y. Dumas) a bryophyte species favoured by introduced Scots pine dead wood in lowland areas and b) heath star moss (*Campylopus introflexus* Bridel) – an invasive bryophytes species favoured by the introduced Scots pine in lowland forest (particularly in mixed stand with oak) posing a potential risk for native bryophyte species Montereau, Forest of Orléans, France (photo: Y. Dumas).

Other species are able to change their feeding behaviour in order to adapt to supplies offered by an introduced tree species. For example, in Spain, some species of birds use eucalypt flowers as a food source during periods when their natural food sources are scarce (Calviño-Cancela and Neumann 2015). Therefore, where natural forest disappeared, stands of introduced species may be considered as having a positive effect on biodiversity. Introduced tree species may also contribute to biodiversity at the landscape level as their characteristics may favour other native or introduced species in the region of their introduction. For example, conifer plantations have increased the wooded area and provide habitat for some forest bird species in Belgium (Baguette et al. 1994) or for certain beetle species in Britain (Humphrey et al. 2003). This could be considered as an 'artificial local biodiversity' contributing to the protection of certain rare species.

Afforestation using introduced tree species, however, plays an important role in agricultural landscapes as it improves the connectivity between isolated patches of forests and can be highly beneficial to some endangered species (Brockerhoff et al. 2008). Along with the example of the Iberian lynx in Spain, the rare species of fungi linked to native Scots pine stands have been detected in Sitka spruce (*Picea sitchensis* (L.) Bong. Carr.) plantations in Britain are also an important case. These stands create a refuge if they are located close to the native forest (Humphrey et al. 2003). Nonetheless, the beneficial effect is still detectable even one hundred kilometres away from stands of native Scots pine.

Silvicultural practices play an important role in increasing biodiversity in forest stands dominated by introduced as well as native tree species.

Intensive vegetation management leads to simplification of the understory layer, which may result in reduced biodiversity. For example, Santos et al. (2006) noted that less intensive management promoted a more complex vegetation structure and a greater degree of associated bird diversity in plantations in Spain comprising mostly of maritime pine (*Pinus pinaster* Aiton), with minor proportion of stone pine (*P. pinea* L.) and Aleppo pine (*P. halepensis* Mill.)

The presence of deadwood and old trees is also very important as these elements promote the occurrence of species restricted to these specific microhabitats (Wallace and Good 1995). For example, the bryophytes species *Lepidozia reptans* (L.) Dumort and rustwort (*Nowellia curvifolia* (Dicks.) Mitt.) (Figure 72a) are favoured by the presence of lying deadwood of introduced tree conifer species.

Although the high density Sitka spruce plantations do not support rich ground flora, the diversity of the ground flora can be improved by thinning (Wallace and Good 1995). Since plants are the first link in the food chain, the lack of light in the conifer plantations can have a cascading negative effect on biodiversity, starting with foraging species such as butterflies (Sparks et al. 1996).

Despite the large number of published studies on the effects of introduced tree species on several taxa, it is difficult to establish a general assessment for particular introduced tree species without studies specifically dedicated to such species.

Studies focusing on the effects of introduction of tree species on biodiversity often concern only a small number of taxa or ecological groups frequently resulting in a mixture of negative, positive and neutral effects. Consequently, drawing generally applicable conclusions still remains difficult. The research results generally relate to the average species richness, but often do not address their heritage/conservation value (e.g. red-list species). For a fixed species richness, the heritage value may be lower if the community is composed of a large number of generalist and opportunistic species as for instance the case of Monterey pine (*Pinus radiata* D. Don.) plantations of northern Spain (Onaindia et al. 2013). The heritage value of such plantations comprising on introduced tree species is lower (Figure 72b). In northern Portugal, Lomba et al. (2011) record more invasive species under eucalypt plantations than under mixed pine-eucalypt forest stand.

The introduction of tree species is often considered as part of the solution for forest adaptation to climate change. There is an urgent need to assess biodiversity related to introduced tree species and how such biodiversity compares with the biodiversity linked to native tree species that they are likely to be replaced under the current climate change forecast. This would allow assessing the risk of biodiversity loss according to the tree species planted along with the probability of adapting it to the biogeographical context.

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4.7 Natural disturbances and invasive introduced plants – a specific view on fire

Daniel Kraus, Joaquim S. Silva, Alexander Held, Marc Castellnou and Frank Krumm

Disturbed ecosystems are more vulnerable to invasions by introduced species and thus ecosystem invasibility can be linked to disturbances (e.g. Myers 1983, Larson et al. 2001). Studies, mainly in the Mediterranean region, are presented in this chapter as examples of how disturbances interact with introduced plants and influence ecosystem development. In particular, fires may produce perfect conditions for plants to invade an ecosystem through interdependent mechanisms (e.g. Gaertner et al. 2014) that often result in dense stands of one particular introduced species. In turn, these formations may exhibit flammability characteristics which facilitate the occurrence of more fires, and thus establishing conditions that lead to continued environmental degradation. This may be fundamentally different from physical degradation processes whose interruption, and even reversal, were possible thanks to reforestation work (Figure 73) over the nineteenth and twentieth centuries (Vieira 2007).

Figure 73. Traces of physical degradation in mountain areas of Portugal (photo: reproduced from Vieira 2007).

Biological degradation processes caused by invasive species are often irreversible.

Disturbances are more and more perceived as an intrinsic part of ecosystem dynamics (e.g. Pickett and White 1985), but the effects of anthropogenic disturbances on ecosystem processes may not be equivalent to natural ones. Increasingly human activities have changed frequency and size of fires so that the effects of these fires on ecosystems are different than fires in the past (Roberts and Gilliam 1995) and have resulted in subsequent changes to vegetation structure and function. There is a range of theories to explain the success of invasive species in non-native habitats. One important aspect is that many invasive species possess contrasting traits, i.e. the ability to colonise areas and also to persist within the environment (D'Antonio and Meyerson 2002). That means these species are well equipped with well-dispersing propagules to opportunistically take advantage of disturbances. At the same time, they have the ability to compete effectively with native species for available resources (see also Denslow 2003) and may also benefit from the scarcity of natural enemies (the enemy release hypothesis, see also Chapter 4.5) in the areas they invade (Colautti et al. 2004). However, it is not only the ecological traits of the invaders that determine whether ecosystems are invaded (Ewel 1986). Another important aspect of ecosystem invasibility is related to species diversity. Although empirical results are often mixed (Levine and D'Antonio 1999) it seems that ecosystems with a lower diversity of species and functional groups are more invasible (Elton 1958) because many empty niches can make them more vulnerable to colonisation by introduced species. This theory of vacant niches applies equally well to increasingly isolated habitats under scenarios of intensified disturbance such as increased fire frequencies.

▶ *Increased burn frequencies can progressively exclude fire-vulnerable components of biodiversity.*

In ecosystems without fire adaptation, fires can have profound consequences for forest structure and composition as even surface fires can cause mortality of thin-barked adult trees (Barlow et al. 2003). Over repeated burn cycles, such ecosystems are depleted of species that can neither resist fires (the stems die because they have thin bark) nor recover from fires (they do not have the ability to re-sprout or regenerate after fires). Additionally, even if they have traits that allow them to recover, if the fire interval is too short, they will not have time to reach reproductive maturity (i.e. obligate seeders). The result is a significantly altered, and reduced, species composition.

In the long term, ecosystem functioning can be highly and irreversibly affected by frequent fires where fire regimes have been altered by human influence. Frequent fires allow less time for fuel load to accumulate between successive burns and thus only develop into low-intensity fires. This may lead to short-term pulses in nutrient availability and increased mineralisation of soil organic matter which generally benefits seedlings and grasses that re-sprout after burning. Frequent fires are often associated with human-driven disturbances, where ecosystems are much more prone to be invaded, often leading to a progressive degradation of the ecosystem. In contrast, infrequent fires tend to burn hotter because fuel accumulation is greater between successive fire events. Infrequent fires are common in natural ecosystems where fire is part of the natural cycle of ecosystem regeneration. However, where such high-intensity fires are not part of ecosystem functioning they can result in reduced soil nutrient availability and reduced soil water-storage capacity (Neary et al. 1999). Over time, an increase of hot and intense fires may result in the conversion of relatively productive forests to degraded vegetation forms if they occur frequently enough to prevent soil recovery between successive disturbances (Brown and Lugo 1990).

Only a few introduced species that are planted widely in the Mediterranean are adapted to fire.

Among the introduced species with the highest significance in these processes, woody species must be considered above all, firstly because they lead to high fuel loads, and secondly, because they have the capacity to dominate ecosystems. In this regard it is important to differentiate between introduced species that have shown a capacity to regenerate profusely (e.g. acacias, *Acacia* spp.) and introduced species that have not shown the capacity to regenerate profusely (e.g. eucalypts, *Eucalyptus* spp.).

The management of vegetation in burned areas with presence of introduced species will depend on: (i) the severity of the disturbance; (ii) the vegetation characteristics (plantations or established from uncontrolled colonisation); (iii) the floristic composition before the fire; and (iv) objectives for the burned area (Moreira et al. 2010). In many cases, colonisation through self-regeneration is the result of poor management or absence of management (Silva et al. 2011). Therefore it is likely that unmanaged areas colonised by invasive species will remain abandoned after fires and the invasion problem will continue or even deteriorate (Keeley et al. 2011).

Mandle et al. (2011) stated that “fire regimes influence and are influenced by the structure and composition of plant communities”, resulting in complex relationships between each of these components. There is evidence that invasive behaviour of some introduced species can be promoted by certain fire regimes (Keeley and Brennan 2012). Invasive species can also significantly alter fire regimes, eventually leading to a self-perpetuating fire cycle (D’Antonio and Vitousek 1992, Gaertner et al. 2014). The rapid regeneration and growth of some species in recently burned areas results in a faster build up of fuel load, which can lead to higher intensity fires than would otherwise be the case, which in turn can lead to increased regeneration of fire-adapted introduced species (e.g. Keeley et al. 2012). Depending on the species concerned and the fire regime, this cycle can be extremely difficult to stop and is surely one of the most intractable problems in the management of burned areas (Vallejo et al. 2012). The germination of acacias, for instance, is stimulated by fire passages as the soil seed bank reacts on high temperatures and might break the dormancy of the seeds (e.g. Hanley, 2009). The case of mimosa (*Acacia dealbata* Link) is particularly relevant given that its seeds can remain viable in soil for over 200 years in its native range in southeast Australia (e.g. Hunt et al. 1999). The second case is the silky hakea (*Hakea sericea* Schrad. & J.C. Wendl.), which stores seeds in serotinous fruits, and regenerates only by seed. After the passage of fire the woody, seed-containing follicles of silky hakea open and the seeds are dispersed over long distances. Most seeds are dispersed within a 100 m radius of the parent, but in some conditions seeds can be dispersed several kilometers (Le Maitre et al. 2008) (Figure 74).

Figure 74. Post-fire regeneration of *Hakea sericea* in central Portugal (photo: H. Marchante).

> *Introduced trees with invasive behaviour can change any of the components of the fire regime: frequency, intensity, average size, fire type and seasonality.*

The main influence of the presence of introduced tree species on fire regime is through a profound change in the fuel characteristics. The fuel properties may change in terms of flammability, fuel load, vertical and horizontal continuity and degree of compaction (Brooks et al. 2004). However, not all changes in the fire regime are associated with an increased risk of fire. In fact, there are studies that report the possibility of a lower flammability of invasive plant formations (Brooks et al. 2004, Mandle et al. 2011.) compared to the formations present before invasion. This is the case with black locust (*Robinia pseudoacacia* L.), which is native to the eastern United States and is reported to be invasive in the pine barrens of the north-eastern United States. The pine barrens are ecosystems dominated by pines (e.g. *Pinus rigida* Mill., *P. banksiana* Lamb., *P. resinosa* Aiton) and which depend on fire to prevent invasion of less fire tolerant species. The combustibility of black locust is lower than that of the pines, and black locust invasion can therefore lead to a permanent change in species composition unless actions are taken to remove black locust (Richburg et al. 2004). Among the many examples we can refer the opposite findings with stands of acacia in Portugal, where acacia is associated with greater combustibility, according to the assessment made by Fernandes (2009).

The changes caused in the communities of plants by the spread of invasive plants in a post-fire scenario are still poorly understood, but are surely a result of a multitude of factors. Taking into account the complex relationships between fire and the invasion processes by exotic plants, Keeley et al. (2005) presented a conceptual model for California where they studied, among other things, the fire regime, the structure of communities before and after the fire, and climatic factors. In this work the authors concluded that the critical factors for the invasion process are mainly associated with how quickly the community of native species can cover the ground. In some Mediterranean landscapes the invasibility potential has increased with the development of large infrequent wildfires over the past decades (Table 23) due to the proximity of urban and peri-urban areas to severely disturbed ecosystems (wildland-urban interface). This triggered the dispersal of mainly introduced ornamental plants into abandoned land.

Table 23. Generations of large wildfires and the potential for invasibility by introduced plants in Euro-mediterranean landscapes (modified from Costa et al. 2010)

Generation	Main factor	Fire behaviour	Invasibility potential
1. 1950s and 1960s	**Continuity** of vegetation cover leads to large perimeter growth, little fragmentation through active farmland	Forest fires between 1000–5000 ha. Surface fires, wind driven.	low
2. 1970s and 1980s	**Rate of spread.** The accumulation of combustible biomass leads to fast spreading fires with high spotting potential.	Forest fires between 5000–10 000 ha. Wind and topography driven.	intermediate
3. 1990s	**Fire intensity.** The accumulation of combustible biomass reaches canopy closure, crown fires with high convective potential.	Crown fires with high spotting potential. Forest fires between 10 000–20 000 ha. Extreme heatwaves reinforce high intensity fires.	high
4. since 2000	**Wildland-Urban Interface fires** are increasing affecting mainly abandoned land	Forest fires in close proximity to urban settlements and abandoned land, usually larger than 1000 ha	very high
5. since 2000	**Mega fires.** Simultaneous large wildfires in high-risk areas with extremely rapid and virulent fire behaviour crossing the urban and peri-urban areas	Simultaneous crown fires affecting also wildland-urban interface.	very high

After the introduction of non-native species, the subsequent stages of the invasion process, if there are any, can lead to alterations of the fuel properties, floristic composition and other ecosystem properties (Vilà et al. 2009). Brooks et al. (2004) present a comprehensive model that illustrates the fire cycle created from the invasion of introduced species. This cycle is developed according to four stages: in phase 1, the seedlings reach a new region; in phase 2, the introduced species becomes naturalised or invasive, but does not yet have a significant ecological impact; in phase 3, the introduced species has a significant ecological impact, but without changes in the fire regime; in step 4, the introduced species changes the fire regime establishing a cycle associated with the process of invasion (Figure 75).

▶ *There are different considerations for restoration of fire-affected plantations of introduced tree species.*

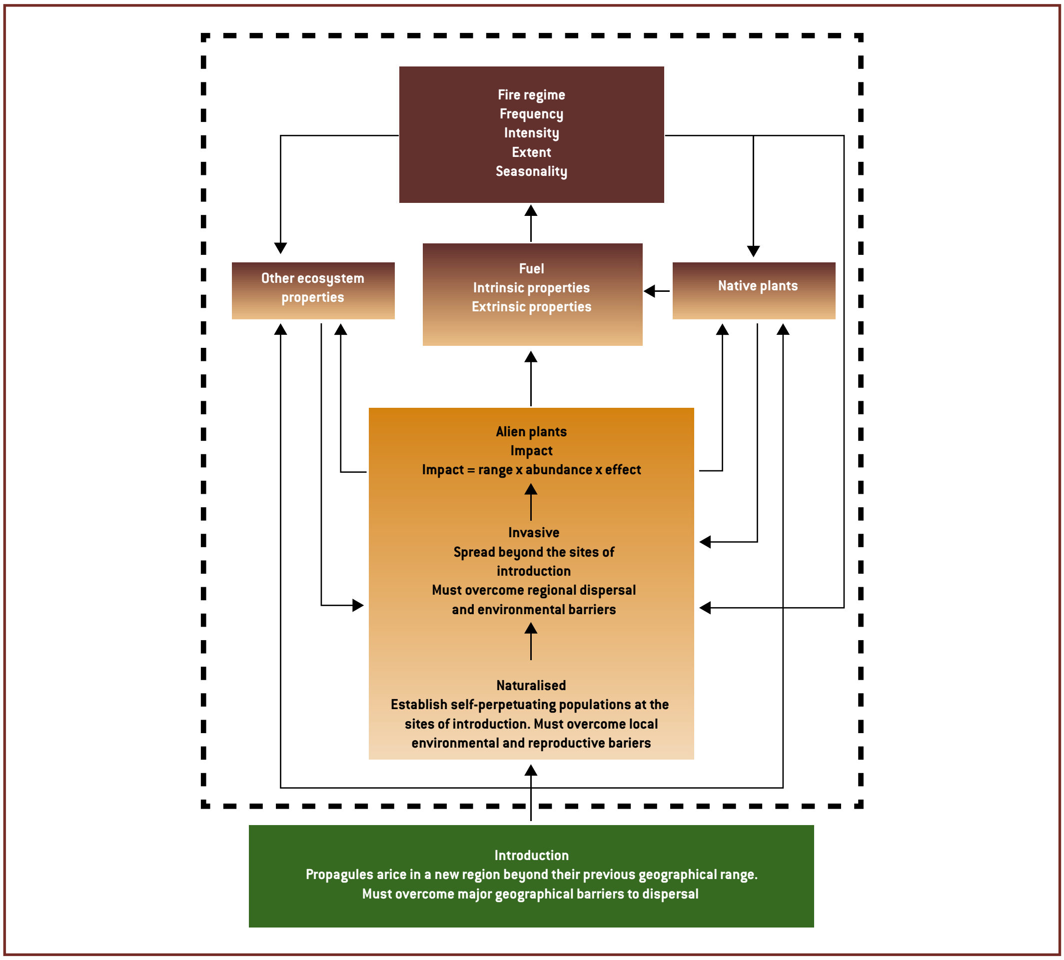

Figure 75. The invasive plant fire cycle: green, phase 1; light orange, phase 2; orange, phase 3; red, phase 4 (modified from Brooks et al. 2004).

Rehabilitation of a burned forest plantation can be a fairly simple process (e.g. Moreira et al. 2012). If there are no other constraints, rehabilitation may simply consist of salvage logging and replanting the burned area with the same tree species. However, rehabilitation is not always as simple, depending on the approach to be adopted, which will obviously depend on the severity of the fire, species and management objectives. The first two aspects are linked, since different species are associated with different fuel characteristics, which in turn influence the fire regime. Despite their high combustibility (e.g. Fernandes et al. 2011), eucalypt plantations are also very resistant to fire because eucalypts can resprout (e.g. Catry et al. 2013). This feature may simply mean that the best solution for a burned plantation is to make a coppice cut and wait for the vegetative regeneration. The conservation of soil and water should always be a concern in good management practices in order to minimise soil loss and the change in hydrological conditions. Furthermore, environmental concerns can and should be considered, particularly when it comes to replacing a burned plantation of an introduced species. In fact, the occurrence of a forest fire presents an opportunity to implement environmental mitigation measures such as the establishment of ecological corridors in the plantation area (Silva et al. 2007a). In a burned plantation the post-fire regeneration of native plants may be considerable, representing an opportunity for conversion of old plantations to other types of vegetation, which be of more value from a conservation and biodiversity point of view (Moreira et al. 2013).

Uncontrolled colonisation by invasive introduced plants can be challenging for species that are well adapted to fire.

Burned areas containing invasive introduced species can present a heterogeneous structure and composition, because in many cases the plant formation may also include naturally regenerated native vegetation. Therefore, the type of ecosystem, the severity of the fire and, consequently, the system response may vary widely. In such situations the objective is often to assist the regeneration of native species, but may include other objectives; particularly with regard to fire prevention through structural modification of the fuel. Post-fire management may be a long-term task, including various approaches, and involving several steps. Therefore, the management of burned areas with invasive vegetation can be highly demanding in technical and economic terms, which makes it very important to plan and monitor the measures implemented.

Given the opportunistic nature of most invasive species, a burnt plantation comprising of non-native tree species may permit the establishment of other introduced species.

In the case of commercial plantations, the pressure of international markets have led forest-based industries to certify their products according to sustainable criteria developed by different certification schemes (e.g. Georgiadis and Cooper 2007). Thus, besides the common goal of intensive wood production, managers are being directed towards more sustainable and diversified management models. In order to achieve objectives of improving ecosystem services such as biodiversity conservation and landscape, these new management models involve commitments in order to achieve a balance between the goods and services to society (Carnus et al. 2006). One of the requirements is reflected in the maintenance of natural vegetation patches within the managed area. The occurrence of fires presents an opportunity to convert areas of lower productivity into conservation areas (Silva et al. 2007b). However, there are still few reported cases of conversion of burned forest plantations into more natural vegetation types, at least for southern Europe. Depending on the species concerned, this type of conversion can involve considerable effort. Some species that are particularly adapted to fire can be particularly difficult to control, especially where there is a strong vegetative regeneration capacity, such as is the case with eucalypts. The existence of abundant regeneration from seeds may require additional efforts in order to avoid the spread to neighbouring areas (Calviño-Cancela and Rubido-Bara 2013).

Fire in intensively managed plantations leads to a greater degree of disruption than fire in other ecosystems. This may promote the establishment of invasive introduced species (Fernandez-Lugo et al. 2009), or it may instead allow for more efficient control. In the particular case of mismanagement or abandonment this may eventually lead to a conversion to mixed stands (Silva et al. 2011). Other aspects may need to be considered in assessing the risk of invasion. In particular, the proximity of roads, urban areas and human disturbance in general have proven to have a strong influence on the increase of introduced plants (e.g. Von der Lippe et al. 2013). Finally, we must consider post-fire regeneration and establishment of introduced species from self-regeneration or uncontrolled colonisation. In this case, the pre-fire vegetation is already the result of an invasion. Fire occurrence can, however, increase the area occupied by the invasive species.

Given the importance that has been attributed to the management of invasive species, there is a pattern of priorities that is established internationally (Silva and Marchante 2012). In general, the management of invasive species should incorporate a phase sequence including: prevention; early detection and rapid response; eradication; containment and control; restoration and mitigation; monitoring; and evaluation (e.g. Hulme 2006). These steps are usually sequential, but not necessarily, given that some of them may be applied simultaneously. Before deciding to invest in costly management options, it is essential to establish priorities on which species and areas should be addressed, taking into account such factors as: the level of impact; likelihood of success; the value of the ecosystem after recovery; and availability of resources (Pyšek and Richardson 2010). Fire and the establishment (deliberate or through invasion processes) of introduced plants, are changing the landscapes of vast areas radically and, in some cases, irreversibly.

> ▶ *New technologies allow insight into the dynamic expansion of invasive introduced species.*

The use of unmanned aerial vehicles (UAV), also known as drones, has been repeatedly referred to as one possible approach to monitor the spread of introduced species (Dvořák et al. 2015). Another approach is the use of aerial images available online through Google Earth and Google Street View systems (Visser et al. 2014). It is now possible to obtain images from different years in order to evaluate the development of the areas occupied by introduced species. In the case of Google Street View, we can survey densities or even growth, based on observation of images collected along roads. There is an enormous wealth of information that may be collected with a minimum investment of resources and time (Deus et al. 2016).

It seems likely that the frequency and the extent of disturbances across Europe will continue to increase with further land-use changes, forest expansion, projected climate warming and fires (e.g. Seidl et al. 2014, Millar and Stephenson 2015). As one of the major goals of modern forest management is to create resilient forests, it is crucial to better understand disturbance dynamics and its relations to forest ecosystems.

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Resprouting eucalypts after a forest fire in a pine forest (photo: J. Silva).

5. Case studies of introduced tree species

Examples of selected introduced tree species to the European continent are presented in the fifth section. The different case studies focus on the ecology, management and economic relevance of certain species. The invasive behaviour of selected species across Europe and across different ecosystems is also addressed in this section.

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Verena Quadt, Gerald Oitzinger and Karoline Zsak

5.1 Black locust: from global ecology to local management – a case study from the Czech Republic

Michaela Vítková, Jan Pergl and Jiří Sádlo

Introduction and the introduced range

Black locust (*Robinia pseudoacacia* L.; Figure 76) is a nitrogen fixing, deciduous tree species growing in open and light habitats, often cultivated and considered as invasive in many countries (Cierjacks et al. 2013). Its native range is the south-eastern part of North America where it occurs in two separate areas: an eastern population centred around the Appalachian Mountains ranging from Pennsylvania in the north to Alabama and Georgia in the south, and a western population present in parts of Missouri, Arkansas and Oklahoma (Fowells 1965). Black locust has been widely planted across the globe and it can now be found in most European countries (DAISIE; http://www.europe-aliens.org/) and also in temperate and subtropical parts of Asia, Africa, Australia and South America (e.g. Weber 2003, Dufour-Dror 2012). It has also been considered as naturalised throughout the northern part of the USA, southern Canada and northern Mexico (Huntley 1990). Although the native range of black locust has a humid temperate climate, it has been successfully introduced into a range of climatic zones including cold oceanic Patagonia, subtropical South Africa, and dry continental Turkey (e.g. Li et al. 2014).

Figure 76. Black locust (family *Fabaceae*) is one of the first tree species introduced to Europe from North America (photo: M. Vítková).

Black locust was introduced to Europe in the first half of 17th century as an ornamental tree species in gardens and parks (Ernyey 1927). Its economic potential was first recognised in the 18th century; it began to be planted for forestry purposes (Keresztesi 1988), which resulted in 'black locust mania'. At the end of 19th century and beginning of the 20th century it was planted in sandy areas and dry deforested habitats that were formerly used as pastures. Such developments substantially changed the look and function of many areas where black locust had started to become dominant.

Black locust, a tree species native to North America, has been widely naturalised in many temperate and subtropical regions across the world; in the Czech Republic it currently covers 0.5 % of the total forested area (14 087 ha).

Black locust currently occurs in many parts of the Czech Republic at altitudes below ca. 750 m. It is most commonly found in areas with warm climate below the altitudes of ca. 400 m (Figure 77). The species is distributed mainly in rocky valleys in central Bohemia (Figure 78) and western Moravia as well as in some sandy areas in Czech and Moravian lowlands. Black locust is also found in urban and industrial, including mining, areas. According to National Forest Inventory of the Czech Republic (2014), black locust forest stands cover 14 087 ha (0.5 % of the total forested area) and contribute with 0.43 % (54 790 m^3, of which 93 % was established by natural regeneration) to the annual timber production. The forest stands dominated by black locust were either artificially established or regenerated naturally between 1920 and 1940.

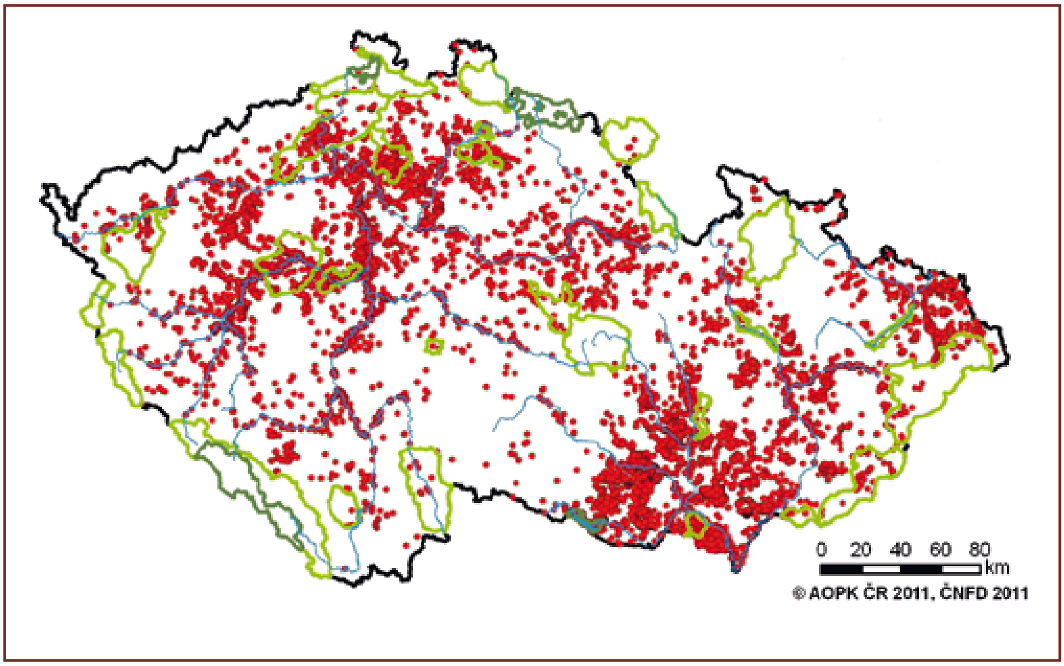

Figure 77. Distribution of black locust in the Czech Republic (green polygons are large-scale protected areas). The map was compiled from various sources such as Czech National Phytosociological Database (Chytrý and Rafajová 2003) and Nature Conservancy Central Register (AOPK CR).

> *Black locust is a controversial tree species as it has certain positive socio-economic, but also some negative environmental impacts. However, its economic benefits should not override the fact that it is considered as one of the 100 worst invasive species in Europe.*

Figure 78. Many black locust stands occur on steep rocky slopes in river valleys. They were used for upgrade of slow-growing forests or less productive pastures threatened by soil erosion (photo: M. Vítková).

Species status

Black locust is listed in several European databases of invasive species as highly invasive (DAISIE 2006, CABI 2016 and NOBANIS 2016) and according to the DAISIE platform is considered as one of the 100 worst invasive species in Europe (DAISIE 2006). In addition, Richardson and Rejmánek (2011) included it in the list of 40 of the most invasive woody angiosperm species in the world. It has also been included in national 'Black lists' in e.g. Norway (Gederaas et al. 2012) and Switzerland (Info Flora 2012).

Although black locust is currently rated as invasive in the Czech Republic (Pyšek et al. 2012, Pergl et al. 2016a), it represents an example of a highly controversial species due to its positive socio-economic effects – e.g. timber and biomass production, beekeeping, ornamental purposes or soil restoration and stabilisation (Rédei et al. 2008), and its negative environmental effects on native vegetation (Vítková and Kolbek 2010). Simultaneously, it is a prominent invader having negative impacts on native vegetation. Therefore, an optimal strategy for management of black locust should reflect its spatial and environmental context. The management approach should be based on a stratified approach which considers: (i) specific site conditions, (ii) decisions at a local scale, and (iii) existing environmental and cultural values.

Environmental aspects

In general, tree species have greater influence on the environmental conditions at a particular site than herbs due to their impact on light regime, litter decomposition and water availability (Richardson and Rejmánek 2011). Black locust is a light-demanding pioneer species that can substantially, and rather quickly, change the habitats which it invades. At sites where it becomes dominant causes a vegetation change towards ruderal and nitrophilous species. Since it is rather short-lived and less competitive in later successional stages, it does not commonly occur in abundance in mature mixed forests. Although black locust tolerates extremely diverse soil properties, it prefers well aerated and drained soils, and it does not grow well on compacted and frequently water-logged soils (Vítková et al. 2015).

▶ *Black locust is light demanding, nitrogen fixing pioneer tree species able to tolerate diverse soil properties; its presence in habitats may cause vegetation change towards ruderal and nitrophilous species.*

In Europe, black locust occurs in a variety of habitats; e.g. in natural open land, woodlands, ruderal or urban habitats, forests and plantations for biomass production. Habitats most prone to black locust invasion are dry grasslands or shrublands on rocky and sandy soils. However, mesic forest vegetation or even riparian forests are often invaded in Mediterranean Europe (Motta et al. 2009). In the Czech Republic, black locust is considered highly invasive in xeric to mesic and semi-open habitats such as ruderal or shrub vegetation as well as in dry grasslands and forests with a light canopy such as dry thermophilous or acidophilous oak forests, relict pine forests, maple forests on scree slopes, or disturbed stands of oak-hornbeam (*Quercus petraea-Carpinus betulus*) forests.

Habitats that are generally resistant to black locust invasion include: (i) areas with poorly aerated soils (e.g. gleysols), (ii) intensively managed sites where the vegetation is permanently disturbed (e.g. trampled sites, mown lawns and meadows or arable fields), (iii) dense forests with competitive shade tolerant tree species such as European beech (*Fagus sylvatica* L.) and (iv) mountain and subalpine areas.

▶ *Habitats most prone to black locust invasion are dry grasslands or shrublands on rocky and sandy soils.*

It is important to note that when black locust is planted in a mixture with other species, it quickly reaches the upper layer of the canopy. Other tree species mostly survive in its presence and occur in an intimate mixture with black locust; this applies to both native species (e.g. oaks – *Quercus* spp.; elms – *Ulmus* spp.; and hornbeam – *Carpinus betulus* L.) as well as introduced tree species (e.g. ash-leaved maple – *Acer negundo* L.; tree of heaven – *Ailanthus altissima* (Miller) Swingle). In old stands, where black locust dominates, seed germination of shade intolerant species (e.g. oak and silver birch – *Betula pendula* Roth) and species which are intolerant to higher nitrogen levels (e.g. beech and conifers) is not successful. However, some shade tolerant tree species (e.g. maples – *Acer* spp., ash – *Fraxinus* spp., and elm) and on steep slopes drought tolerant shrubs such as hawthorn *(Crataegus* spp.), blackthorn (*Prunus spinosa* L.) and wild rose (*Rosa* spp.) will regenerate and are able to replace black locust (Vítková 2014).

Although black locust regenerates mainly through re-sprouting from root and stem suckers, reproduction from seeds is crucial for long-distance dispersal and colonisation of remote sites. Black locust is insect pollinated with pods containing seeds with highly impermeable seed coat resulting in low germination rate but long viability in the seed bank (Roberts and Carpenter 1983). Black locust seedlings are sensitive to shading, which means that seedling mortality is high in forests with closed canopies or in habitats where there is a dense ground vegetation. Black locust has the ability to create clonal stands due to its connective root system which may grow by up to 1 m per year (Kowarik 1996). The suckers grow faster and reach reproduction maturity earlier than seedlings (Vítková and Kolbek 2010). It is also important to note that mechanical damage to the stem or to the root system leads to an increase in the number of ramets, which consequently results in an increase in stem density and creation of a compact clonal colony which may cover hundreds of square meters (Chang et al. 1998).

Figure 79. The ground vegetation in black locust stands is most often dominated by nitrophytes, such as nettles, goosegrass and elder and occurs on mesic sites with deeper soils on alkaline bedrock (photo: M. Vítková).

Black locust spreads mostly vegetatively using root and stem sprouting. Its occurrence in dense forests is only minor and usually presents remnants of earlier disturbances such as forest clearings or fires.

According to laboratory experiments, black locust shows strong allelopathic effects on two edible crops and two weeds (Nasir et al. 2005). Its impact on germination of seed bank under nature conditions have yet to be tested. Vegetation change towards ruderal and nitrophilous species in the presence of black locust is caused by the changes in the availability of soil nutrients rather than allelopathy (Vítková and Kolbek 2010).

Black locust is able to fix atmospheric nitrogen through symbiotic *Rhizobium* bacteria occurring in its root nodules (Batzli et al. 1992); since the litterfall of black locust is low and its decomposition takes a long time due to the high lignin content (Castro-Díez et al. 2012, Vítková et al. 2015), nitrogen fixation represents the key input in the nitrogen cycle in black locust stands (Liu and Deng 1991). In soils with a favourable moisture regime, soil nitrogen pool increases, nitrification and net nitrogen mineralisation rates rise and available mineral forms of soil nitrogen tend to accumulate in the A-horizon (Van Miegroet and Cole 1984, Montagnini et al. 1991). Such changes of soil nitrogen support expansion of nitrophilous plants in herb and shrub layers such as nettle (*Urtica dioica* L.), goosegrass (*Galium aparine* L.), greater celandine (*Chelidonium majus* L.), cow parsley (*Anthriscus sylvestris* (L.) Hoffm.), garlic mustard (*Alliaria petiolata* (M.Bieb.) Cavara & Grande), and elder (*Sambucus nigra* L.) (Vítková and Kolbek 2010; Figure 79). In drier habitats, the ground vegetation tends to be dominated by perennial grasses such as false oat grass (*Arrhenatherum elatius* (L.) P.Beauv. ex J.Presl & C.Presl.), sterile brome (*Bromus sterilis* L.), bush grass (*Calamagrostis epigejos* (L.) Roth), and nitrophilous plants occur on suitable microsites with organic matter deposition. Where black locust has become established it has mostly replaced native and species-rich vegetation including oak or hornbeam forests and dry or mesophilous grasslands. Both grasslands and some forest communities have relict origins; however, they were sustained, modified and spread by human management since the Holocene climatic optimum (Pokorný et al. 2015).

In general, black locust stands have plenty of light reaching the forest floor over the whole vegetation period as the foliage holds for a relatively short period of time; i.e. the leaves appear late in spring (May) and begin to fall rather early, usually during summer droughts (August). High light levels reaching the forest floor enable the survival of local light demanding species in the herb layer or dense shrub layer.

Nitrogen fixation represents the key input in the nitrogen cycle in black locust stands. In mesic habitats, available mineral forms of soil nitrogen accumulate in the A-horizon and nitrophilous plants dominate in herb and shrub layers.

Although it is clear that black locust has negative and irreversible environmental impacts where it becomes dominant, it should be noted that there are some positive effects on biodiversity. It provides habitat for some rare and endangered species of plants such as rare ruderal plants, for example burr chervil (*Anthriscus caucalis* M. Bieb.) or geophytes from the genera *Gagea*, *Muscari* and *Allium*, saprophytic fungi (e.g. *Crepidotus luteolus* Lambotte Sacc., *Geastrum rufescens* Pers.: Pers., *Lepiota griseovirens* Maire), or invertebrates (mainly saprophagous beetles, e.g. *Anommatus reitteri* Ganglbauer) (Vítková and Kolbek 2010, Ślusarczyk 2012, Stejskal and Vávra 2013). In species-poor landscapes dominated by agricultural production, black locust stands preserve biodiversity and play a significant role as migration corridors for woodland animals. Their dense undergrowth of shrubs and complex canopy structure provide nesting opportunities and a food source for many bird species. In addition, Hanzelka and Reif (2015a) observed higher bird abundance in black locust stands than in native oak; however, it was further reported that habitat specialists dominated in oak forests in comparison to habitat generalists (Hanzelka and Reif 2015b). In derelict urban areas, Buchholz et al. (2015) demonstrated that black locust invasion does not decrease the diversity or the number of endangered species and diversity of carabid beetles and spiders.

▶ *Black locust preserves biodiversity in species-poor agricultural landscapes and urban environments where it provides habitat for some rare and endangered species as well as nesting opportunities and a food source for birds.*

Economic aspects

Black locust is an economically important species in several countries as it is commonly used as a source of fast growing and long-lasting quality timber that is resistant to insects and fungi (Keresztesi 1988). Due to its exotic appearance, lack of serious natural enemies in the invaded range, fast growth and high production of nectar, it is commonly planted not only for timber production, but also for firewood, erosion control, amelioration and reclamation of disturbed sites, as well as for honey production, animal forage and as an ornamental tree (Göhre 1952, Cierjacks et al. 2013). Until now, it has been planted widely in cities due to its high tolerance of air pollution, salinity and dry or infertile soils (Hillier and Lancaster 2014). Black locust has been planted for the purpose of biomass production in short-rotation energy plantations in Hungary, Germany, Greece, Italy, Poland, Slovakia, Austria, China and the United States (Rédei et al. 2010, Straker et al. 2015).

▶ *Economic utilisation of black locust has different priorities across the European continent.*

In some countries (e.g. Hungary, Germany, Poland), more emphasis is placed on the economic benefits such as timber, biomass and honey production while in the other countries (e.g. Czech Republic, Switzerland, Great Britain), the interest of nature conservation resulting in restrictions on planting of black locust except for gardens and urban areas prevails.

In the Czech Republic, black locust has been planted mostly for protective purposes such as soil stabilisation and reforestation of bare, sandy or rocky areas as well as a fire-barrier along railways (Figure 78), or during mine reclamation. Nowadays, black locust is only planted in gardens and urban environment and new plantations are not being established due to its negative impacts. Management of existing stands dominated by black locust often aims to replace black locust with other vegetation types, especially in protected areas.

Management of black locust

Since this species causes conflict among different stakeholder groups (e.g. nature protection, forestry, urban landscaping, public), integrated action plans towards management of the existing populations of black locust should be developed where economic and biodiversity aspects should be taken into an account (Pergl et al. 2016a,b). Therefore, site specific approaches where black locust is tolerated in selected areas, but strictly eradicated in other, especially valuable sites, is considered the best option. Several practical scenarios demonstrate some of the management approaches that may be use in areas where black locust dominates:

> *The best approach in black locust stands seems to be based on stratified management tolerating black locust in selected areas and strictly eradicating it from naturally valuable habitats.*

Abandoned plantations. Although it can take a long time, old black locust stands and scattered black locust trees in forests are naturally replaced during succession by more competitive trees. Black locust will disappear from the community by shade tolerant trees over 70 years. Succession without any management can be selected only when we are able to fulfil two conditions: (i) competitive shade tolerant trees must already be present in the understory or in the near neighbourhood – e.g. ash (*Fraxinus excelsior* L.), sycamore (*Acer pseudoplatanus* L.), Norway maple (*A. platanoides* L.), field maple (*A. campestre* L.), or in dry sites tall shrubs such as hawthorn (*Crataegus monogyna* Jacq.); and (ii) in order to eliminate the risk to biodiversity and human infrastructure, there should be no adjacent high conservation value sites, traffic corridors or built-up sites. It is important to avoid any disturbance such as felling broken or dead trees otherwise the black locust stand will regenerate.

Plantations with regular forestry management. Black locust plantations can be tolerated but its spread in the surroundings should be restricted. Such approach can be applied in agricultural landscape where regular management such as ploughing or moving prevents vegetative spread and survival of seedlings. Care has to be taken in the case where black locust stands are in contact with fallow land, grasslands or semi-natural habitats with retaining local biodiversity such as rocky slopes in which young plants of black locust should be regularly removed.

Intensive short-rotation biomass plantations under coppice management (common e.g. in Hungary) are a special case of forest plantations. Such areas are characterised by the intensive growth of coppice shoots and suckers and when abandoned, their spontaneous conversion to native vegetation is very slow (Vasilopoulos et al. 2007, Radtke et al. 2013).

Sites in vulnerable locations. In protected areas and sites prone to the black locust invasion such as open thermophilous forests and grasslands, eradication of black locust is recommended. Focus should be on black locust populations in the close vicinity of vulnerable sites. Rapid eradication is an extreme approach that has to be justified by needs of nature protection or by threats to infrastructure. It is connected with high financial costs and environmental risk (soil erosion, application of herbicides, and strong regeneration ability of black locust). Although there is no widely accepted and efficient method of eradication, a combination of mechanical and chemical approach is recommended as the most effective (Box 23). All black locust trees must be removed together since clones are connected by roots and single surviving stems can regenerate quickly. Subsequent targeted control of the regrowth from root and stem suckers and seedbank is necessary for at least 3–5 years. Where there is little or no natural regeneration, it is the time for artificial regeneration methods to ensure adequate regeneration of target replacement species. This usually does not occur earlier than the third year after felling of the black locust. If possible, usage of shade tolerant species is the best option.

Semi-spontaneous stands in urban or mining sites. This category contains heterogeneous set of stands, that may originate from planting or spontaneous natural regeneration, and may differ in structure (closed forest vs. semi-open stands), and composition (share of native and introduced species). For such stands local context needs to be taken into account for appropriate management. Black locust should be locally eradicated in cases where high conservation value sites are threatened by invasion.

Isolated black locust trees. Solitary or alley of trees occurring along roads have often been planted at memorial sites, e.g. near chapels or roadside crosses. There is usually no reason to remove these trees, especially in cities or if proper management of neighbouring sites is applied.

Social aspects

The attitudes towards the management of black locust differ fundamentally among different groups of researchers, land managers and policy-makers in Europe as they perceive its impacts differently. In some European countries (e.g. Hungary, Slovakia and Germany), black locust is considered mainly for its benefits and is removed only from highly valuable habitats, whereas in other countries, it is listed on local list of dangerous invasive alien species (IAS) with a ban on introduction and planting (e.g. Spain and Great Britain). Such controversy in the perceptions towards black locust resulted in the species being absent from the black list of IAS of EU concern (for more details, please see Chapter 3.2.).

In the Czech Republic, black locust is a popular tree species as it is a part of cultural and historic heritage. It is mentioned in songs, poems and recipes. Possibility of large-scale eradication thus causes unease among beekeepers as well as others benefiting from the advantages black locust provide. The significance of black locust in terms of providing jobs in forestry, facilitating for honey production or delivering positive landscaping values has to be taken into account; it should not, however, override the needs for nature protection at high conservation value sites.

> *Since black locust is a part of the cultural and historic heritage in many European countries, large scale eradication is not considered as a recommended management approach.*

Although there is a lack of agreement on the management of black locust in many European countries, large scale eradication is not considered to be a suitable management. Instead, an integrated and site-specific management strategy seems to be an appropriate approach. The current ambivalent public opinion to the occurrence of black locust and its management is the result of centuries of experience with the species, where enthusiasm related to its use in forestry and other purposes is contrasted with its rejection due to e.g. its negative effect on biodiversity, or the potential threat as a vector of pests such as the European fruit Lecanium (*Parthenolecanium corni* Bouché; Kolbek et al. 2004).

Conclusion

In spite of the varied economic benefits that black locust provides, it is an invasive species with serious implications for nature conservation. The traits supporting black locust cultivation such as vitality, exceptional sprouting ability, rapid growth, abundant production of seeds, or nitrogen fixation complicate its removal from sites of high conservation value. The attitude to black locust is diverse among different stakeholder groups with the perceptions towards this species varying regionally. Since individual stands differ in their economic value and environmental benefit or risk, the site-specific management approach appears to be the best attitude that can be applied to most of introduced tree species also including black locust (Pergl et al. 2016a,b).

Figure 80. Stem and root suckers appearing after using ring-barking method without application of herbicide (photo: M. Vítková).

Black locust is a tree species with negative environmental impacts comparable to that of species such as knotweeds (*Fallopia* spp., please see Chapter 3.8. for details) or giant hogweed (*Heracleum mantegazzianum* Sommier & Levier) (Hejda et al. 2009) and therefore its management has to be carefully planned (Pergl et al. 2016b). A site-specific approach to management of black locust may be more appropriate, rather than large-scale eradication programmes as may be suitable for other species. For many decades, this species has been a part of the European environment and the complete eradication is thus highly unlikely. In addition, in areas intensively managed for agriculture where the risk of further spread is rather low, black locust presence increases the diversity in the landscape matrix and provides shelter for many organisms. Co-existence of black locust, people and nature thus can in some areas create sustainable system persisting for many decades.

Box 23. black locust control

For a rapid eradication of black locust from a site, removal of trees by cutting (at high or low stump) followed by immediate application of herbicide is the best choice. For removal of single black locust trees or stepwise canopy opening, killing the standing main trunk gradually over a period of several years may be preferred. A common method is girdling, i.e. removal of the outer bark (down to the phloem layer) around the entire circumference of the stem. Since this method does not prevent sucker formation below the girdle on the stem (Figure 80), Böcker and Dirk (2008) recommended incomplete girdling. In the first year a strip of bark about 5 cm wide is removed from about 9/10 of the trunk circumference; if possible, the strip should be cut into the xylem, and preferably during winter season. In the second year, the strip is completed. When the tree has fully dried up (usually in the third year), it can be felled. An efficient method is based on a combination of cutting or girdling, application of herbicides, eliminating the root and stem suckers by foliar spraying of diluted herbicide and long-term grazing by goats to control re-sprouting. The best period for application of herbicides is the end of vegetation season (second half of August and September), when assimilates are translocated to the roots (Vítková 2014).

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5.2 Douglas fir in Freiburg City Forest: an introduced tree species in the light of multifunctional management objectives

Nicole Schmalfuss and Lucie Vítková

Freiburg City Forest is located in the southwestern part of Germany in the state of Baden-Württemberg covering forested area of 5 129 ha (Figure 81). The city forest serves the 220 000 inhabitants of Freiburg and its surrounding municipalities. The management of this forest has proven to be a successful approach fulfilling multiple aims under the label of Forest Stewardship Council certification (FSC).

The Municipal Forestry Office was established in 1835 in order to manage Freiburg City Forest. For more than 180 years the Municipal Forestry Office has continued its work irrespective of several administrative reforms in the forest sector in Baden-Württemberg. This work has been based on the successful identification of management objectives satisfying the multiple needs of Freiburg City Council as well as the city's citizens. The current management aims are to maintain ecological and social functions of the city forest and to create financial revenues.

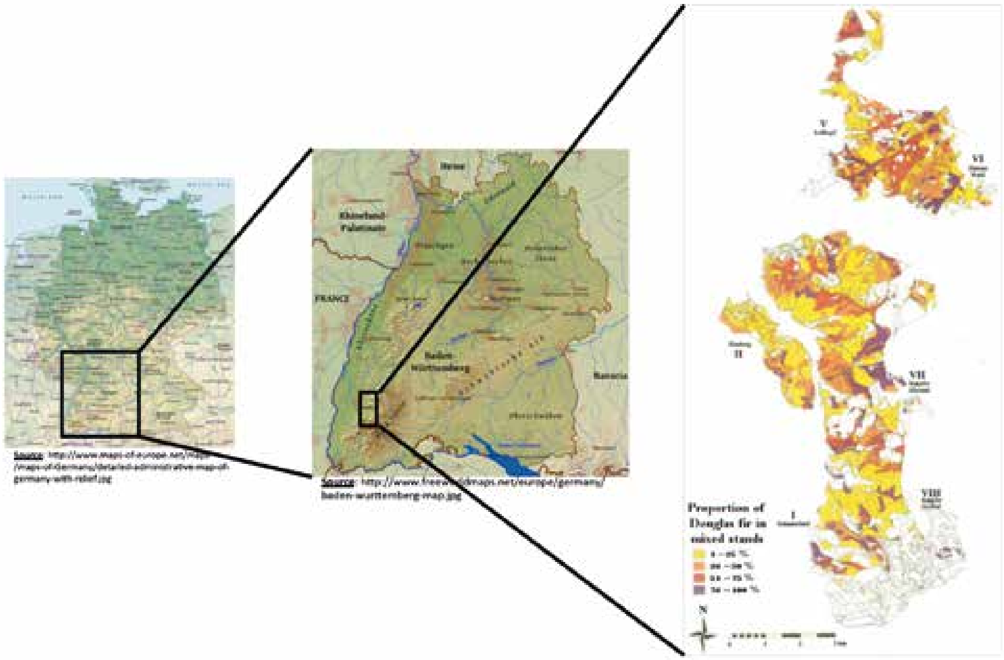

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Figure 81. Location of Freiburg City Forest with a map showing the proportion of Douglas fir within the mixed stands in the mountain forest stands. The lowland forests are excluded due to absence of Douglas fir.

Freiburg City Forest is an example of a successful multifunctional forest management where the major management aim is to maintain ecological and social functions and to create financial revenues.

The city forest spreads around Freiburg and is located in the two contrasting climatic and geological areas of the Upper Rhine Valley and the Black Forest. The altitude range of the city forest spans from 200 to 1 284 m a.s.l. Such location also reflects city forest's different forest types; i.e. lowland alluvial forests found below 400 m a.s.l. and upland mountain forest located above 400 m a.s.l.

The lowland forest accounts for about 40 % of the city forest area and is dominated by oaks (*Quercus* spp.), hornbeam (*Carpinus betulus* L.), ash (*Fraxinus excelsior* L.) and sycamore (*Acer pseudoplatanus* L.). The mean annual temperature in the lowland forest is 10.4°C with the mean annual precipitation being 880 mm.

The upland forest covers 60 % of the city forest and is mainly composed of European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* (L.) H. Karst.), silver fir (*Abies alba* Mill.) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Figure 82). The mean annual temperature is 9.4°C in the lower altitudes of the forest (400 m a.s.l.) and 5.1°C in the upper parts (1 250 m a.s.l.). The mean annual precipitation is between 950 mm and 1800 mm, which is also altitude dependent.

Figure 82. Douglas fir and European beech stand representing the altitudes middle ranges of Freiburg City Forest (photo: L. Vítková).

Although native tree species make up the majority of the area of the city forest, Douglas fir, a coniferous tree species of North American origin, fulfils a significant role in the city forest. Douglas fir was first planted in Freiburg City Forest in 1896 and became an important tree species for timber production. This is mainly attributed to its fast growth rate and the possibility for multiple uses of its timber.

Although Douglas fir shows a comparable susceptibility to wind throw as Norway spruce, wind throw risk is not considered as a restricting issue in the city forest as the stands located in the upland areas are on rather well drained soils with tree roots penetrating to sufficient depths. Therefore, the wind throw is considered to be a risk only during extreme wind storms. Furthermore, the wind-thrown Douglas fir trees are subjected to much less economic loss than wind-thrown Norway spruce. Up to now, even after extreme wind events, Douglas fir timber can still be sold without major losses as it tends to retain its value following the wind event and does not require quick management action as is the case of Norway spruce, which is affected by bark beetle following severe wind events (Albrecht et al. 2015).

The proportion of Douglas fir throughout the city forest varies from being absent in the lowland alluvial forest to being rather abundant at an altitude of around 800 m a.s.l. and then again decreasing in abundance towards yet higher altitudes. The proportion of Douglas fir in the tree species mixture of the upland city forest continuously increased from 1912 to 1980 and peaked in the 1990s at 21 % (Figure 83) more or less stagnating since then. The management aims to keep the area dominated by Douglas fir at 20 % in the upland forest as Douglas fir timber harvested from these areas significantly contributes towards city forest's timber income (Douglas fir forms 13 % from the whole city forest's area). However, it is important to note that the FSC certification standard does not allow for more than 20 % of a forest to be composed of introduced species (more information on certification can be found in Text Box III).

Box 24. Proportion of Douglas fir in German forests

According to the latest German National Forest Inventory (2012), Douglas fir forms 2 % of German forests with the largest proportion found in Rhineland-Palatine (51 718 ha; i.e. 6.4 % of the local forest cover) and the lowest in Hamburg and Bremen (117 ha; i.e. 0.9 % of the local forest cover). As for the state of Baden-Württemberg, the state with second largest representation of Douglas fir, and where Freiburg City Forest is located, Douglas fir covers 43 928 ha, which equates to 3.3 % of the local forest cover. It is also important to note that the proportion of Douglas fir in individual federal states increase in comparison to the National Forest Inventory in 2002.

Figure 83. Douglas fir forming an important proportion of Staufen Municipal Forest in southwestern Germany (photo: L. Vítková).

The forest stands where the proportion of Douglas fir exceeds 50 % were established between 1930 and the end of the 1980s when pure Douglas fir was initially planted after clearcutting. This management practice was abandoned at the beginning of the 1990s when the principles of continous cover forest management were first put to practice in Freiburg City Forest. Since then, the forest management preferences were given to promoting small scale openings (i.e. single tree or small patches) where natural regeneration of mixed species has been favoured.

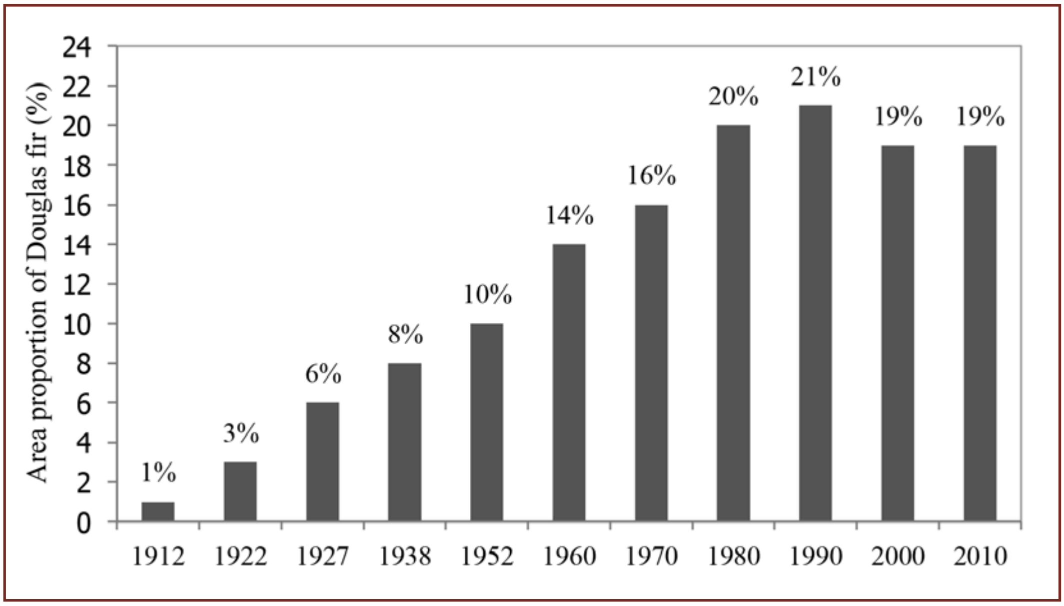

Figure 84. Proportions of Freiburg City Forest area (mountain part) dominated by Douglas fir.

> *The major management objective in Freiburg City Forest with regards to Douglas fir is to produce high quality timber of large size that brings substantial financial revenue.*

As an example, in 2014, the average price for Douglas fir logs (stem wood) was 121 €/m^3 with the average price for all Douglas fir assortments, including pulpwood, being 103 €/m^3. However, the top quality Douglas fir logs yielded prices of around 300 €/m^3 at sale auctions that year. In order to promote timber quality from an early age, specific management focus is on young and medium-aged Douglas fir stands. In such cases, careful pre-commercial thinning is usually carried out once the top height reaches 6 m. Trees of the poorest quality are removed and, if present in the stand, broadleaved species are favoured in order to increase species richness. A high number of stems in the stand is retained in order to suppress formation of large branches. Once the top height in such stands reaches 18 m, 50 final crop trees/ha (Z1 trees) and an additional 50 final reserve crop trees/ha (Z2 trees) are selected and retained. The choice is based on stem quality, growth vitality, light branching as well as convenient spatial distribution of trees. The selected trees are pruned up to 10 m of height in order to increase the future volume of quality timber. The target diameter of the final crop trees is 100 cm. The final crop trees are promoted by a continuous and careful removal of their competitors in order to achieve consistent diameter increment. In addition, careful harvesting is applied to prevent damage to the final crop trees.

Not only do top quality Douglas fir assortments attract high prices, the mean timber price for this species over time are also higher than for Norway spruce, silver fir and European beech (Figure 85). It is also important to note that the annual net profits generated by Douglas fir-dominated stands provide a considerable revenue of 500–700 €/ha/year that is subsequently used for various purposes throughout the forest.

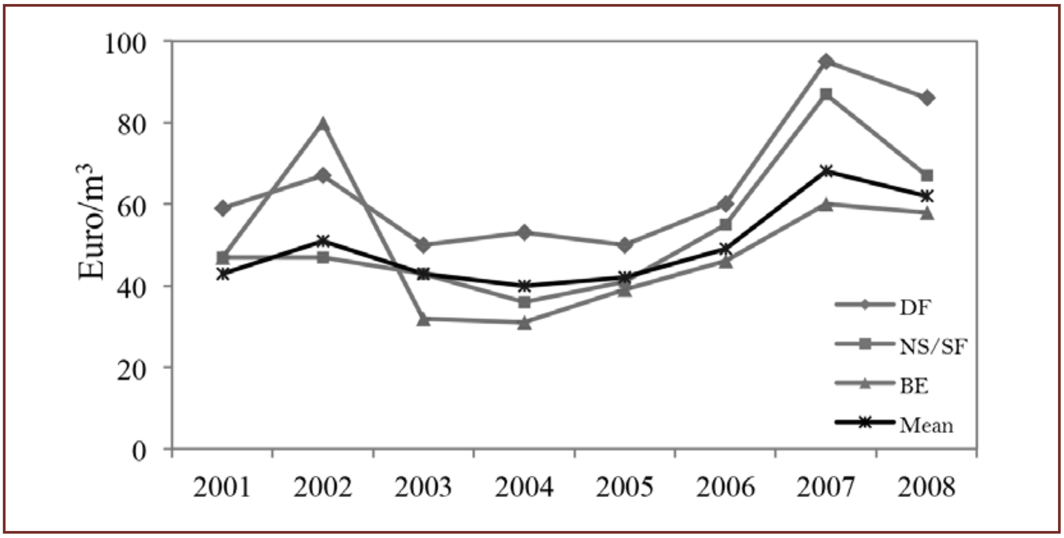

Figure 85. The development of the mean timber prices (€/m^3) between the years 2001 and 2008 for major commercial species in Freiburg City Forest. DF=Douglas fir, NS =Norway spruce, SF=silver fir, BE=European beech and Mean=average values.

Douglas fir plays an important role in Freiburg City Forest as it accounts for 28 % of the total income covering only 13 % of the total forest area.

Although Douglas fir covers only 13 % of the entire area of Freiburg City Forest, it accounts for 28 % of city forest's total income from timber sale, which makes this species of North American origin a substantial contributor to the city forest's income. Douglas fir also has a higher mean annual increment (18 m^3/ha/year) in comparison to other species such as silver fir and Norway spruce (15 m^3/ha/year), European beech and larch (9 m^3/ha/year) or sycamore and ash (8 m^3/ha/year).

Although the conditions favouring the natural regeneration of Douglas fir vary throughout the city forest, the highest densities of Douglas fir natural regeneration can be found on drier south facing slopes as observed by the local managers. The natural regeneration of Douglas fir is usually accompanied by natural regeneration of silver fir and/or European beech. Douglas fir requires at least medium light levels and it does not regenerate well under dense, closed canopies. Natural regeneration of more shade tolerant species such as silver fir and European beech is usually observed in more shaded parts of the stands (Figure 86). Steinmetz (2014) focused on the occurrence of natural regeneration of Douglas fir in the city forest and did not report any major increases in the Douglas fir natural regeneration between the forest enterprise inventories conducted in 1999 and 2009. The proportion of Douglas fir natural regeneration decreased between the two inventories with the exception of the early stages of natural regeneration (below a height of 20 cm) where it slightly increased.

The topic of invasive potential of Douglas fir has been the subject of intense debate in Germany (for further details, please see Chapter 3.3.). The fact that Douglas fir has been planted at such considerable rates in Freiburg City Forest has also created debate; in simple terms, foresters consider Douglas fir as suitable addition to the mixed-species mountain forests regardless of its non-native origin, while nature conservationists see it as a tree species that should not be present in local forests. Nonetheless, unless heavier cut allowing higher light level reaching the forest floor is applied in order to provide conditions for Douglas fir to regenerate, natural regeneration of shade bearing species such as silver fir is generally observed. Competing vegetation is also considered as a hindrance to the natural regeneration of Douglas fir (Steinmetz 2014).

Another important point to note is that Douglas fir is considered as a possible alternative to the native conifer species (e.g. Norway spruce and silver fir) whose native range is likely to shift and substantially reduce due to the climate change. The issue of climate change means that management objectives must be reassessed and include species that create positive revenue streams.

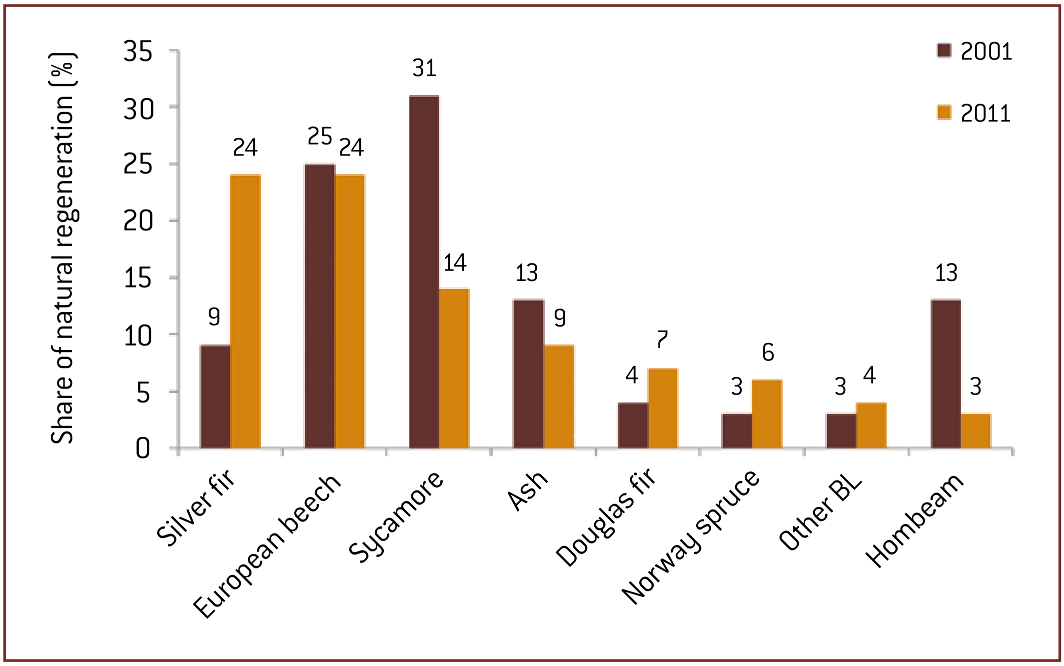

Figure 86. The share of natural regeneration of major tree species found in Freiburg City Forest under shelter in mature stands in the upland parts of the forest (proportions of natural regeneration that are ≥3 % are shown).

About 18 % (938 ha) of the city forest are designated as special forest habitats, with the most common habitat being the rare near-natural forest communities occupying 67 % of the entire designated area. The special forest habitats are managed in order to preserve and enhance their valuable structures and species biodiversity. Detailed information on the role and occurrence of introduced Douglas fir in the designated habitats can be found in Chapter 5.3.

The principles of continuous cover forest management are incorporated into the management of Freiburg City Forest.

The forest management principles of 'continuous cover forestry' have been adopted in Freiburg City Forest for the past 25 years. One of the aims has been to transform even-aged and even-sized stands of Douglas fir (but not only) towards an uneven-sized forest structure (Figure 87). About 11 % (549 ha) of Freiburg City Forest have been categorised as 'Dauerwald', which is considered as a mixture of trees of all sizes and species. Such type of management in the city forest usually results in the use of a single-tree selection system where only a few trees from the upper diameter classes (>100 cm) are cut. A relatively short harvesting cycle is applied (i.e. once every five years) as the management decisions and the harvesting depends on the volume increment and quality of individual trees. Harvesting of individual trees is spread uniformly across the stand resulting in rather closed canopy. In the case small gaps occur, the canopy closes rapidly leading to low light conditions at ground level. The presence of European beech in the middle storey tends to enhance this effect. As Douglas fir has an intermediate light demanding character, this led to a decrease of natural regeneration of Douglas fir between 1999 and 2009 (Steinmetz 2014).

According to the objective of keeping the proportion of Douglas fir in the upland forest at 20 %, slight changes in silvicultural management have been adopted in the last five years in older stands of Douglas fir. Where natural regeneration of Douglas fir is desired, the single tree harvesting of trees of larger diameters is complemented by thinning of poor quality trees (e.g. those with heavy branching, poorly developed crowns, etc.) in order to establish suitable light conditions facilitating successful natural regeneration of Douglas fir, which is otherwise outcompeted by other, more shade bearing species.

Figure 87. Douglas fir stands of varying forest stand structure (photos: L. Vítková).

Recreation in Freiburg City Forest plays an important role as 4–5 million people visit the forest each year.

One of the management objectives of the city forest is to make the forest not only freely accessible to everyone, but also to enhance the recreation potential of the forest. This may be demonstrated by the number of visitors to Freiburg City Forest, which is estimated by the Municipal Forestry Office to be between 4 and 5 million each year. Visitors say that they appreciate the presence of the older Douglas firs that can reach large proportions (diameters exceeding 100 cm at 100 years of age) and consider Douglas fir an integrated component of the pleasing aesthetical value of the forest. Due to the high visitor pressure in the city forest, extra money is spent on maintenance and creation of infrastructure in order to satisfy visitor needs. The income from the sale of Douglas fir timber substantially contributes towards the social function of the forest. Freiburg City Council spends €1 million each year to be used for activities related to recreation, environmental education and increase of public awareness regarding forest ecosystems. Some 437 km of marked footpaths, 126 km of mountain bike paths and 78 km of sign-posted bridle (horse riding) paths have been created in the city forest. There are also 68 km of jogging and fitness parkour paths. Barbeque sites and huts have also been installed in the city forest to increase the forest use.

As a proof of how the Freiburg City Forest serves multiple forest management, and how the administration provides necessary information for public, around 150 events are organised by specially trained foresters each year, especially for school and kindergarten children. In line with educational objectives, the children spend some time in the forest learning to understand forests as complex natural ecosystems.

Freiburg City Forest has been managed in a way that it accommodates for various recreational demands of the 4–5 million visitors every year and at the same time gains revenue from timber harvesting. The management applied has been in accordance with FSC certification standards where traditional forest practices have been combined with the principles of continuous cover forest management. Although there has been much debate regarding the presence of introduced Douglas fir, this species of North American origin plays an important role contributing to the aesthetic and economic value of the city forest.

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5.3 Quantifying invasiveness of Douglas fir on the basis of natural regeneration in south-western Germany

Anja Bindewald and Hans-Gerhard Michiels

Introduction and the introduced range

Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) is a non-native tree species to Europe where it was introduced from the west coast of North America in 1828 (Kownatzki et al. 2011). Douglas fir has been used for forestry purposes in Central Europe since 1880, and in southwestern Germany, in particular, it has developed to be the most important introduced tree species used in forestry (Knoerzer 1999). The area where it dominates has been expanding and this trend can be attributed to several of its characteristics (Otto 1997):

- Excellent wood properties;
- Superior increment when compared to other tree species across a wide range of site conditions;
- Ability to regenerate naturally in existing forests;
- Relatively fast decomposition of its litter (in comparison to other coniferous species such as Norway spruce (*Picea abies* (L.) H.Karst.) or European larch (*Larix decidua* Mill.);
- Low susceptibility to pests.

Although Douglas fir formed only 3.3 % (43 928 ha) of the total forest area in the State of Baden-Württemberg (southwestern Germany) in 2012 (NFI 2012), the timber volume produced between 2005 and 2015 from state forests accounted for an average about 47 000 m^3 and was worth €4 million per year (ForstBW 2016). The importance of Douglas fir in the forests in Baden-Württemberg and in other parts of central Europe is expected to increase since our climate is becoming drier and Douglas fir is considered to be more drought-resistant than other widespread tree species in central Europe such as for instance Norway spruce (e.g. Oberer 2011). According to Kleinschmit (1991), in the medium-term, Douglas fir has the potential to become one of the most important forest tree species in Europe.

> *Douglas fir is one of the most commercially significant tree species of non-native origin in south-western Germany; its importance is expected to increase due to the climate change.*

Species status

Currently, Douglas fir causes a conflict between nature conservation and forestry that is based on the assessment of its invasive potential. In Germany, different perspectives were described in:

- Nehring et al. (2013) who classified Douglas fir as non-native invasive tree species in Germany based on its dominance on treeless rocky locations (Figure 88) and acidophilous, nutrient-poor and dry warm sessile oak forest (*Quercus petraea* (Matt.) Liebl.) sites (Figure 89) with sparse tree cover.
- Spellmann et al. (2015) who concluded in their analysis that the species cannot be regarded as invasive.

Both publications considered different criteria for the assessment of invasiveness, which also reflects different interests and motivations (see Chapter 3.3 for more detail).

Figure 88. Young Douglas fir on a cliff Scharfenstein in Münstertal, southern Baden-Württemberg (photo: A. Reif).

Figure 89. Naturally regenerating Douglas fir in sessile oak forests. Left: primary *Quercetum*, Hirzberg in Freiburg; right: secondary *Quercetum*, Messerschmiedfels near Staufen, southern Baden-Württemberg (photos: A. Reif).

> *The use of Douglas fir in forestry is controversially discussed and leads to conflicts of interest between forestry and nature conservation.*

Assessment of invasiveness

Risk assessment protocols for invasiveness generally contain criteria matching the main stages of invasion (Verbrugge et al. 2012):

1. Entry;
2. Establishment;
3. Potential for spread;
4. Adverse impacts – primarily on native species and ecosystems; e.g. Vanderhoeven and Branquart (2010).

Although the data monitoring the invasion process are poor and mostly only descriptive (Gavier-Pizarro et al. 2012), invasiveness of introduced species is frequently assumed without clear scientific evidence heavily depending on expert opinions (Strubbe et al. 2011). Consequently, the replicability and thus stability of the assessments are limited (Essl. et al. 2011).

Douglas fir's potential to naturally regenerate in protected ecosystems is assessed in this chapter; all currently available data on natural regeneration of Douglas fir collected in specific areas across the State of Baden-Württemberg (south-western Germany) focusing on potential trends between 2002 and 2012 were included. One important aspect of the analysis was to assess the current potential of Douglas fir to regenerate in specific forest habitats as well as at different altitudes where suitable seed source is available. Such information provide an improved basis for the assessment of invasiveness, and thus for identification of appropriate management approaches.

Methods

A range of inventory data is available for forests in the State of Baden-Württemberg; the data were derived from different inventory systems operating at different spatial scales and partly at different inventory periods. The data used for this chapter were based on the following inventories:

1. *German National Forest Inventory (NFI)*: provides data on the state of the forests based on methodology used consistently across whole Germany (see methodology Polley et al. 2010). The NFI uses a systematic cluster sample with sampling intensities varying across individual states. In 2012, data sampling within Baden-Württemberg included 11 500 sampling plots in a systematic 2 x 2 km grid that was applied to the total forest area of 1.3 million ha (NFI 2012). The data on natural regeneration were collected by measuring stand area (ha) covered by young stems (trees > 20 cm and < 4 m in height) in circular plots (0.03 ha). Forest stand type was determined for each sample plot by assessing the dominant species of the tree species composition (e.g. Douglas fir stand type – Douglas fir accounts for at least 50 % of the stand's basal area). The data on natural regeneration of Douglas fir as well as data on Douglas fir forest stand type, from the second and third NFIs were used in order to assess potential trends between 2002 and 2012.

2. *Forest Structure Mapping*: surveys protected and unmanaged forests in Baden-Württemberg. This inventory was carried out in 82 forest nature reserves covering 4 298 ha. Individual inventory plots are distributed in a 50 × 50 m, 50 ×100 m, 100 × 100 m or 100 × 200 m grid with permanent circular sampling points of 0.1 ha in the undisturbed core area (see methodology Wevell von Krüger et al. 2015). Data on natural regeneration (i.e. trees below 7 cm diameter breast height; hereafter diameter) were used. The natural regeneration was further divided into three different height classes: (i) seedlings and stems <11 cm tall; (ii) stems 11–150 cm tall; and (iii) stems > 150 cm but < than 7 cm in diameter. The species composition of trees > 7 cm in diameter were extracted for each inventory plot to assign the respective forest stand type (defined as in the NFI methodology as described above). Tree species compositions where dominant tree species could not be determined were classed as 'mixtures' of the most frequently occurring species (e.g. 'beech-spruce-fir-mix').

3. *Selective Forest Habitat Mapping:* monitors rare and protected habitats on a 10 year cycle with yearly updates for different regions throughout Germany. Currently there is an entire area of 81 795 ha where the key habitats in the State of Baden-Württemberg are monitored. Thirty two per cent of this monitored area (i.e. 26 450 ha) include the total of 9 700 sites that are classed as rare near-natural forest habitats. Plant species composition is recorded and site characteristics are identified in order to assign the specific habitat type and plant association for each sampling plot; methodology by Kerner and Geisel (2015) and nomenclature by Rennwald (2000). Natural regeneration of Douglas fir was distinguished from artificial regeneration (i.e. planted) with no further information on height or diameter of individual trees being provided in the inventory dataset.

Results

1. Proportion of Douglas fir natural regeneration according to the three different inventories

Table 23: Douglas fir natural regeneration presence in Baden-Württemberg according to three different inventory methodologies.

	National Forest	**Inventory**	**Forest Structure Mapping**	**Selective Forest Habitat Mapping**
Reporting year	2002	2012	1994–2010	2015
Total area where sampling was carried out (ha)	1 323 119	1 323 958	4 298	81 795
Inventoried area with Douglas fir regeneration (ha)	2 112	4 346	71	165.9
Proportion of forest area with Doulas fir natural regeneration (%)	0.16	0.33	1.66	0.20

The results based on the three inventory types indicate that natural regeneration of Douglas fir occurs only on a very small proportion of the forest area in the State of Baden-Württemberg.

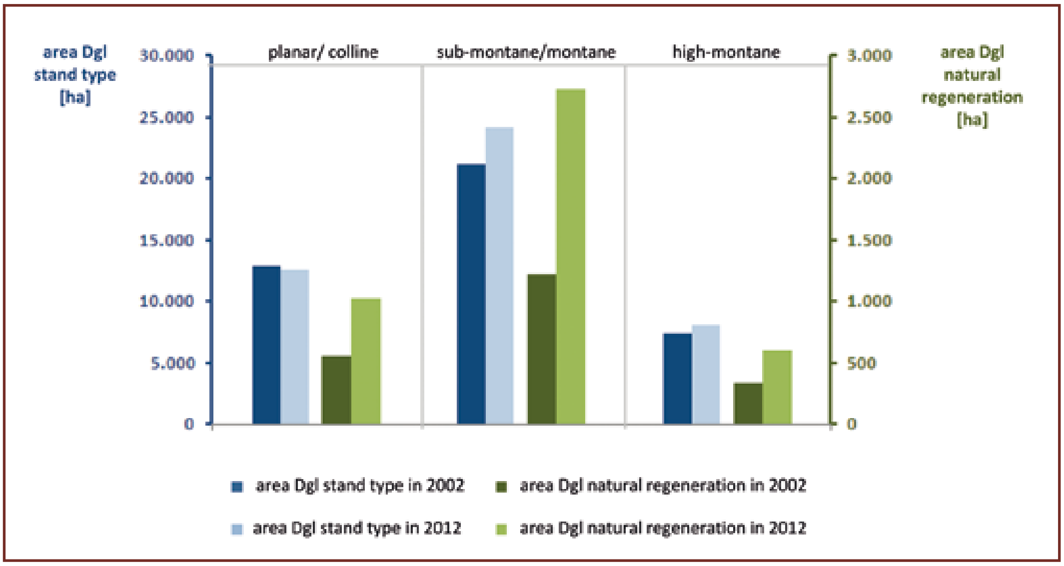

Figure 90: The area of natural regeneration of Douglas fir (trees below 4 m in height) in comparison with the forest area of Douglas fir stand type at different altitudes in Baden-Württemberg: comparison of NFIs conducted in 2002 and 2012; Dgl= Douglas fir.

2. Natural regeneration in National Forest Inventory 2002 and 2012

According to the NFI, the proportion of Douglas fir natural regeneration in the monitored plots more than doubled between the two NFIs in 2002 and 2012 (Table 23). However, it is important to note that the forest area dominated by Douglas fir also increased by about 8 % (3 316 ha) within the last 10 years. The inventory results revealed that Douglas fir primarily regenerates in forests at sub-montane altitudes (Figure 90). However, except for the planar/colline zone, the distribution of Douglas fir natural regeneration at different altitude levels appears to be associated with forest management rather than being a result of an invasion process (NFI 2012).

The largest proportions of the area where natural regeneration of Douglas fir (NFI conducted in 2012) was found were in the forests dominated by mature Douglas fir or in the forests dominated by other coniferous species (Norway spruce, silver fir (*Abies alba* Mill.), Scots pine (*Pinus sylvestris* L.) and European larch).

Coniferous species account for more than half of the total forest area (54.1 %) in Baden-Württemberg with mature Douglas fir-dominated stands accounting for 3.2 % (Figure 91). Douglas fir regeneration occurred on only 0.3 % of the total area of coniferous forests but formed nearly 4 % of the total forest area where mature Douglas fir was the major species (Figure 91). This clearly indicates that Douglas fir regeneration mainly occurs beneath its own canopy. However, natural regeneration of Douglas fir can be considered negligible with a proportion of less than 1 % of the area in other forest types dominated mainly by broadleaved tree species; e.g. poplars (*Populus* spp.), willows (*Salix* spp.), maples (*Acer* spp.), elms (*Ulmus* spp.) or bird cherry (*Prunus avium* L.).

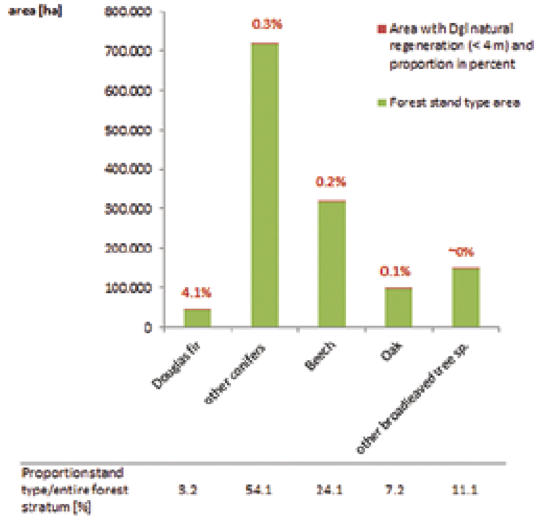

Figure 91. Natural regeneration of Douglas fir (below 4 m height) in forest stands dominated by different tree species for the State of Baden-Württemberg. The area of natural regeneration is related to the area of each forest stand type; Dgl = Douglas fir (NFI 2012).

3. Natural regeneration in unmanaged forest areas – Forest Structure Mapping

This data set was studied with respect to the question whether Douglas fir is capable to establish in forest areas that have not received any forest management for about 20 years. This provides information on the natural regeneration potential in, what may be considered as, naturally developing conditions. The largest proportions of natural regeneration of Douglas fir were mainly found in forest stands whose overstorey is dominated by mature Douglas fir or a mixture or Douglas fir and European beech (Figure 92). When considering the whole inventoried area, the largest proportion of forest stands are dominated by Norway spruce and silver fir or European beech and altogether account for about 60 %. However, those dominated by Douglas fir account for only 1.7 % (i.e. 1.3 % of Douglas fir and 0.4 % of Douglas fir mix) of the unmanaged forest area (Figure 92).

The natural regeneration of Douglas fir is relatively uncommon in stands of e.g. European beech where it formed just below 1.6 % of the area of natural regeneration present. In contrast, areas where mature Douglas fir was reported to be a major tree species or in a mixture with other species such as e.g. European beech, its natural regeneration accounted for more than 20 % of the area of natural regeneration. This indicates that Douglas fir naturally regenerates beneath its own canopy but rather negligibly under the canopies of other species in unmanaged forests. In addition, the natural regeneration of Douglas fir was absent from the sample plots dominated by shrubs suggesting that such habitats do not provide suitable conditions for natural regeneration of Douglas fir according to the Forest Structure Mapping.

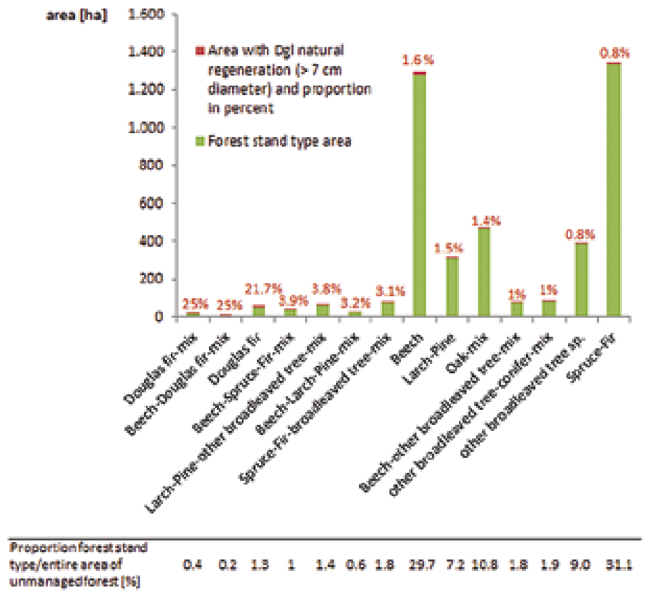

Figure 92. Natural regeneration of Douglas fir (individuals below the diameter of 7 cm) in forest stands of different species compositions in Baden-Württemberg. The area of natural regeneration is related to the area of each forest stand type. Sampling plots that could not be matched with a particular forest stand type were omitted; Dgl = Douglas fir (Forest Structure Mapping 1994–2002).

The results of the Forest Structure Mapping inventory indicated that Douglas fir has the potential to reach advanced stages of natural regeneration as it was reported to be between 11 cm and 150 cm in height in 57 sampling plots (from a total of 5 488) where it represented the largest proportion of reported Douglas fir individuals.

▶ *The natural regeneration of Douglas fir is negligible in managed as well as in unmanaged forests with the exception of areas where Douglas fir is the dominant tree species in the canopy.*

4. Natural regeneration in rare protected forest habitats – Selective Forest Habitat Mapping

The data gained from the Forest Habitat Mapping allowed analysis of the current status of Douglas fir natural regeneration in those forest habitats that are at particular risk due to being rare and/or covering only a small area. The natural regeneration of Douglas fir was reported on 0.2 % of the total area sampled during the Forest Habitat Mapping. The largest recorded area where the natural regeneration of Douglas fir was recorded was 'natural formations' habitats and 'rare near-natural forest types' with 0.46 % and 0.37 %, respectively (Table 24).

Table 24: Natural regeneration of Douglas fir in protected habitats in the State of Baden-Württemberg (Selective Forest Habitat Mapping 2015).

Habitat type	Habitat with Douglas fir (ha)	Entire size habitat (ha)	Portion of habitat with Douglas fir (%)
Natural formations	40.6	8 904	0.46
Rare near-natural forest types	98.8	26 450	0.37
Forest with animals worthy of protection	6.3	4 356	0.14
Forest with plants worthy of protection	5.6	4 143	0.14
Structurally rich forests	11.4	10 500	0.11
Succession areas	2.5	5 453	0.05
Dry habitats	0.2	4 585	~0.00
Running water	0.4	9 234	~0.00
Marsh and wetland habitats	0.1	4 936	~0.00
Sum	165.9	*81 795	0.20

*total area surveyed including habitats where Douglas fir was absent

Natural formations (areas where the natural regeneration of Douglas fir was predominantly found) are habitats usually covering only very small areas (Kerner and Geisel 2015) where acidic open rocky heaps, acidic rock formations, single rocks or cirques are the major features present. The largest area where natural regeneration of Douglas fir was found within the rare near-natural forest habitats was located in the sessile oak (*Quercus petraea* (Matt.) Liebl.) forest communities on dry sites with acidic soils (63.2 ha, *Luzulo-Quercetum and Luzulo-Quercetum* with Silene nutans, Figure 93). Douglas fir natural regeneration area further accounted for 23 % of the whole area of Luzulo-Quercetum forests and 26 % of the whole area of mixed-broadleaved forests (*Deschampsia flexuosa-Acer pseudoplatanus community*, Figure 93) being dominated by sycamore (*Acer pseudoplatanus* L.). Rocks, steep slopes, screes and ravines on nutrient-poor sites are features commonly appearing in the latter forest habitat that is, however, rare in Baden-Württemberg as it accounts for only 0.09 % of the total area of rare near-natural forest (Figure 93). Low canopy density and absence of the shrub layer, and thus a high light availability for natural regeneration, is one of the key features of this habitat providing suitable conditions for successful natural regeneration of Douglas fir (or any light or medium light demanding tree species). The success of Douglas fir in sessile oak forests is due to its high competition ability attributed to its drought stress tolerance that is especially pronounced on acidophilous, nutrient-poor and dry sites. Therefore, it has been recommended to remove the naturally regenerating Douglas fir from these valuable habitats and to set up appropriate buffer zones around the key protected areas in order to avoid seed deposition from mature trees appearing in the proximity of the rare habitats (e.g. Walentowski 2008).

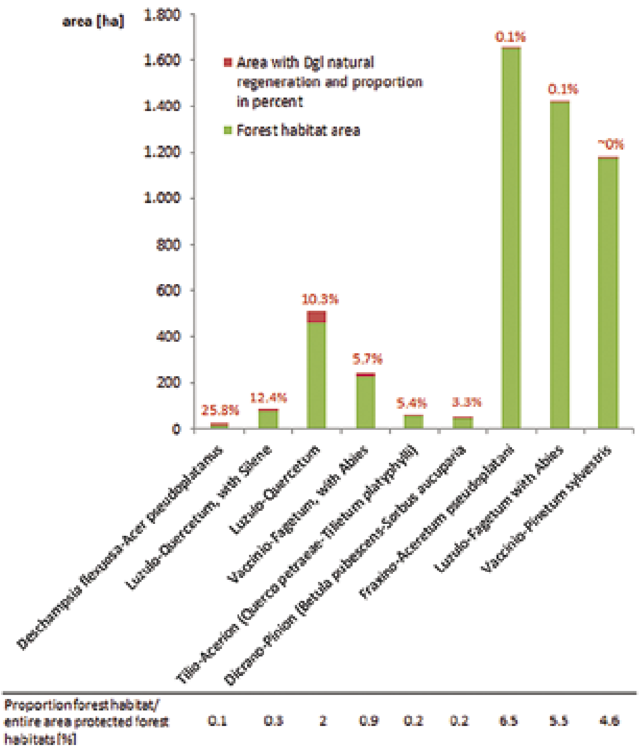

Figure 93. Natural regeneration of Douglas fir in different protected near-natural forest habitats in Baden-Wurttemberg (Forest Habitat Mapping 2015). The area of natural regeneration is related to the area of each forest habitat; Dgl = Douglas fir.

The natural regeneration of Douglas fir can be found only in several protected forest habitats such as natural formations and rare near-natural forest types.

Discussion

Natural regeneration of Douglas fir in the forests of Baden-Württemberg is currently occurring at a very low level. This introduced tree species does not naturally regenerate substantially in managed semi-natural forests with the exception of areas where it forms a dominant tree species in the canopy. In such areas, the natural regeneration of the species is typically desired and the past management reflects such situation. In commercial forestry, an adaptive management approach helping the forest to cope with the predicted climate change is to choose and encourage 'alternative tree species' (i.e. non-native) to regenerate (Mitchell et al. 2016). Therefore, the potential of Douglas fir to spread is also associated with forest management practices as no overwhelming evidence of its wider spread has been detected given the data used in this study. The area of natural regeneration is likely to increase with the increasing proportion of mature Douglas fir trees throughout the forest stands of Baden-Württemberg.

The data on protected areas where no management is applied (Forest Structure Mapping) provided similar results as natural regeneration of Douglas fir was rare with the exception of stands where Douglas fir has already been the dominant tree species in the canopy. Although there is only a small proportion of Douglas fir natural regeneration that exceeded a height of 150 cm, it is still an indication that Douglas fir has the potential to reach advanced stages of natural regeneration. However, for future research, it would be useful to include the natural regeneration of height classes in the analysis as well as including trees above 7 cm diameter.

Natural regeneration of Douglas fir currently occurs at a rather low level in the State of Baden-Württemberg, but will likely increase with the increasing proportion of mature Douglas fir trees.

Douglas fir may be considered as a potentially invasive species in special protected sites in the State of Baden-Württemberg as it is particularly successful in regenerating in *Luzulo-Quercetum* and *Deschampsia flexuosa-Acer pseudoplatanus* forest associations. So far, long-term consequences in protected habitats remain unknown, especially in terms of seed input and seedling establishment or the capability of adult Douglas fir individuals to survive extreme weather events. Considering the competitive strength of Douglas fir at those sites, this introduced tree species may have a negative influence on the native biodiversity. Therefore, it is recommended to manage such areas by designating appropriate buffer zones (ForstBW 2014) in order to protect the valuable habitats. Since Douglas fir regeneration was reported on only a small proportion of the protected forest habitats (98.8 ha) it may still be possible to successfully eradicate this tree species from such habitats. Still, the conservation of the protected habitats depends on available financial resources that would ensure long-term nature protection. The number of seed-producing trees, and thus the area where Douglas fir natural regeneration occurs, may increase in future as 45 % of all Douglas fir stand types are currently only less than 40 years of age (NFI 2012) with the oldest ones reaching an age between 120 and 135 years. It is important to consider the time since introduction as the invasions of many woody species may happen with after a considerable time lag, which may be the case of 170 years for tree species (Kowarik 1995).

Douglas fir may be considered as invasive tree species in special protected rare habitats. However, the control of natural regeneration is still possible, if the financial resources are available.

Low levels of Douglas fir natural regeneration in the State of Baden-Württemberg are most likely caused by Doulas fir being only competitive on drier sites on nutrient-poor and/or slightly acidic soils. Its natural regeneration does not appear to be favoured on sites where the nutrient levels and water availability are higher; these conditions are not favourable for its germination and early establishment and its natural regeneration is usually outcompeted by other more shade-tolerant tree species.

Data for the current assessment of Douglas fir natural regeneration is limited since the age or height of trees could not be taken in an account in most cases. It was also beyond the scope of this chapter to analyse the presence of seed trees that is related to the propagule pressure, which is, however, a key element in the process of understanding the invasion success (Lockwood et al. 2005). Nonetheless, the studies indicating the critical distance between Douglas fir mother trees and the protected habitats showed a lot of variation as Burschel and Huss (1997) considered this distance to be 60 m while Walentowski (2008) reported it to be 2000 m.

In general, the provided evidence supporting conclusions about invasiveness of introduced tree species appears to be insufficient; especially since many risk assessment tools often only rely on qualitative data or small datasets. Information on natural regeneration can present valuable quantitative data that may be used for the risk assessment of introduced tree species as they may help indicate the establishment success, potential to spread as well as adding valuable evidence regarding propagule pressure. In this context, however, the analysed data offer information on the current forest area where natural regeneration occurs and does not allow for predictions on future developments such as whether the species is capable to increase its area outside of Douglas fir forest stand types. Such predictions play a significant role for rare protected habitats and could be enhanced by analysing time series, which, in that case, were not possible due to the lack of data. Information on the natural regeneration potential of introduced tree species indeed covers only one aspect of invasiveness, which may offer information regarding the competitive strength and thus the potential to supress other tree species. However, such data does not provide information on other important criteria of invasiveness such as ecological integration within the native flora and fauna (e.g. effects on biodiversity of lichen populations), hybridisation with native tree species, transmission of diseases and pathogens, or impacts on ecosystem such as changes of the water and nutrient cycling (as per Spellmann et al. 2015). When a native species is outcompeted or in a direct competition with an introduced species, such as Douglas fir, the resource availability for native species is influenced, and this may have considerable ecological implications. However, according to Mitchell et al. (2016), such implications have not been considered in terms of determining the suitability of alternative (introduced) tree species to be used in local forests.

▶ *Data on natural regeneration are a valuable factor when assessing invasiveness.*

It is difficult to assess the whole spectrum of criteria used to assess invasiveness in the State of Baden-Württemberg with regards to Douglas fir (as well as other tree species) in this study as the data available is limited. Combining data on the distribution potential of introduced tree species considering the above mentioned nature conservation aspects can improve management approaches and thus the protection of valuable habitats. However, further research efforts are necessary in order to collect additional data and further develop solid standardised risk assessment tools providing reliable assessments of introduced tree species invasiveness.

▶ *Further develop solid standardized risk assessment tools providing reliable assessments of introduced tree species invasiveness.*

According to the three inventory datasets, the natural regeneration of Douglas fir occurs at a low level in the State of Baden-Württemberg. In managed, as well as in unmanaged forests, the natural regeneration of Douglas fir is rather negligible with the exception of areas where mature Douglas fir is the dominant tree species in the canopy. In special protected rare habitats, Douglas fir naturally regenerates on open rocky heaps and in sessile oak forest communities on dry sites with acidic soils and mixed broadleaved forests dominated by sycamore, thus may be considered as invasive species in these specific conditions.

Controlling the natural regeneration is still possible if sufficient financial resources are available. However, the area of Douglas fir natural regeneration is likely to increase in future. It is therefore important to apply appropriate management. Designating buffer zones around valuable protected habitats is considered as convenient option. Although it was not possible to assess the ecological integration of Douglas fir in natural forest communities in this context, data on natural regeneration should be considered as a valuable part of the invasiveness assessment. Further research on Douglas fir using forest inventory data can improve the management of the species and the protection of valuable habitats.

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5.4 Challenges and opportunities – Sitka spruce in Ireland

Padraig O'Tuama, Paddy Purser, Faith Wilson and Áine Ní Dhubháin

As a result of centuries of forest clearance for agriculture and industry only 1 % of the land area of the island of Ireland was forest at the beginning of the 20th century. An afforestation programme was launched in 1904 and in the early years of this programme Scots pine (*Pinus sylvestris* L.) was favoured, Scots pine being one of only three native conifers–juniper (*Juniperus communis* L.) and yew (*Taxus baccata* L.) being the other two (Joyce and O'Carroll 2002). However, over time Sitka spruce (*Picea sitchensis* (Bong.) Carr.) became the commonly planted species. The natural range of the species is confined mainly to a narrow coastal belt close to the Pacific coast of North America, extending from latitude 61°N in the western Gulf of Alaska to latitude 39°N in northern California, a distance of about 2 900 km. Sitka spruce had been introduced to Ireland in 1835 as a specimen tree (Twomey et al. 2002) but its value as a forest tree became evident from its performance in a trial established in the east of Ireland in 1905 where it grew well on difficult sites such as those with wet ground, with exposed grassy areas. On these sites, annual increment of 24 $m^3ha^{-1}yr^{-1}$ were not uncommon (O'Carroll 1984). Elsewhere the species grew successfully at elevations in the range of 305 to 550 m (Joyce and O'Carroll 2002). By 1925, Sitka spruce was being extensively grown on damp soils, and appeared to be the most rapidly growing species of the spruce genus (Forbes 1925).

Figure 94. Sitka spruce forest in Gougane Barra Forest Park in County Cork planted in 1940 grown on peaty gley soil (photo: P. O'Tuama).

Early trials showed Sitka spruce to be the most suitable species for the sites available for afforestation in Ireland.

Government policy during much of the 20th century limited the land available for afforestation to upland peat soil types and to lands deemed marginal for agriculture and consequently limited the species range that could be successfully established (Gray 1963). The development of cultivation and drainage techniques such as mounding and ploughing made it possible for such sites to be afforested and Sitka spruce was chosen due to its proven production potential (White 1956). By 1956 Sitka spruce had become the most widely planted species in the Forestry Division's afforestation programme on blanket peat (O'Gruineil 1956, White 1956) and on peat covered moorlands (Parkin 1957).

Sitka spruce accounts for 52 % of the forest area in Ireland and will account for 83 % of the total harvest over the next two decades.

The significance of Sitka spruce in the afforestation programme continued to increase and by 1985 it accounted for 60 % of the planting programme. At this time private afforestation which had been negligible up to then began to develop in response to the availability of subsidies. The range of site types available for afforestation consequently expanded to include well drained mineral soils. The high growth rates achieved by Sitka spruce on these better soil types – Farrelly et al. (2009) noted annual increment as high as 32 $m^3ha^{-1}yr^{-1}$ on better soil types – combined with the afforestation subsidies made afforestation an attractive alternative land use option for landowners (Upton et al. 2013). Consequently, afforestation has in recent years been largely undertaken by the private sector (typically farmers) with Sitka spruce accounting for 65 % of afforestation in Ireland in 2014 (Forest Service 2015). Today Sitka spruce is the most important commercial species in Irish forestry, accounting for 334 560 ha or 52 % of the total forest estate in 2012 (Forest Service 2013). It accounts for a slightly higher percentage of the growing stock volume; i.e. 59 % or 57.56 million m^3 with a gross annual volume increment of 5.39 million m^3. The species accounts for 78.7 % (2.84 million m^3) of the total mean annual harvest volume (3.65 million m^3) (Forest Service 2013).

The clearcut system is the dominant silvicultural system in use in Ireland and the vast majority of forest stands, including those composed of Sitka spruce are managed using this system (Vítková et al. 2013). The Irish forest products sector has adopted the shortwood harvesting system from Scandinavia whereby different log grades are cut to length in the forest and forwarded to the forest roadside, stacked and hauled to different processing mills. Over the last two decades, these mills have invested in state-of-the-art processing lines capable of utilising smaller logs from smaller trees. This, combined with the afforestation of more productive sites and fear of windblow, has contributed to shortened rotation lengths for Sitka spruce which is now rarely grown to the age of maximum mean annual increment.

Sitka spruce wood is particularly suited as a raw material for particleboard and fibreboard manufacture.

Figure 95. Mature Sitka spruce in Ballinagapogue Forest in County Wicklow following (photo: L. Vítková).

The end-uses for Sitka spruce sawn material include: roofing, flooring and studding. It is also used to produce pallets and fencing material (once treated with preservative) and is considered to be an ideal raw material for all types of particleboard (Cahalane 1987); its relatively lower density makes it particularly suited to oriented strand board and chip board production; its relatively long fibres making it suit to fibreboard manufacture (Joyce and O'Carroll 2002).

Due to the significance of Sitka spruce in the forest estate it is not surprising that it comprises a significant proportion of the wood harvested in Ireland. This total harvest of all species was 3.65 million m^3 in 2012; the total harvest is expected to increase to 6.4 million m^3 by 2028 as the timber output of private forests established since 1980 comes on-stream (COFORD Wood Mobilisation Group 2015). It is estimated that spruce wood (primarily Sitka) will comprise 83 % of the forecast total volume production over the next two decades. Thus the socio-economic contribution of the growing and processing of Sitka spruce is substantial with the most recent estimates indicating that the total employment supported by the forest sector was 12 000 (COFORD 2014) with total output (including indirect and induced effects) being about €2.3 billion in 2012 (COFORD 2014).

The greatest threats to Sitka spruce stands in Ireland are those posed by wind, Hylobius abietes *and* Heterobasidion annosum*.*

Sitka spruce is subject to a number of abiotic and biotic threats in Ireland. When assessing these, it is difficult to assign risk associated with the species itself versus the forest management system used. Many of the risks to Sitka spruce are considered to be compounded by the monocultural and even-aged management system which, while designed to optimise timber production, may not provide the same resilience and resistance to risks that more mixed, diverse or natural woodlands are considered to provide. These threats include:

- **wind damage** – expected to become more serious with climate change models predicting more frequent and severe storm events (Purser et al. 2004);
- **deer damage** – Ireland's ever increasing land area under forestry is resulting in greater habitat area for deer species. This means that sustainable deer management practices will become an essential part of forest management if significant damage to Sitka spruce is to be avoided;
- **butt rot** – caused by the fungus *Heterobasidion annosum* and considered the most serious disease affecting Sitka spruce in Ireland (Joyce and O'Carroll 2002);
- **green spruce aphid** (*Elatobium abietinum*) – to date has affected productivity during periods of high populations but of potential greater threat given climate change models predictions of milder winters in Ireland;
- **large pine weevil** (*Hylobius abietis*) – a threat to Sitka spruce and other species replanted on, or close to, restock sites where there are large quantities of breeding material in the form of tree stumps and residual logs with bark intact;
- two different **bark beetles**, the great spruce bark beetle (*Dendroctonus micans*) and the European spruce bark beetle (*Ips typographus*) – these are currently not found in Ireland but nevertheless represent a serious threat to Sitka spruce.

Figure 96. Windthrow in Sitka spruce stand in Ballinagapogue Forest in County Wicklow following a storm in 2014 (photo: L. Vítková).

> *It is difficult to assess and isolate the impacts of Sitka spruce as a non-native conifer species on the flora and fauna of Ireland from the effects of how it has been planted as a monoculture often located on sensitive habitats and inappropriate locations.*

The domination of Sitka spruce in Irish forests has affected Irish biodiversity in a variety of ways. The ecological impacts of the planting of this species and the subsequent silvicultural method (clearcut) used relate to the original habitat and associated biodiversity that it replaced. The underplanting of scarce native woodlands and semi-natural old estate woodlands with introduced tree species including Sitka spruce (as well as Norway spruce (*Picea abies* (L.) Karst), silver fir (*Abies alba* Mill.), beech (*Fagus sylvatica* L.), sycamore (*Acer pseudoplatanus*, L.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), etc.) was common, particularly in the 1940s, 1950s and 1960s. The introduction of these species, which cast a dense shade, interrupts the natural structural dynamics of the woodlands affecting natural regeneration within the stand as well as the development of an understorey and the ground flora. Of more serious concern from an ecological perspective was the establishment of monocultures of Sitka spruce and other conifers on peatland habitats. These were the main afforested soil types in Ireland, both overall (accounting for 52 % of all afforestation) and in every ten-year period after 1956 when the major afforestation era started (Wilson et al. 2012). The peatlands that were most frequently afforested in Ireland were blanket bogs and wet heaths (Smith et al. 2006). Until 1955, the majority of afforestation occurred on well drained soils. The proportion of planting on peat increased between 1956 (12 %) and 1985 (71 %), and subsequently declined to 43 % between 1996 and 2005. There has been a general downward trend of peatland planting since 1990 (Black et al. 2008) arising from changes in forest policy. Afforestation on certain environmentally sensitive sites, including Natura 2000 sites, is now not allowed. Nevertheless, the legacy of the earlier afforestation of peatland has been a loss of extensive areas of ecologically important habitats in both the lowlands and uplands including the loss of many peatland habitats and species rich grasslands as well as impacting on a number of protected animal species. A range of Annex I habitats and Annex II faunal and floral species of the EU Habitats Directive have been found to be negatively affected by afforestation of introduced species (NPWS 2013a, 2013b, 2015). It is difficult to assess and isolate the specific impacts of Sitka spruce in this regard although it has been the main species used. It is also difficult to assign risk associated with the species itself versus the forest management system (clearcut system) and operations used e.g. drainage, monoculture.

Damage to biodiversity arose from direct loss of habitat, alterations of natural drainage patterns, fertilisation, siltation, acidification of watercourses, shading, regeneration of introduced tree species, soil erosion, decline in water quality, eutrophication, etc. The natural cycle of carbon sequestration by peatlands was also negatively affected.

The impact of some of this damage is being reversed through a series of projects funded under the EU LIFE-Nature Programme. These include projects by Coillte Teo. (a private limited company co-owned by the Ministry of Agriculture, Fisheries and Food and the Ministry of Finance, and which is responsible for the management of much of the public forest estate) for the restoration and conservation of 571 ha of raised bog habitat, almost 2 000 ha of blanket bog habitat and 550 ha of priority native woodland habitats within Natura 2000 sites mostly through the restoration of natural hydrology and drainage patterns on peatland sites and the removal of conifers. The Kerry LIFE project (2014–2019), which has recently commenced aims to restore populations of freshwater pearl mussel (*Margaritifera margaritifera* Linnaeus, 1758) in the southwest of the country and will trial various forest management prescriptions.

Irwin et al. (2014) recently examined the species diversity and community composition of plants, invertebrates and birds in Sitka spruce dominated and Norway spruce dominated plantations in Ireland, with that of oak- (*Quercus* spp.) and ash (*Fraxinus excelsior* L.) dominated semi-natural woodlands in the same area. Their study showed that species richness in spruce plantations can be as high as semi-natural woodlands, but that the plantations and semi-natural woodlands support different assemblages of species. For many taxa species richness values in Norway spruce plantations showed greater similarities to those of native woodlands than those in Sitka spruce dominated forest plantations.

A study of the ground flora of various commercial plantations (the plant communities of mature Sitka spruce, Norway spruce, Japanese larch (*Larix kaempferi* (Lamb.) Carr.) and ash plantations) and native woodlands in Ireland (Coote et al. 2012) found that none of the coniferous plantation plant communities were similar to either semi-natural oak or ash woodlands.

In some cases faunal species have benefitted from Sitka spruce plantations providing rich foraging and breeding habitat for a variety of bird species as for instance raven (Corvus *corax* Linnaeus, 1758), coal tit (*Periparus ater* Linnaeus, 1758), long eared owl (*Asio otus* Linnaeus, 1758), crossbill (*Loxia curvirostra* Linnaeus, 1758), etc. in many cases allowing species to extend their range such as the pine marten (*Martes martes* Linnaeus, 1758), buzzard (*Buteo buteo* Linnaeus, 1758) (Balmer 2013) and many non-native deer species (Carden et al. 2011), or provided a refuge from non-native competitors i.e. the plantations provide red squirrel (*Sciurus vulgaris* Linnaeus, 1758) with refuge from grey squirrel (*S. carolinensis* Gmelin, 1788) (Waters and Lawton 2011).

It is difficult to assess and isolate the impacts of Sitka spruce as a non-native conifer species on the flora and fauna of Ireland from the effects of how it has been planted as a monoculture often located on sensitive habitats and inappropriate locations. The general silvicultural method of the clearcut system with an average rotation length of about 40 years has also contributed to these impacts; there are only a small number of sites that contain older stands. Its potential to become an invasive species under the wider understanding of the term is also unknown as Sitka spruce only begins to produce seed at about 30 years of age. At present, Sitka spruce is an 'amber' listed invasive species in Ireland whose impact on conservation goals remains uncertain due to a lack of data showing impact (or lack of impact).

Sitka spruce is one of the non-native conifers introduced into Ireland almost two hundred years ago and the species has flourished in wet climatic conditions resembling its natural range, exhibiting growth rates that are among the highest in Europe. It has been and continues to be the dominant species used in Irish forests and consequently will account for most of the timber output from Irish forests, at least over the next two decades. It also plays a significant role in the burgeoning private forestry sector in Ireland. The greatest threats to Sitka spruce stands in Ireland are those posed by wind, *Hylobius abietes* and *Heterobasidion annosum*. In earlier years it was planted, in monoculture, on sites that are now recognised as sensitive, and this has had significant negative environmental consequences. More recent afforestation of the species has, however, been on less sensitive areas. Natural regeneration of Sitka spruce does occur and can be prolific following clearfell of more mature stands in certain circumstances (Joyce and OCarroll, 2002). However, it is the view of the authors that, unlike some invasive species, it has not regenerated outside of forest areas and in this regard is not considered a threat for widespread invasive dispersal.

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5.5 Tasmanian blue gum in Portugal – opportunities and risks of widely cultivated species

Joaquim S. Silva and Margarida Tomé

> *The Tasmanian blue gum is one of the most widely cultivated broadleaf species on the planet.*

Plantations of eucalypts (*Eucalyptus* spp.; family Myrtaceae) account for the largest area of non-native forests in Europe; these plantations are mainly located in the Iberian Peninsula (Schelhaas et al. 2006), and due to their continued expansion, eucalypts currently occupy around 1.5 million ha in Portugal and Spain (MAAMA 2012, ICNF 2013). The two most important eucalypt species in Europe are Tasmanian blue gum (*Eucalyptus globulus* Labill.) (hereafter blue gum) and red gum (*Eucalyptus camaldulensis* Dehnh). Blue gum is currently the most commonly occurring tree species in Portugal as it occupies 812 000 ha, which equates to 26 % of the total forest area (ICNF 2013). Around 20 % of eucalypt stands in Portugal are managed by pulp companies, while the remaining area is managed by individual landowners.

Figure 97. Leaves and flower buds of blue gum (photo: H. Marchante).

Blue gum is a species native to south-eastern Australia (Tasmania and Victoria). It was first introduced to Europe in 1804 as an ornamental tree to botanical gardens. In Portugal, this eucalypt species was introduced in the middle of the 19th century. The fast growth of this species captured the attention of foresters and botanists soon after its introduction. However, its ability to drain wet areas was the major purpose for its first use in forestry (Figure 98), especially in coastal marshlands (Radich 2007). The first pulp company using eucalypt wood (Caima Pulp) was established in Portugal in 1907. The expansion of blue gum was essentially driven by the increasing demand for raw material by the pulp industry, particularly after the 1960s. The first Portuguese National Forest Inventory (NFI) estimated the area of eucalypt plantations to be 150 000 ha (DGFRA 1966a, b).

Figure 98. An example of one-year-old eucalypt at the swamp of Juncal Gordo, central Portugal, in 1911 (photo: M.A. Rei).

Blue gum plantations are normally coppiced every 10 to 12 years along three rotations.

Blue gum plantations are even-aged monocultures managed according to a coppice system (10 to 12-year rotations) for pulp production. The planted rotation is normally followed by two coppice rotations. The main climatic factors limiting the expansion of plantations in Portugal are water availability and low temperatures (Ribeiro and Tomé 2000) resulting in the current species distribution confined mainly to the coastal regions of northern and central Portugal and along the River Tagus. The expansion of blue gum has been mostly conducted by individual landowners, and to a lesser extent by the pulp companies. Hence, there are many examples of stands established in unsuitable areas mostly in inland and drier regions. In these areas, the site indices (dominant height at 10 years of stand's age) are below 14 m, whereas on good sites, most plantations have site indices above 20 m at 10 years of age, corresponding to a mean annual increment above 14 m^3/ha (Tomé 2000). On the best sites, site index can be close to 28 m corresponding to annual increments of more than 30 m^3/ha (Tomé 2000). Tree breeding programs were developed in the last 50 years, leading to gains in productivity between 25 % and 50 % (Borralho et al. 2007). Genetically improved planting material from these breeding programs is used in most industrial plantations managed by pulp companies, but at present, only a small proportion of private landowners use such improved planting stock.

There is a growing number of forest owners who have joined forest certification programs (for further details on how issues of introduced species are dealt with by certification, please see Text Box III). Both the Program for the Endorsement of Forest Certification (PEFC) and the Forest Stewardship Council (FSC), have been adopted by the industry and by individual landowners (mainly through regional forest owners associations), contributing to the enhancement of the productivity and the environmental performance of the plantations. Besides these advantages, there are more immediate motivations for joining certification programs. The certified paper products can be sold on international markets, resulting in a higher price of certificated wood paid by the pulp companies to the individual landowners, which may be particularly attractive for the small landowners.

Figure 99. A typical second rotation eucalypt stand managed by a pulp company in central Portugal (photo: H. Matias).

▶ *Given its high growth rate, blue gum plantations have a high capacity to sequester carbon from the atmosphere and to extract water and nutrients from the soil.*

There have been many studies regarding the environmental impacts of eucalypt plantations. Carbon sequestration is an important issue given the current concern with greenhouse emissions and global warming. Given its high growth rate, blue gum plantations have a high capacity to sequester carbon, although this capacity is offset by the relatively high decay rate of paper products (Skog and Nicholson 1998). As with other highly productive tree species, carbon sequestration is highly influenced by the availability of water and nutrients in the soil. The increases in above and belowground carbon in an experiment in Portugal six years after planting were between 5.9 kg C/m^2 in control plots and 11.4 kg C/m^2 in experimental plots where irrigation and fertilization was applied (Madeira et al. 2002).

A common criticism about eucalypt plantations stems from their ability to extract water from the soil, therefore competing with other organisms. An experiment carried out in Portugal showed that eucalypts intercepted less water in the canopy than native maritime pine (Pinus pinaster Aiton.), therefore leading to a lower water loss to the atmosphere (Valente et al. 1997). However, the transpiration rates of the two species followed a similar pattern for a similar leaf area index (Loustau et al. 1996, David et al. 1997). On the other hand, the run-off can significantly increase in the year following clearcutting (David et al. 1994). This effect was, reported to last for 1–3 years due to the fast growth of the canopy. Blue gum plantations are associated with soil water repellency which may also contributes to increase run-off (Walden et al. 2015).

Blue gum plantations extract a large amount of nutrients from the soil although an important proportion of the nutrients can be returned to the soil if the leaves, branches and bark are left on the site after harvesting (Madeira et al. 2007). Recent harvesting practices do not include debarking on the site as the bark is used for energy generation at the pulp mills. Nutrient restoration via litter decomposition has been found to be faster than in maritime pine (Ribeiro et al. 2002) and oak stands (Canhoto and Graça 1996) but slower than in alder (*Alnus glutinosa* (L.) Gaertn.) stands (Pozo et al. 1998). However, a recent meta-analysis showed that blue gum plantations significantly inhibited litter decomposition in streams when compared to native forests (Ferreira et al. 2016). As to physical characteristics, the soils of eucalypt stands have been found to be more compacted leading to lower hydraulic conductivity and infiltration rate as opposed to cork oak (*Quercus suber* L.) stands (Madeira 1989).

▶ *Eucalypt plantations are in general less diverse in species richness than other common land use systems.*

One of the most studied impacts of plantations is the change in biodiversity, compared to natural ecosystems. Studies in Portugal (Madeira et al. 2007) showed that blue gum plantations had a lower density of soil arthropods than maritime pine stands and other native vegetation. Similar results were found in relation to soil colembola and riparian macro-invertebrates (e.g. Abelho and Graça 1996). With regard to the vertebrate diversity, several studies compiled by Onofre (2007) show that eucalypt plantations are in general less diverse in bird richness than other common land use systems in Portugal. Onofre stresses that one component of this finding is related to the intensive short-rotation silviculture, while another component is due to the exotic nature of eucalypts to which the native fauna is not well adapted to.

Abandonment of plantations by landowners is a serious problem in Portugal given the increase in fire hazard and the low economic and ecological value of these areas; in many cases the abandonment is driven by fire occurrence (Silva et al. 2011). Occurrence of mixed stands is an indicator of abandonment as most actively managed forests are monocultures. In 2005, there were 173 000 ha of mixed stands of eucalypts and pines representing an increase of 75 % when compared to 1995 (AFN 2010). Mixed stands of eucalypts and pines are very frequent and represent the highest fire hazard among all forest types in Portugal (Moreira et al. 2009). However, the abandonment of plantations might also enhance the naturalisation process of the species given the absence of understorey management and the increase in propagule pressure (Silva and Marchante 2012).

A highly relevant environmental issue is the fire susceptibility of eucalypt plantations, particularly in Portugal where forest fires are a major concern (San-Miguel and Camia 2009). The accumulation of high quantities of biomass, the dry environment in the understory and the presence of flammable oils may contribute to the high fire hazard of eucalypt plantations (Fernandes et al. 2011).

> *The pulp and paper sector is a very important part of the Portuguese economy with blue gum wood being the main raw material for the pulp and paper industry.*

In 2012, the pulp and paper sector contributed to the industrial GDP with 8 % and to the national GDP with 4.4 %, representing 4.9 % of the total national exports. Also, a substantial number of jobs is supported by the forestry and industrial production chains, corresponding to 1.2 % of employment, (CELPA 2015). Thanks to these remarkable figures there are very contrasting views and perceptions about the role and importance of eucalypt plantations in Portugal. Urban citizens, who do not directly benefit from the plantations, tend to be against eucalypts, which are perceived as presenting lower aesthetic and recreational value than alternative land uses. Rural landowners, on the other hand, tend to have a contrasting view because of the income provided by these plantations. In fact, eucalypts are often cultivated in very small land plots, and much of the plantation area is fragmented and owned by myriad of small landowners. In the areas where eucalypt plantation expansion is the greatest (central and northern Portugal), there are around 10 million registered land plots with an average area of less than 1 ha (DGRF 2006). In these regions, eucalypts are seen as an important source of revenue, not only by the landowners, but also by other people who get direct or indirect economic benefits from plantations, including, for example, employees from small harvesting and transport enterprises.

However, this was not always the case, particularly during the 1980s. At that time, there was a marked expansion of plantations, mainly driven by pulp companies and encouraged by state policies. Protests took place in rural areas where, in some cases, newly established eucalypt plantations, particularly in northern Portugal, were destroyed by the members of the rural communities. Protest actions organized by the local NGOs involving the chaining of environmental activists to bulldozers working for the pulp companies also happened during this period of time. It is worth mentioning that, at that time, eucalypt area covered less than half of todays area. With time, many people have come to accept the eucalypt plantations. In 2013, a national newspaper announced the results of the last NFI showing that blue gum had become the main tree species in the country. However, there were no significant protests. Therefore, it seems that the society has become used to the presence of eucalypts in large areas of the Portuguese landscape. The popular negative perception that still exists is very likely driven by aesthetic and recreational values, but there is also a strong association between eucalypt plantations and forest fires. In addition, according to a study that surveyed the landscape preferences of the inhabitants from Serra do Açor, eucalypt plantations were the least preferred option (Páscoa et al. 2005).

▶ *Blue gum is naturalised in Portugal but the assignment of an invasive status has been controversial.*

Using clear and consistent terminology and definitions is crucial when talking about invasiveness of an economically important species such as blue gum. In Portugal, the species is not officially listed as invasive in the still-in-force Decree Law 565/99, which contradicts the assessment presented by Marchante et al. (2014) in the Portuguese guide on invasive plants. Rejmánek and Richardson (2011) stated that the reproductive characteristics of eucalypts do not favour a strong invasive character, particularly when compared with other widely planted species such as pines. Indeed, the eucalypt seeds are small and dehiscence is not particularly adapted to wind dispersal. In addition, the seeds are short-lived, which prevents the formation of a soil seed bank. It is also important to note that recently established seedlings endure a high mortality rate when competing with dense native vegetation (Rejmánek and Richardson 2011).

One of the first known references to a possible naturalisation of blue gum in Portugal refers to 1954 (Goes 1977). More recent studies suggest that blue gum is able to naturally regenerate in large areas of the Portuguese landscape, particularly in burned areas; Águas et al. (2014) for instance found natural regeneration in 93 % of sample plots established in burned areas of pure stands of blue gum and in 98 % of mixed stands. Moreover, the same study concluded that the size distribution and the existence of fruit-bearing wildlings, were strong evidence that blue gum is able to establish new self-perpetuating populations, which is the necessary condition to assign a naturalisation status. Fire seems to play a significant role on dehiscence from living capsules in the canopy, by causing the necrosis of capsule tissues and subsequent seed release (Santos et al. 2015). A recent study carried out at a countrywide scale along roadsides, confirms the ability of the species to produce offspring all across the Portuguese territory. The survey showed the existence of natural regeneration from lateral seed dispersal in 60 % out of 3111 samples (Catry et al. 2015). Climatic factors (e.g. precipitation, temperature range, frost days) were reported to be the major driver of the abundance of natural regeneration in the above-mentioned study, together with topography and soil type.

A critical aspect regarding the invasive status of a cultivated introduced tree species is the capacity to spread outside the cultivated areas. The assessment of lateral dispersal in Spain (Calviño-Cancela and Rubido-Bará 2013) and seedling establishment in Portugal (Fernandes et al. 2016) revealed that 97 % of seeds and 92 % of seedlings of blue gum were found within 15 m from the plantation edge, with maximum distances of 80 m for seeds and 75 m for seedlings. In Portugal, the only documented case of eucalypt dispersal beyond 100 m was reported from Tapada Nacional de Mafra (Catry 2000), a conservation area near Lisbon, where areas dominated by blue gum have increased from 4 ha to 64 ha between 1974 and 1995; i.e. complying with the definition of invasive species proposed by Richardson et al. (2000). Heathfield et al. (2001) simulated these naturally established thickets using a seed dispersal model with a maximum dispersal distance of 200 m. They concluded that a combination of factors may have facilitated this documented invasion process: fire occurrence (e.g. Santos et al. 2015), a sloping terrain (Catry et al. 2015), a favourable climate (Catry et al. 2015) and a high propagule pressure (Simberloff 2009). These conditions are relatively common in the coastal regions of central and northern Portugal, suggesting the need for a proper management of eucalypt plantations and their surrounding areas, in order to control any escape (Calviño-Cancela and Rubido-Bará 2013).

Figure 100. Eucalypt wildlings escaped from an abandoned plantation, on a roadside near Coimbra, Central Portugal (photo: J. Silva).

Opportunities and risks of a widely cultivated species.

In spite of the economic importance of eucalypt plantations in Portugal, there are important constraints based on mismanagement resulting in low productive stands and increase of the susceptibility to forest fires, particularly associated with the smaller areas that represent an important part of the eucalypt cover in Portugal. The reproductive characteristics do not favour invasion, as opposed to some legume or pine tree species. However, the presence of natural regeneration is fairly common, particularly in the moist coastal climates of central and northern Portugal. The high incidence of forest fires and the abandonment of plantations may strongly favour the recruitment of new plants. Nonetheless, many knowledge gaps still remain open. Besides the Tapada de Mafra case study, there is no other documented evidence of invasion processes.

The effect of colonisation by blue gum on native vegetation is still a comparatively unstudied issue. Although it grows much faster than native species, Moreira et al. (2013) found considerable densities of native species in burned eucalypt stands, suggesting a reasonable resilience of local ecosystems. As for the opportunities, the possibilities presented by forest certification in terms of improving both the production as well as the environmental performance of eucalypt plantations, particularly among owners of small plots, must be stressed. It is also important to note that the spread of best practices in eucalypt stands should be the primary aim of forest management in Portugal, especially given the difficulties originating from the existence of a large number of poorly managed small-scale forests scattered throughout the landscape.

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5.6 Integrating black cherry in forest management in the Netherlands and Belgium

Bart Nyssen, Jan den Ouden, Kris Verheyen and
Margot Vanhellemont

The possibilities of integrating black cherry (*Prunus serotina* Ehrh. var. *serotina*) into the forests on sandy soils in the Netherlands and Belgium is addressed in this chapter. We present a toolbox for forest managers that will help them in integrating black cherry into the forest management. This case study is, in major part, based on the Dutch/Belgian book '*Amerikaanse vogelkers van bospest tot bosboom*' (black cherry, from forest pest to forest tree) (Nyssen et al. 2013).

▶ *Black cherry is a valuable timber species native to North America that was introduced into Europe in the 17th century.*

In the eastern part of North America, black cherry is a commonly occurring species and is considered as the most widespread native *Prunus* species on the American continent (Marquis 1990). It can be found within most forest types in the eastern part of North America. However, it only occurs as a co-dominant species in the man-made cherry-maple forest-type. In such forest type, black cherry is a primary component along with red maple (*Acer rubrum* L.), sugar maple (*A. saccharum* Marshall), and white ash (*Fraxinus Americana* L.) (Uchytil 1991).

The first known introduction of black cherry to Europe took place in France in 1623. As for other European countries, black cherry was first planted in Britain in 1629 and in Germany in 1685. In the Netherlands, black cherry was first introduced in 1740 where it was planted in the botanic garden in Leiden. The first introduction in Belgium likely took place at the same time, although it is not properly documented. Since its first introduction to Europe, black cherry has been planted in arboreta, parks and gardens due to its aesthetic qualities (i.e. spring blossoms, summer fruits and colourful foliage in the autumn). At the end of the 19th century, black cherry was planted in several species trials in Germany, but also in Belgium and the Netherlands, in order to test its timber production potential (e.g. Schwappach 1896).

▶ *Black cherry was widely used in forest restoration programmes in the 20th century.*

The big expansion of black cherry in the Netherlands took place in the first half of 20th century as black cherry started to be used as an admixture species to prevent spread of disease and fire in Scots pine (*Pinus sylvestris* L.) plantations and to enhance litter decomposition. Black cherry was also used to create firebreaks between individual pine stands and to stabilise mobile sand dunes. Black cherry became rather common in the Dutch and Belgian forests starting in 1920s (Muys et al. 1992). Its popularity has also been apparent since the 1950s in the north-western European sand belt where large areas of unproductive land (mainly heathland and drift sand) were reforested with black cherry. In the 1960s it became apparent in the Netherlands that dominance of black cherry on some sites seriously hindered the natural regeneration and plantation of native Scots pine (the main commercial tree species in the Netherlands), which was usually managed using a clearcut system (Figure 101). The natural regeneration of black cherry was already present in the understorey of the mixed Scots pine and black cherry stands, and when the mature Scots pine was clearcut, this regeneration was released and became dominant. Forest managers started to consider black cherry as a contributing factor to reduced biodiversity, and programmes for eradication of black cherry were established (Bakker 1963). These eradication programmes further allowed native species such as silver birch (*Betula pendula* Roth), rowan (*Sorbus aucuparia* L.) and alder buckthorn (*Rhamnus frangula* Mill.) to become more common. With the exception of a period of 'reflection' between 1970 and 1985 (Staatsbosbeheer 1984), the eradication programmes lasted until recently when the rising costs and often limited success of eradication led forest managers to reconsider the status of the species and search for alternative management strategies (Figure 102).

Figure 101. Natural regeneration of black cherry in a Scots pine forest following the formation of thinning racks (photo: B. Nyssen).

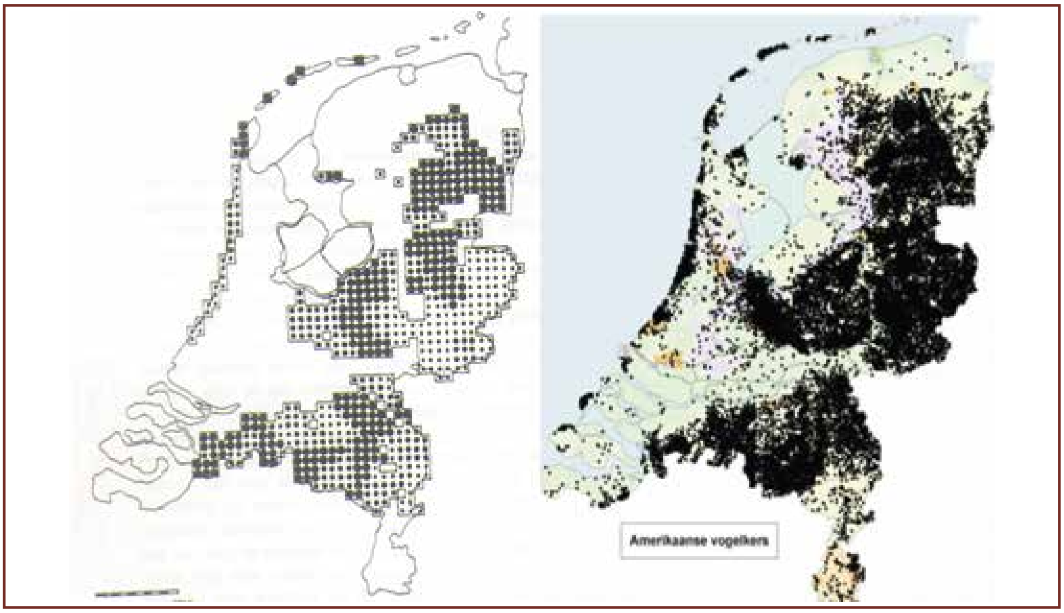

Figure 102. The occurrence of black cherry in the Netherlands before (Iven 1963) and after the eradication programmes (Beringen and Odé 2012).

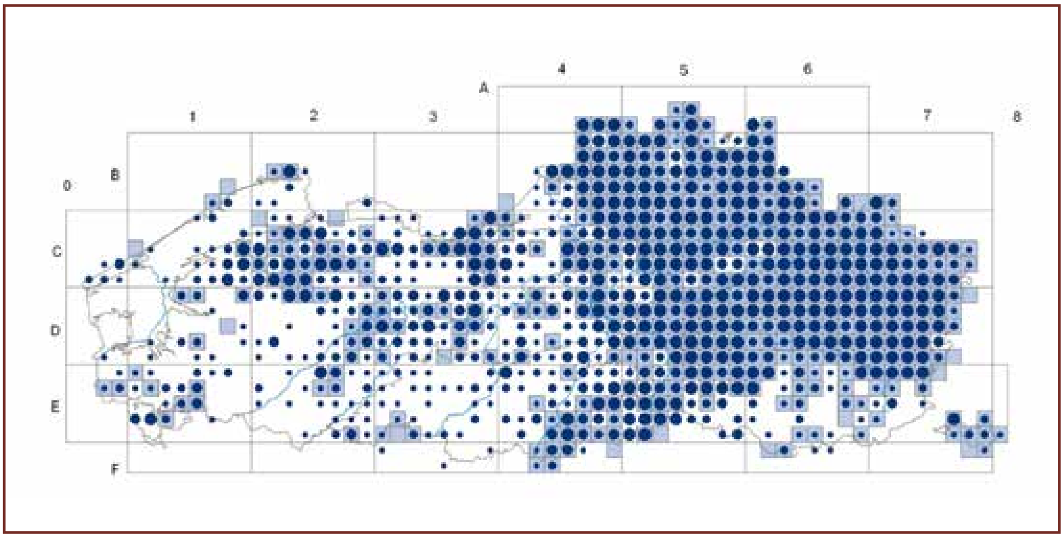

Figure 103. The occurrence of black cherry in northern Belgium; the light blue squares represent the black cherry's spread in the period between 1939 and 1971, while the black circles represent its spread in the period between 1972 and 2004 (Landuyt van 2006).

Black cherry is naturalised in the north-western European sand belt that reaches from northern Belgium across the Netherlands and Denmark to northern Poland.

Naturalisation of an introduced species is described as the process during which the species establishes new self-perpetuating populations, undergoes widespread dispersal and becomes incorporated within the resident flora (Richardson et al. 2000). Black cherry affects the composition of the herb layer (Starfinger 1990) and in open vegetation types, such as heathlands, it has a negative impact on the local ecosystem as it directly competes for light with other plants. Black cherry easily colonises heathland similarly to some native tree species such as Scots pine, silver birch and alder buckthorn. In addition, the presence of black cherry is deemed negative when forest owners wish to keep their pine forest in the pioneer stage comprising of Scots pine, silver birch and oak with a herb layer species composition of heliophilous (i.e. light-demanding) plants such as wood sage (*Teucrium scorodonia* L.), hawkweed (*Hieracium* spp.), goldenrod (*Solidago virgaurea* L.) and common cow-wheat (*Melampyrum pratense* L.). The establishment of black cherry mainly changes the light conditions in these forests as it forms a shrub layer similar to that of silver birch, rowan and alder buckthorn. The expansion of black cherry in forests on sandy soils is not considered a problem as such because these forests generally do not contain rare or endangered plant species and high conservation value biotopes (Starfinger and Kowarik 2011). Black cherry acts as late pioneer species shading out light-demanding species such as purple moor grass (*Molinia caerulea* (L.) Moench) and heather (*Calluna vulgaris* (L.) Hull) and promotes typical forest vegetation such as May lily (*Maianthemum bifolium* (L.) F.W. Schmidt) and Solomon's seal (*Polygonatum multiflorum* (L.) All.) (Nyssen et al. 2013; Figure 104).

Figure 104. May lily and Solomon's seal in a mature stand of black cherry on sandy soil (photo: J. Tonckens).

> *Black cherry is a host for many species that are, in part, the same species also being hosted by native Prunus species such as bird cherry (*Prunus padus L.*), wild cherry (*P. avium L.*) and blackthorn (*P. spinosa L.*).*

Black cherry was recently found harbouring a less dense, but more diverse, herbivore community than the native bird cherry, with similar proportions of specialist and generalist species (Schilthuizen et al. 2016). The herbivory on black cherry doubled over the past century indicating that evolutionary processes may generate a specialised herbivore community developing on an introduced plant; such communities may develop to an extent that they may reduce the invasive potential of the introduced species over time (Schilthuizen et al. 2016). Many studies have found that a wide range of species are associated with black cherry such as insects (e.g. Nowakowska and Halarewicz 2006, Meijer et al. 2012), birds (e.g. Deckers et al. 2008), mammals (e.g. Sebert-Cuvillier 2008) and fungi (Möller 1998). An example of a butterfly species found on black cherry is the scarce swallowtail (*Iphiclides podalirius* Linnaeus; Figure 105).

Figure 105. The native scarce swallowtail caterpillar that can be commonly found on all *Prunus* spp. leaves, including that of black cherry (photos: R. Hille and R. Thassos).

Figure 106. This forest manager tried many methods for eradicating black cherry from the native Scots pine forests (e.g. cutting it down, pulling it out or treating its stumps and leaves with glyphosate); now, he is thinking about other solutions (photo: B. Nyssen).

Many Dutch and Belgian foresters now consider black cherry to be a valuable component of the forest.

Once black cherry is accepted within the regular forest management, the costs of eradication will disappear and may even be replaced by revenues from timber production. Depending on the timber quality, black cherry timber can be sold at the same price as wild cherry with the prices ranging between €65 and €2 500/m^3 (Van der Burgh et al. 2000). In canopy gaps, black cherry seedlings grow straight stems (e.g. Grundler 2011) and can be integrated in the management of the stand. Currently, three strategic management options are available when managing forests where black cherry is present: eradication, acceptance or enhancing the resilience of the forest. The option chosen depends on the impact black cherry has on the management goals (Petersen et al. 2015). Figure 107 presents a decision scheme for forest owners and managers when choosing a management strategy in forests where black cherry is present.

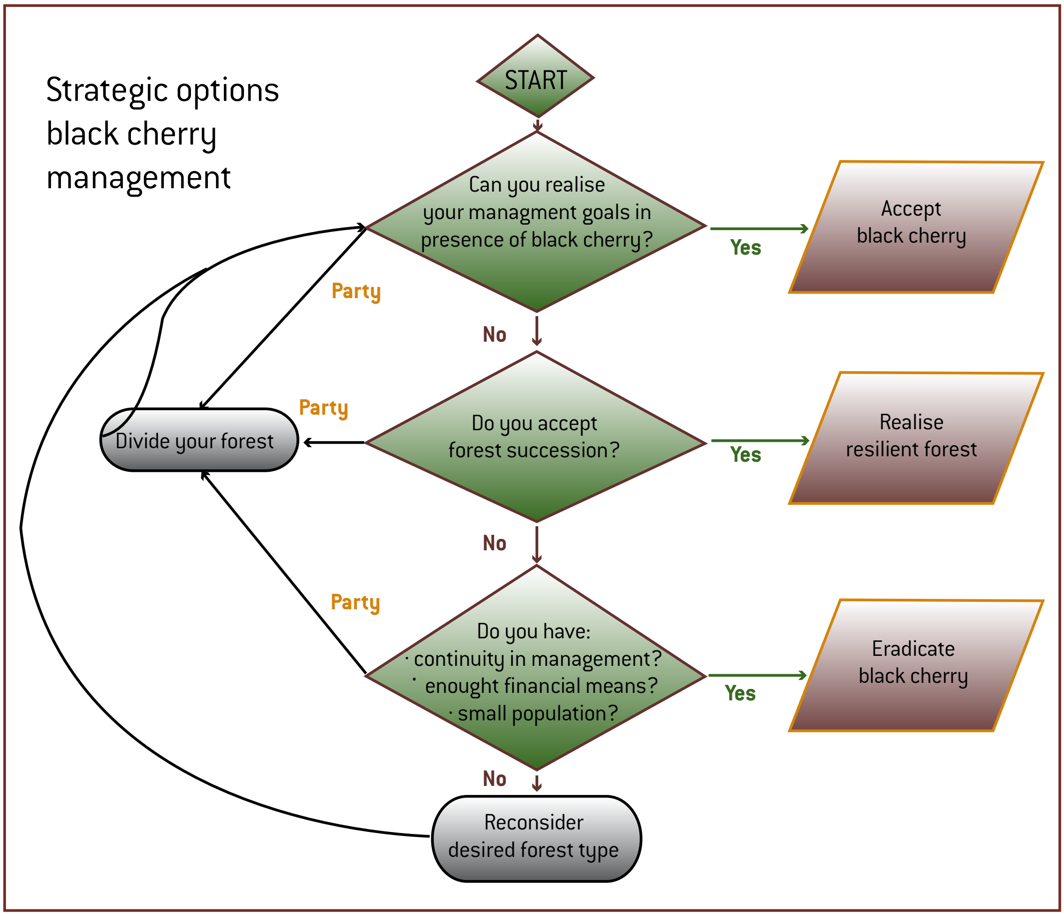

Figure 107. Decision making tool of strategic management options for black cherry.

Eradication of black cherry is necessary when its presence is incompatible with the goals of forest management.

Eradication of black cherry is necessary when the objectives of management are to maintain specific open vegetation types, such as heathland, grassland, Natura 2000 forest habitat types (especially 9190 Old acidophilous oak woods with *Q. robur* on sandy plain) or open forest types with light demanding tree species. The best chances for successful eradication are when the population is small and confined, and a systematic approach with a thorough follow-up management is applied. The eradication measures are very costly; the local eradication of black cherry may take up to 20 to 30 years and is done in two phases. In the first phase, the seed trees are removed; a combination of chemical and mechanical measures has proven to be the most effective. The stumps of the trees that had been cut are treated with glyphosate. The cost of this measure is between €200 and €2 200 per hectare for every intervention depending on the abundance and the age of the trees. In the second phase, an inspection of the entire area that had been subjected to the eradication measures is necessary to be applied every five years to prevent the development of new seed trees (Nyssen et al. 2013). On a forest-wide scale, this treatment can be successful as long as the area is frequently monitored and the establishment of new seed trees is prevented. This is necessary because half a century of intensive eradication programmes in the Netherlands – estimated to have cost €200 million – have proven that eradication of black cherry is no longer possible at the landscape scale (Figures 108 and 109). Black cherry seeds are effectively dispersed by birds and mammals (Sebert-Cuvillier 2008), which allows for black cherry seedlings to be established again in open forests.

Figure 108. Natural regeneration of black cherry from fox excrement (photo: J. den Ouden).

> *This impossibility of eradication at the landscape scale has led forest managers to accept black cherry in their forests.*

When the presence of black cherry does not hinder the fulfilment of management objectives, the acceptance of the species presence may be considered as the most suitable option. If timber production is a management goal, then black cherry is a valuable alternative to wild cherry. In the Netherlands and Belgium, the guidelines for the production of black cherry quality timber (on sandy soils) have been developed using German, Belgian and Dutch experiences; North American guidelines (i.e. Perkey and Wilkins 2001; Box 25) were also considered.

> *Absence of late-successional tree species that could compete with black cherry results in the increase of invasibility of these forests.*

Scots pine forests in the eastern parts of the Netherlands and northern parts of Belgium have been planted in the 20th century on heathlands and managed with the aim to produce timber. Thus, Scots pine has always been favoured over native broadleaved tree species. The open structure of the even-aged Scots pine stands promoted black cherry invasion. Moreover, late-successional tree species such as European beech (*Fagus sylvatica* L.), hornbeam (*Carpinus betulus* L.), sweet chestnut (*Castanea sativa* Mill.), sycamore (*Acer pseudoplatanus* L.) and small-leaved lime (*Tilia cordata* Mill.), which could compete with black cherry were never planted as the soil conditions of the heathlands were not suited for these species. As a result of this, these late-successional species have had little chance to colonise these forests once the soil conditions have ameliorated. Recent ecological research helps to understand the role of black cherry in the dynamics and functioning of these forest ecosystems (e.g. Verheyen et al. 2007, Vanhellemont 2009).

Box 25: Management guidelines for black cherry on sandy soils where the aim is timber production

1. Regenerate under light shelter or in gaps with a minimum width of 10 m and a maximum width of 1.5 times the height of the surrounding trees.
2. Select the desired species composition in mixed natural regeneration groups.
3. Designate control paths in large-scale regenerations.
4. When the crown base is about 2 m, select 200 ‘option trees’ per ha.
5. Inspect every 3 years to make sure the main shoot of the ‘option trees’ is developing well.
6. Select 40 vital well-formed future crop trees per hectare when the crown basis is at 5 to 6 m height.
7. Gradually free the crop trees from competition to minimise the growth of epicormic shoots growing from the stem; cut a maximum of 1 or 2 competitors.
8. Remove dead branches and prune living branches beneath the desired crown onset height.
9. Subsequently free future crop trees completely every 3 to 6 years.

Black cherry will reach its maximum crown expansion at an age of 45 to 50 years. On sandy soils a diameter at breast height of 50 to 60 cm at age 50- to 80-years-old is possible.

The resilience of a forest against black cherry dominance is promoted by the reduction of light levels in the understorey. The most effective strategy for the reduction of black cherry is the introduction of shade-tolerant and shade-casting species and the creation of multiple crown layers. The replacement of black cherry can be achieved by planting more shade-tolerant tree and shrubs species before there is sufficient light for black cherry to regenerate; i.e. up to 10 % relative light, which are conditions where most shade-tolerant tree species can grow and such conditions can prevent the natural regeneration of black cherry by shading it out (Retter 2004). European beech, hornbeam, lime (*Tilia* spp.), maple (*Acer* spp.), Norway spruce (*Picea abies* (L.) H. Karst.), firs (*Abies* spp.), hazel (*Corylus avellana* L.), rowan, alder buckthorn and holly (*Ilex aquifolium* L.) can be considered amongst the species suitable for this purpose.

Figure 109. a) Forest development on sandy soils under black cherry canopy, in the presence of shade tolerant tree species such as European beech, sycamore, sweet chestnut, lime, hazel, holly and yew at Norg (The Netherlands). b) natural establishment of sycamore under black cherry at Kessel (Belgium) (photos: B. Nyssen).

A canopy entirely comprised of black cherry does not hinder the regeneration of most native tree species. In the thicket phase, black cherry casts a lot of shade on the forest floor and prevents shade-intolerant species such as Scots pine and pedunculate oak from establishing. Very shade-tolerant species such as European beech, small-leaved lime and yew can establish below a dense canopy of black cherry that is formed at the early pole stage of black cherry (Hamm et al. 2015a). In the later pole stages, the canopy formed by black cherry becomes sparser enabling the establishment of other species such as sycamore, hazel and sweet chestnut (Niinemets and Valladares 2006). When the black cherry reaches its mature phase, sessile oak (*Quercus petraea* (Matt.) Liebl.), rowan and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) can establish beneath its canopy. However, it is important to note that if shade tolerant tree species are absent, black cherry replaces itself and dominates the species composition.

The litter of black cherry is easily degradable and enhances the establishment of natural regeneration of late successional species such as small-leaved lime (Hamm et al. 2015b). The litter layer under mature black cherry trees is relatively thin and the survival of seedlings is therefore easier than in the thick litter layers commonly found in, for example, Scots pine forests (where black cherry is absent). This is specifically the case for the late-successional species that profit from the increased nutrient availability of the litter layer and the topsoil under mature black cherry trees (Hamm et al. 2015b). On poor sandy soils, the black cherry leaf litter degrades relatively quickly and increases nutrient availability (Vanderhoeven et al. 2005). This litter enriches the sandy soils that are commonly dominated by species with litter that does not degrade as quickly, such as Scots pine and oaks (Lorenz et al. 2004). Scots pine stands where black cherry is present can develop a mull or moder humus form instead of the typical mor of pine forests (Bilke 1995). The topsoil under mature black cherry can have significantly higher nutrient concentrations and it can be less acidic than under a Scots pine or oak canopy (Crétin 2013). Black cherry's uptake of nitrogen from the soil is relatively high resulting in a distinct prevention of nitrate leaching into groundwater (Lorenz et al. 2004).

Black cherry can be controlled and integrated into forests on sandy soils by reintroducing native tree species that can compete with black cherry in the understorey.

Where black cherry is dominant, shade-tolerant species can be favoured or introduced. A next step in integrating black cherry is to actually use black cherry, since it has much to offer. It can contribute to biodiversity and soil improvement and its wood is classified as a valuable timber. In the Netherlands, Belgium and neighbouring countries, forest managers have started looking into these new possibilities to cope with black cherry which, depending on the management goals, may either be a great nuisance, or a species with interesting potential.

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5.7 The spread of tree of heaven in Switzerland

Jan Wunder, Simon Knüsel, Daniela Gurtner and Marco Conedera

Introduction history around the globe

The genus *Ailanthus* is native to a large part of Asia reaching from the tropics to the temperate zone. Fossil records from the Tertiary show that it used to be present in North America, Europe and western Asia (Kowarik and Säumel 2007). The genus has regained, and even expanded, its long-lost range as humans have introduced the tree of heaven (*Ailanthus altissima* (Mill.) Swingle) to many temperate, Mediterranean and subtropical ecosystems around the globe. Tree of heaven is a deciduous tree originating from north-eastern and central China, a region characterised by a long history of human settlements and very high population densities. Within its large native range, tree of heaven appears to be a relatively rare tree species with few adult stands found in nature reserves, e.g. in Shangdong province (Kowarik and Säumel 2013, Figure 110). In the 1740s, the species was first introduced to Europe (Hu 1979). Several decades later, plantings followed in North and South America, South Africa, Australia and New Zealand. Tree of heaven was planted as an ornamental tree in many cities where it was highly valued for its tolerance to air pollution and its contribution to air quality improvements during the industrialisation period, surviving even the London smog (Webster 1910 in Kowarik and Säumel 2013).

Figure 110. The tree of heaven with cultivated Chinese chestnut (*Castanea mollissima* Blume) and *Pinus densiflora* (background) in Wangshimen Tianshangrenjia Scenic Areas, Shangdong province, China (photo: J. Wunder).

In Europe, a second plantation wave followed around 1850 for the purpose of the silk industry; the tree provided a food source for the introduced Ailanthus silk moth (*Samia cynthia* Drury), which was thought to substitute the domesticated silk moth (*Bombyx mori*

L.) that was attacked by the Pébrine disease (Arnaboldi et al. 2003). In addition, tree of heaven was planted for erosion and wind protection; the bee-keepers also value the tree's honey for its special taste (Kowarik and Säumel 2007). In its native region, the tree has played an important role in the traditional Chinese medicine over centuries, e.g. for the treatment of asthma, epilepsy and eye diseases (Hu 1979). Clinical research is currently testing the usage of several chemical compounds of tree of heaven against malaria, cancer and HIV (Sladonja et al. 2015). In China, the wood of the tree is mainly used for kitchen utensils and as fuel wood (Hu 1979, Figure 111).

Tree of heaven is a deciduous tree originating from north-eastern and central China, a region with a long history of human settlements and very high population densities.

Figure 111. A plantation of the tree of heaven near Jiejiabucun, ca. 10 km south-east of Wangshimen Tianshangrenjia Scenic Areas, Shangdong province, China (photo: J. Wunder).

Introduction history in Switzerland

About 150 years ago, the tree of heaven was introduced to the warmer regions of southern Switzerland and to several larger cities and milder urban areas north of the Swiss Alps, e.g. Basel, Zurich and Geneva. In southern Switzerland, the first introduction driver was the silk production in the late 1860s, which was followed by plantations in quarries to provide shade, especially in central Ticino in the 1900s. Around 1920, the first spontaneous occurrences of the tree of heaven in the wild were reported between Bissone and Maroggia, near Caslano in southern Ticino (Voigt 1920).

> *About 150 years ago, the tree of heaven was introduced to the warmer regions of southern Switzerland as well as to several larger cities and milder urban areas north of the Swiss Alps, e.g. Basel, Zurich and Geneva.*

Figure 112. Juvenile tree of heaven above Lago Maggiore, Ronco sopra Ascona, Ticino, Switzerland (photo: J. Wunder).

From the 1950s onwards, the tree increasingly spread into fallow land and several sweet chestnut (*Castanea sativa* Mill.) forests. Sweet chestnut is a non-native archaeophyte that was successfully planted and intensively managed over centuries in large areas of southern Switzerland (up to an altitude of about 1000 m a.s.l.) forming the so-called chestnut belt. Around 60 years ago, many of the formerly cultivated sweet chestnut groves and coppice forests were gradually abandoned due to general land-use changes and the contemporaneous outbreak of the chestnut blight (*Cryphonectria parasitica* (Murr.) Barr) – a pathogenic fungi originating from China that was accidentally introduced to Europe in the late 1930s (Conedera et al. 2001). The subsequent successful naturalisation of the tree of heaven from the urban areas to the surrounding fallows and abandoned orchards at lower elevations continued relatively slowly, and largely unnoticed, until the advent of the 21st century. In the meantime, the tree of heaven has become widespread at low elevations in southern Switzerland with populations occurring on sites with difficult access; e.g. steep rocky slopes. The nationwide eradication of this species is currently considered unrealistic, especially given the moderate financial resources available and the strict ban on herbicide applications in Swiss forests (BAFU 2016, Figure 112). Hence, the current attempts to eradicate the tree of heaven in the forests include mechanical control methods (e.g. pulling up of seedlings or girdling of older trees) whereas in urban areas, a combination of mechanical and chemical control is often applied (e.g. cut stump treatment) either during regular maintenance of infrastructure or during one-time targeted tree elimination schemes (e.g. in the community of Sierre, Canton of Valais, ca. CHF 90 000 during 2015 and 2016).

Various data sources across Switzerland clearly show that the tree of heaven is currently spreading into many forests outside its main colonisation area, i.e. the sweet chestnut belt in southern Switzerland (Figure 113). Juvenile individuals of the tree of heaven can currently be found on sites at higher altitudes in Ticino (above ca. 1200 m a.s.l.), especially in disturbed forest stands (e.g. burnt areas; Maringer et al. 2012). Although less pronounced, a naturalisation process can now be observed in many places north of the Alps. First sub-spontaneous individuals can be found in fallows and forested areas probably originating from female seed trees in urban areas. To date, there are at least 90 records of the tree of heaven in forests with a milder climate north of the Swiss Alps (Gurtner et al. 2015).

> *Young trees of heaven can currently be found on sites at higher altitudes in Ticino (above ca. 1200 m a.s.l.) as well as in forests with a milder climate in certain parts of northern Switzerland.*

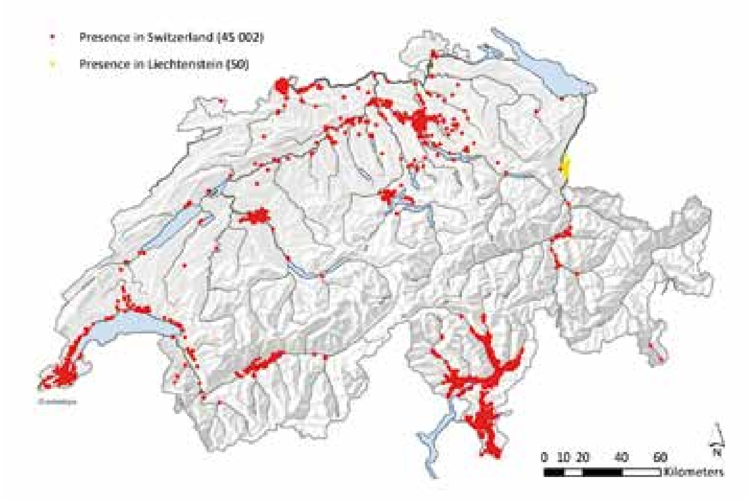

Figure 113. Current distribution of the tree of heaven in Switzerland and the Principality of Liechtenstein (Gurtner 2015). The numbers in brackets represent the estimated number of trees per country (Reproduced by permission of Swisstopo - JA 100118).

The sites colonised by tree of heaven are characterised by mean annual temperatures between 6 and 12°C and by a total annual precipitation within the range of 600 and 2150 mm. The mean annual temperature and non-climatic factors such as the proximity to roads and railroads seem to be the main drivers of the current spread of the tree of heaven (Figure 114; Gurtner 2015, Kowarik and Säumel 2007). Consequently, the tree will benefit from a warmer climate, which will strongly increase both its suitable area (which will almost double) and also the probability of its presence across the entire range (Gurtner 2015). This is in line with the findings based on a plantation experiment where trees of heaven were planted along a climatic gradient in eastern Austria (Pötzelsberger and Hasenauer 2015).

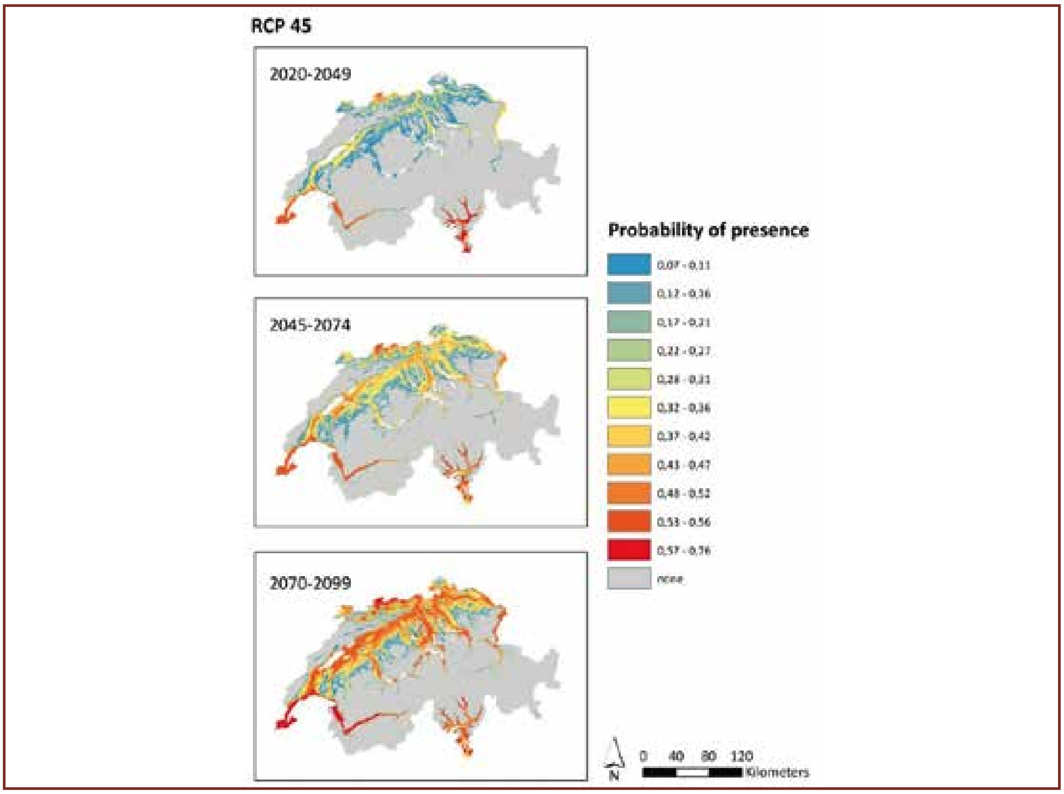

Figure 114. Model outputs for future scenarios of the distribution of the tree of heaven in Switzerland (Gurtner 2015). The colours reflect the probability of its presence. For every time period, the IPCC scenario RCP45 for changes in the annual average temperature (IPCC 2013) was down-scaled to Switzerland. RCP stands for relative concentration pathway and it is a greenhouse gas concentration trajectory used in the IPCC's fifth assessment report (AR5, IPCC 2013). The number corresponds to the increase in radiative forcing compared to pre-industrial values. The RCP45 is a mild scenario that assumes the increase in radiative forcing to be 4.5 W per m^2 (by the year 2100).

Selected ecological characteristics of tree of heaven

> ▶ *Recent observations in southern Switzerland suggest that the shade tolerance of saplings of tree of heaven is higher than previously thought, thus highlighting the potential of the tree to colonise undisturbed forests.*

The key ecological characteristics of the tree of heaven with respect to recent findings in Switzerland are summarised below.

Regeneration: The tree of heaven is an early successional tree species. It is a dioecious tree that regenerates both generatively (via seeds) and vegetatively (by root or stem sprouts and by adventitious shoots and roots from shoot fragments; Kowarik and Säumel 2007). Recent observations in southern Switzerland suggest that the shade tolerance of young saplings of tree of heaven is higher than previously thought, thus highlighting the potential of this tree species to colonise undisturbed forests where only little light reaches the ground level (de Boni 2013, Knüsel et al. 2016, Figure 115).

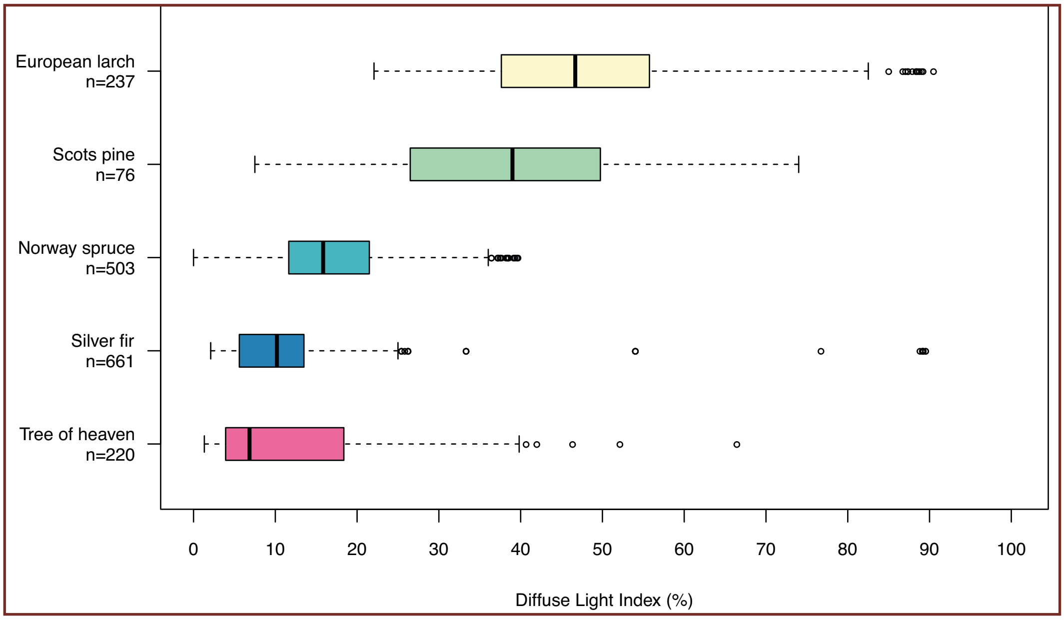

Figure 115. Diffuse light index (DLI: average transmission of diffuse (indirect) radiation over a growing season) of natural regeneration of tree of heaven with heights ranging from 40 to 450 cm (Knüsel et al. 2016). Regeneration of tree of heaven is compared to the natural regeneration of four native tree species growing in near-natural forests in Switzerland: European larch (*Larix decidua*, Krebs 2001), Scots pine (*Pinus sylvestris*, Perren et al. 1992), Norway spruce (*Picea abies*, Frehner 2000) and silver fir (*Abies alba*, Cadotsch 2011).

Kowarik and Säumel (2007) report a maximum flight distance for seeds of ca. 450 m. Observations in Switzerland show that most seeds of the tree of heaven are being dispersed within a radius of 500 m from the mother tree (Gurtner 2015). However, in few cases distances of ca. 2 km between the juvenile individuals and the closest seed-bearing tree have been reported, e.g. in Leysin VD, the Principality of Liechtenstein, and in Ticino (Maringer et al. 2012, Wunder et al. 2014). An explanation for these long dissemination distances may be a combination of strong foehn storms and a secondary dispersal along forest roads by cars or via rivers and urban streams (e.g. Planchuelo et al. 2016).

Growth: In the forest gaps in Ticino, the height increment of young individuals of tree of heaven can reach up to 2 m per year (Spiess 2014), which exceeds the growth of any native competitor. In contrast, adult individuals of tree of heaven reaching the upper canopy in forest stands show a slower growth in diameter as compared to the sweet chestnut (Figure 116; Knüsel et al. 2015).

Interestingly, the existence of mixed stands of tree of heaven and sweet chestnut of similar ages contradict the often assumed direct allelopathic suppression of potential competitors of tree of heaven (e.g. Csiszár 2009). In addition, it should be kept in mind that tree of heaven is benefiting from an indirect selective effect due to the poor palatability of its foliage that is largely avoided by browsing animals. However, exceptions were also found – such as browsing by red deer (*Cervus elaphus* L.) (Mátrai et al. 2004) and white-tailed deer *Odocoileus virginianus* Zimmermann (Carter and Fredericksen 2007).

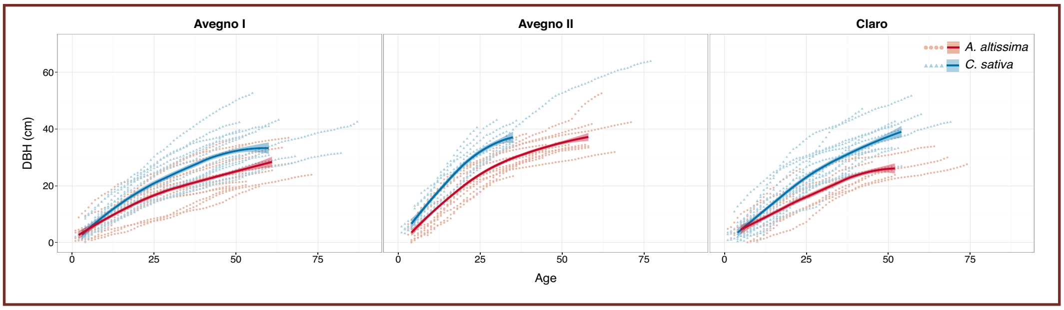

Figure 116: Diameter growth curves calculated from tree-ring width data. Points or triangles represent the values of diameter at breast height for individual trees. Bold lines represent loess-functions fitted to the diameter data (shaded areas are the 95 % confidence intervals of the loess-functions). Loess-functions are only plotted if data for at least five trees are available. (Figure amended from Knüsel et al. 2015, with permission from Elsevier).

Stress tolerance: Knüsel et al. (2015) used tree-ring methods to demonstrate that the tree of heaven has a higher drought tolerance as compared to sweet chestnut. The resulting relative competitive advantage of the tree of heaven is most striking during exceptional droughts such as the heat wave in 2003 that also contributed to a large-scale chestnut dieback.

The oldest stands of the tree of heaven in Switzerland have reached an age between 70 and 80 years showing no signs of stand scale dieback.

Tree vitality and mortality: The oldest stands of the tree of heaven in Switzerland have reached an age between 70 and 80 years showing no signs of stand scale dieback. While most trees appear to be very vital, trees with heart rot were detected in some stands (e.g. Plozza and Schmid 2012). Interestingly, internal stem rot has not yet been reported in old tree of heaven individuals planted along streets that are typically affected by additional stressors such as a reduced root space and potential damages due to traffic and road works. For example, older individuals of ca. 80 years of age without any evidence of heart rot can be found in the city of Zurich.

Management approach and research needs

Given the present expansive behaviour of the species combined with a lack of knowledge on its long-term effects on various forest services and functioning, forest managers tend to consider the tree of heaven as an unsuitable invasive species. This clearly implies that the spread of the tree of heaven has negative impacts on Swiss forest ecosystems, particularly on their biodiversity and forest stability. Regarding the biodiversity loss, there are several studies describing negative effects of tree of heaven on floral diversity (e.g. Motard et al. 2011), soil properties (e.g. Castro-Díez et al. 2011) or the multi-functionality of riparian ecosystems (e.g. Constán-Nava et al. 2015). However, it is still not clear if tree of heaven directly alters ecosystem functioning or if its colonisation is the consequence of land-use or global change. As a general rule, the patches of pure tree of heaven populations usually originate from the first colonisation of disturbed sites and are therefore very small. Where propagule pressure is present, however, the species also colonises forest patches subjected to active silvicultural treatment such as thinning or regeneration cuts. Most of the adult stands of tree of heaven in southern Switzerland are mixed with other tree species such as sweet chestnut, small-leaved lime (*Tilia cordata* Mill.), common ash (*Fraxinus excelsior* L.), black locust (*Robinia pseudoacacia* L.), yew (*Taxus baccata* L.) and holly (*Ilex aquifolium* L.). Yet, the natural regeneration in such forest stands consists mainly of the tree of heaven due to the generally high and selective browsing pressure in Ticino that tend to avoid this non-native species. Furthermore, the entire chestnut belt by ungulates is still dominated by a single (once managed and non-native) tree species, sweet chestnut, making these monocultures very vulnerable to pathogens and drought stress.

▶ *It is still unclear whether the tree of heaven alters important components of ecosystem functioning such as forest stability. More research is required to decide, which regions will be suitable for integrating tree of heaven into the local forest ecosystems, and where control or eradication measures may be the best practice.*

With regards to the reduced forest stability, many individuals of the tree of heaven with severe heart rot were found several sites in southern Switzerland, e.g. near San Vittore, Canton Ticino (Plozza and Schmid 2012) while on almost none or only small heart rots were detected on other sites, e.g. near Claro, Canton Ticino (Knüsel et al. 2015). However, it is not yet clear how the frequency, intensity and dynamics of heart rot differs at a stand scale and across the tree of heaven stands and its native competitors.

Our current research activities aim to clarify the risks (and opportunities) caused by this novel 'player' within Swiss forests by assessing its distribution, ecology, and dispersal patterns. Irrespective of the outcome of such assessments, both control and integration measures have to be prepared and tested in order to have them in place when needed. More research is required to decide, which regions will be suitable for integrating the tree of heaven into local forest ecosystems, and where the control or eradication measures may be considered the best practice.

The first research route is represented by the assessment of the current and future ecological niche of the species. Due to its temperature sensitivity, tree of heaven will very likely benefit from a warmer climate. Therefore, further analyses of the colonisation boundary and the stress tolerance of tree of heaven are needed. In addition, information on tree characteristics such as maximum age and size in its native region in China may help to improve succession modelling of the tree of heaven and scenarios on its future development in the Swiss forests.

The second research focus concerns the forest stability and the heart rot decay rates. Ongoing work in collaboration with HAFL Zollikofen, IRSTEA Grenoble and the University of Bern using controlled rock fall impact experiments, disturbance history assessments and in-situ sonic and resistance tomography for heart rot detection should help to clarify this important question. This research is currently being carried out by the framework of the project ALIEN (www.wsl.ch/alienproject).

Novel girdling methods are currently being evaluated showing some promising preliminary results. Apart from control measures, the potential use of the tree of heaven for fuel wood, furniture and medical purposes should also be considered.

Figure 117. Girdled trees of heaven in Ticino, ca. 1.5 years after the initial treatment (photo: J. Wunder). Novel girdling method where three complete rings around the entire stem are cut with a depth of ca. 2 cm using a chainsaw; i.e. cutting the bark, cambium and only a small part of the xylem (photo: S. Knüsel).

The management-oriented part of our research currently focuses on possible mechanical (i.e. stem girdling; e.g. Liess 2007) and chemical control options (i.e. stem injection and cut stump treatment, e.g. Constán-Nava et al. 2010). For the mechanical control of adult trees, we currently evaluate a novel girdling method proposed by Martin Ziegler (Canton Zug) on adult individuals of tree of heaven of different sizes (ca. 20–40 cm in diameter) in two forest stands in Ticino. After bud break in late spring, three complete rings around the entire stem base were incised with a chainsaw up to a depth of ca. 2 cm so that only the bark, the cambium and a small part of the xylem are cut (Figure 117, inlet). Preliminary results of this ongoing experiment show that after two growing seasons most of the treated trees are dying back without any significant re-sprouting from the tree base (Figure 117). Chemical control through stem injections and cut treatment is currently investigated in collaboration with the Amt für Umwelt Vaduz in the Principality of Liechtenstein due to the strict ban on herbicide applications in Swiss forests. Biological control using pest agents such as *Verticillium nonalfalfae* (e.g. Mascheck and Halmschlager 2015) may be an additional option if the eradication of tree of heaven in the entire country, and potentially beyond, is the ultimate goal.

Apart from the control measures, the potential use of the tree of heaven should also be considered. For example, this tree species may be useful as a biomass producer due to its high growth rate along with a remarkable heat of combustion of 4.5 kwh/kg exceeding both European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) H. Karst.) (Schumacher et al. 2010). Moreover, the use of the species for medical purposes and the utilisation of its timber for high-value products such as furniture should also be further investigated (Brandner and Schickhofer 2010).

The current spread of the tree of heaven should be closely monitored, particularly in the newly colonised sites in the northern part of Switzerland where a targeted elimination is still timely and possible.

Does the tree of heaven negatively impact native ecosystems? Or, is the ongoing colonisation negligible, and can its effects be regarded as neutral – or perhaps even positive? The risk assessment is still ongoing and does not yet allow these questions to be answered with certainty. Also, answers are likely to differ amongst regions and forest stands colonised by the tree of heaven. Given these uncertainties, caution should be applied i.e. the current spread of the tree of heaven should be closely monitored, particularly in the newly colonised sites in the northern part of Switzerland where a targeted elimination is still timely and possible. In addition, it is necessary to develop and test measures aiming at controlling the species in case it might be required and to look into various options for integrating the tree of heaven into native forests where this is suited.

Figure 118. The tree of heaven in a rock fall protection forest in the Maggia valley, Canton Ticino, Switzerland (photo: S. Knüsel).

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5.8 Eastern white pine in the Czech Republic

Pavel Bednář, Petr Vaněk and Lucie Vítková

Pines (*Pinus* spp.) are an important component of the Northern Hemisphere's forest cover where they occupy a wide range of habitats and are an important source of timber (Hadincová et al. 2007). Introduction of non-native tree species of pines to central Europe has a long history with the first introductions having taken place over 200 years ago. Although the seeds of eastern white pine (*Pinus strobus* L.), a coniferous tree species native to eastern part of North America (Figure 119) were first brought to Europe in 1605, it was first established in Europe in 1705 on the Weymouth Estate in the southern part of England (Musil and Hamerík 2007).

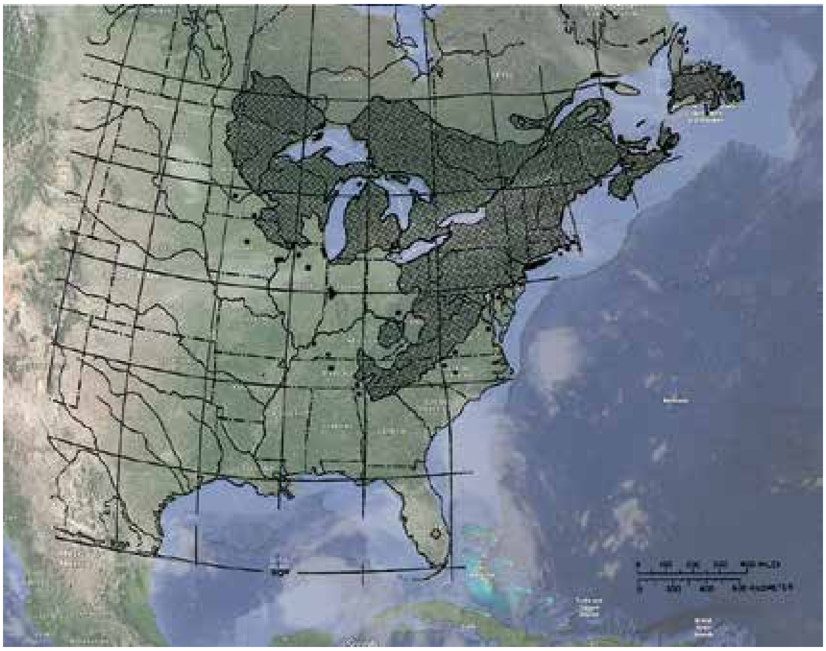

Figure 119. Native range of eastern white pine in the eastern part of North America (altered from Wendel and Smith 1990).

> *The potential of eastern white pine was recognised shortly after its introduction from North America two centuries ago.*

As for its introduction to the Czech Republic (formerly part of Austro-Hungarian Empire at the time of introduction), eastern white pine was first planted in central Bohemia around Hluboš in 1812 (Svoboda 1976). However, according to other sources, the first planting took place in 1785 in Lány Chateau (Mlíkovský and Stýblo 2006). With time, eastern white pine was introduced to several estates throughout the Czech territories (Nožička 1965). At the end of 19th century, the native Scots pine (*Pinus sylvestris* L.) was heavily affected by needle blight and the local foresters looked for a pine species that could replace the native Scots pine. In species trials, eastern white pine appeared to be the most suitable replacement amongst pine species planted; e.g. jack pine (*P. banksiana* Lamb.), Macedonian pine (*P. peuce* Griseb.) and pitch pine (*P. rigida* Mill.). As a result of these experimental plantings, the eastern white pine began to be planted more widely.

The main reason for eastern white pine introduction was as an ornamental species; however, its growth rates, that can exceed in specific conditions many tree species native to Czech forests, played an important role in its use for forestry purposes. Another characteristic that was considered when planting eastern white pine was that it does not tend to suffer frost damage and tolerates high summer temperatures (Soukup et al. 2000). Due to a thick waxy layer of its needles, eastern white pine appears to be resistant to emissions, especially to SO_2 (e.g. Wild et al. 2013). This trait brought attention to eastern white pine during the period of high emission in 1970s and especially in 1980s due to its potential to replace dying Norway spruce (*Picea abies* (L.) H. Karst.) in the north-western part of the country (e.g. Kaňák 2004).

The timber of eastern white pine does not reach the quality of many native species in terms of wood density and strength properties. However, to a lesser extent, it is used as construction timber for wooden houses and for furniture (Zeidler et al. 2010). The main use of its timber is for specialised products such as pencils, matches, beehives, etc.

Excessive natural regeneration of eastern white pine causes shifts in species composition within the ground vegetation layer and changes to the dynamics of native habitats.

Eastern white pine deposits a thick layer of needle litter (Härtel and Hadincová 1998) that is acidic and nutrient poor causing soil acidification (Podrázký and Remeš 2008). This triggers substantial changes to the herbal layer consequently affecting native biodiversity and modifies plant communities. Such changes may be seen in the National Park České Švýcarsko in northern Bohemia where blueberry (*Vaccinium myrtillus* L.), lingonberry (*Vaccinium vitis-idaea* L.), heather (*Calluna vulgaris* (L.) Hull) and wild rosemary (*Ledum palustre* L.) are supressed due to the shade casted by naturally regenerating eastern white pine (Wild et al. 2013). Disruptions as such are undesirable as they have negative impacts on the natural succession and dynamic development of the native habitat.

The habitat types most affected by invasion by eastern white pine are situated in the Elbe River Sandstone Mountains; they are the natural forest stands dominated by Scots pine and European beech (*Fagus sylvatica* L.) on acidic soils (*Genisto gemanicae-Quercion*) as well as the natural dry acidic Scots pine forests (*Dicrano-Pinion*) (Wild et al. 2013). Although the greatest proportion of naturally regenerated eastern white pine (the proportion of natural regeneration covering the ground estimated based on vegetation survey) was found in Scots pine forests on drier nutrient-poor soils (21 %), it did not exceed 9 % in other forest stand types with the exception of an acidic site with European beech and silver fir (12 %) (Wild et al. 2013). The proportion of natural regeneration of eastern white pine was, however, lower on wet or water-logged sites (5 %). It was even lower (0.8 %) on acidic sites with a greater proportion of European beech and on sites on a slope where European beech dominated (0.4 %) (Wild et al. 2013).

Although eastern white pine has not been officially listed as invasive in the Czech Republic, it has behaved invasively in certain areas under specific conditions.

In a study from České Švýcarsko National Park, eastern white pine was reported to have naturally regenerated in native Scots pine woods (*Vaccinio uliginosi-Pinetum*) where it behaved invasively as it suppressed native species (Hadincová et al. 1997). Its natural regeneration was also found to compete with native Norway spruce in cooler and wetter parts of the National Park (Kaňák 2004). Although efforts to eradicate this non-native species were made in the protected areas of the National Park, the presence of eastern white pine in České Švýcarsko National Park is still of concern. The methods used in the protected areas included the removal of mature trees and the total eradication (mechanical means) of eastern white pine natural regeneration with consequent reforestation by native species, especially Scots pine.

Although eastern white pine was first reported as invasive in the sandstone area of the Elbe River Sandstone Mountains at the beginning of the 1950s (Härtel and Hadincová 1998), its invasive character and spreading natural regeneration gained greater attention and started to be more intensively focused on only at the end of the 1990s. Eastern white pine was found suppressing native vegetation by forming dense stands that out-competed the native Scots pine in the Elbe River Sandstone Mountains (Mácová 2008). As a consequence, the relict Scots pine forests in these areas have become endangered (Mácová 2008). Nonetheless, the density of eastern white pine started consequently decreasing in the 1990s due to a decline in its vitality (Kaňák 2004). The decline was caused by various agents including the occurrence of the white pine blister rust (*Cronartium ribicola* (J.C.Fisch.)).

Eastern white pine was found to be invasive in sandstone regions while regenerating only sparsely in areas on different soil type or bedrock (Mácová 2008). This explains the intensive spread in areas where the conditions for its growth are suitable, i.e. Elbe River Sandstone Mountains, which includes the České Švýcarsko National Park and a small area east of Hradec Králové. Apart from behaving invasively in the above mentioned areas, eastern white pine is not reported as invasive in other parts of the country. The native range of eastern white pine in eastern North American is rather extensive as it reaches from the boreal forests of Newfoundland to northern Georgia and northern South Carolina. This large ecological range explains why eastern white pine has the ability to easily naturally regenerate and behave invasively in some habitats. Eastern white pine is able to naturally regenerate and grow in hostile conditions such as rocky outcrops where other native species do not survive with the exception of Scots pine and birches (*Betula* spp.) (Wild et al. 2013).

Although several diseases are found on eastern white pine, within its introduced range, only white pine blister rust causes serious damage.

There are several diseases affecting eastern white pine including Phaeolus *schweinitzii* (Fr.) Pat., *Heterobasidion annosum* (Fr.) Bref. and *Armillaria ostoyae* (Peck). A disease causing noticeable damage to eastern white pine within Czech forests is *Meloderma desmazieri* (Duby) Darker. Although eastern white pines do not necessarily die when infected by *M. desmazieri*, tree death can occur due to a severe needle loss when affected several years in a row. This disease has been sparsely recorded in the area of Elbe River Sandstone Mountains where it affects pure, dense, shaded and weak young trees (up to 5 cm diameter at breast height) that have not been subjected to any forest management (Beznoska 2000).

However, the only disease that causes serious damage to eastern white pine within the Czech forest ecosystem is white pine blister rust (*Cronartium ribicola* J.C.Fisch.). This rust requires two host species to complete its life cycle: in North America and Europe, the hosts are usually pines and currants (*Ribes* spp.); in order to prevent the damages by rusts, elimination of currents was recommended in past. This rust forms blisters on the lower branches of eastern white pine; unless the affected branches are removed by pruning, the rust moves onto the stem encircling it with blisters. Consequently, the needles turn brown and the tree death is inevitable. Nonetheless, it is important to bear in mind that diseases of eastern white pine have not been consistently monitored in the Czech Republic.

Within its native range (Figure 119), eastern white pine is considered a valuable tree species in terms of timber production, because of its rapid growth and its timber qualities (Joyce and Rehfeldt 2013). Although the timber production potential of eastern white pine has been reported from its introduced range (e.g. Beran and Šindelář 1996), it is not considered as commercially important tree species in the Czech Republic. This is mainly due to eastern white pine accounting for only a minor proportion of the local forest cover. However, the ability of eastern white pine to naturally regenerate under forest canopy on nutrient poor sites, where native tree species would fail to do so, often leads to retaining eastern white pine natural regeneration in commercial forests on such sites to avoid additional planting costs.

Studies from the Municipal Forest Hradec Králové found that the production of eastern white pine was greater than that of native Scots pine (Vaněk and Bednář 2013; Box 26). As for the volume production performance elsewhere in Europe, the increment of eastern white pine was reported to exceed that of native Scots pine in e.g. Germany (Waldherr 2000), Switzerland (Svoboda 1953), Estonia (Kasesalu 2000), Bulgaria (e.g. Ratknic et al. 2002), and Croatia (e.g. Perić et al. 2004).

Although the cost of eradication of invasive species in general is not particularly high in the Czech Republic, in comparison to other countries such as South Africa (e.g. van Wilgen and Richardson 2012), it is certainly not negligible. In addition, eradication measures require considerable efforts. Over €245 000 were invested between 1977 and 2002 from the Programme for Landscape Maintenance (support of unprotected areas) to eradicate natural regeneration of invasive species, which also included eastern white pine. In České Švýcarsko National Park, where eastern white pine has been considered invasive, more than €170 000 were spent between 2000 and 2003 on eradicating its natural regeneration (Hentschel and Hentschelová 2003). It is also important to note that where eastern white pine is eradicated, a cost of reforesting such places with native species may become rather expensive (Beznoska 2000).

Box 26. Comparison of eastern white pine and Scots pine in terms of commercial timber production

A study that compared introduced eastern white pine and native Scots pine concluded that eastern white pine has higher volume production than Scots pine, which was particularly pronounced in nutrient-poor and acidic soils. The ability of eastern white pine to tolerate shade (as opposed to light demanding Scots pine) plays an important role in natural regeneration under a closed canopy.

Eastern white pine is commonly compared to Scots pine since the latter is a native species of substantial importance in many areas of the country. Vaněk and Bednář (2013) compared the timber production of eastern white pine and Scots pine and reported that the former had greater production of total timber volume than the latter. Eastern white pine reached a larger mean diameter and mean stem volume.

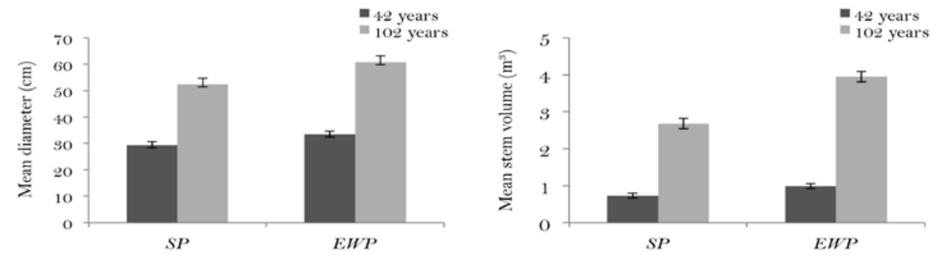

Figure 120. Mean diameter and mean stem volume for Scots pine (SP) and eastern white pine (EWP) from stands in the Municipal Forest Hradec Králové in eastern Bohemia are presented (amended from Vaněk and Bednář 2013). Data for 10 largest trees in the experimental plot are shown for two age classes (42 and 102 years).

Although both pine species are able to grow on nutrient poor sites, eastern white pine grows faster than Scots pine on such sites. Nonetheless, on the other hand, evidence shows that the natural regeneration of Scots pine outcompetes that of eastern white pine on more nutrient rich soils (Hadincová et al. 1997).

The level of natural regeneration of either pine is also influenced by the degree of canopy openness. Since eastern white pine was reported to be much more shade-tolerant than Scots pine, it has a clear advantage for regeneration in stands with closed canopy. The occurrence of natural regeneration has been dealt with differently; in the České Švýcarsko National Park, where its presence is considered to be a problem, the natural regeneration of eastern white pine has been subjected to successful eradication measures in order to further avoid the spread. In commercial forest stands, on the other hand, its natural regeneration has been retained as cost-free natural regeneration.

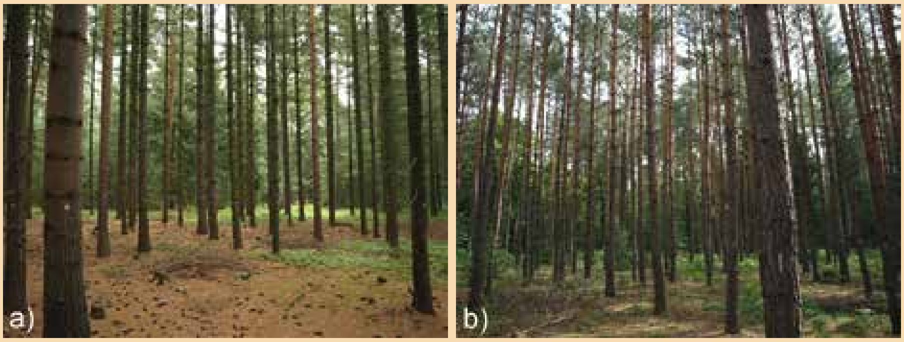

Figure 121. Eastern white pine stand (a) and Scots pine (b) in the Municipal Forest Hradec Králové (photos: P. Vaněk).

Figure 122. Eastern white pine stands in the Municipal Forest Hradec Králové (photos: P. Vaněk).

Afforestation of marginal agricultural land has been encouraged in order to reduce agricultural production in the Czech Republic. This brought attention on using eastern white pine for afforestation due to its ability to grow on nutrient-poor and dry sites where growth and regeneration of native early successional species such as rowan (*Sorbus aucuparia* L.), willows (*Salix* spp.), and birches (*Betula* spp.) is generally poor. Eastern white pine was therefore considered to be used as a part of pioneer vegetation that will later be replaced by later successional species (Kaňák 2004). Eastern white pine could also be considered as an alternative to native tree species whose natural range has been shifting due to climate change. Some studies from its native range in North America reported that the importance of eastern white pine will substantially increase due to enlargement of its ecological optima under climate change (e.g. Jacobson and Dieffenbacker-Krall 1995, Iverson and Prasad 1998). However, this has not been greatly explored since eastern white pine only accounts for a minor proportion of the forest cover in the Czech Republic.

▶ *The contribution of introduced tree species to Czech forestry is relatively minor and the perceptions of such species vary; although it should be absent from protected areas, it could form a minor component of commercial forests.*

Although eastern white pine is an unwanted addition in National Parks, some foresters consider it as an enrichment to tree species composition, an aesthetic enhancement to local forests and a contribution to an increase in production potential (Vaca 1999). There are, therefore, polarised opinions about the species amongst those involved in management of forest ecosystems. Eastern white pine has been considered as naturalised in the Czech Republic (Beznoska 2000); however, introduced tree species, in general, do not play a key role in Czech forestry as they cover only relatively small areas; e.g. black locust (*Robinia pseudoaccacia*) 0.6 %, introduced spruces (*Picea* spp.) 0.4 %, red oak (*Quercus rubra*) 0.2 % or Douglas fir (*Pseudotsuga menziesii*) 0.2 % (Czech National Forest Inventory 2001–2004; ÚHUL 2007). The perceptions would likely differ if introduced tree species accounted for a majority of the forest cover such as in e.g. Ireland where they form three quarters of the forest cover (NFI 2013), and thus dominate the local forestry sector.

The public opinion regarding the origin of tree species occurring in the forests tends to be indifferent until proper education regarding the underlying issues is provided. Members of public have been involved in various eradication and reforestation procedures in České Švýcarsko National Park (České Švýcarsko National Park 2016). The aims of these efforts have been two-fold: (i) to educated public about the value of protected areas; and (ii) to apply eradication measures in order to protect vulnerable parts of valuable habitats. Such environmental education is essential as it allows the public to recognise the importance of native habitat and the efforts necessary to maintain it.

▶ *Additional research on eastern white pine in the Czech Republic is necessary in order to further evaluate its invasive potential.*

With the exception of Elbe River Sandstone Mountains, and in particular the protected core area of České Švýcarsko National Park, where eastern white pine behaves invasively due to suitable conditions facilitating for its natural regeneration and its fast growth, this species has not attracted any special attention as an invasive species in the Czech Republic. This may be due to the lack of monitoring or research focusing on, for example, escapes from cultivation or on propagule pressure in areas where it is invasive. Czech foresters have recognised its timber production potential, especially on sites on water and nutrient-poor soils where many native species do not grow well. Since eastern white pine only forms a minor component of the Czech forest cover, this North American species has not been subjected to much research.

Further studies on eastern white pine are recommended with the focus on its potential to act as alternative species under climate change, on the ways it alters native habitats as well as its invasive and timber production potentials.

It is important to note that the failure to recognise invasive potential cause lead to changes in ecosystems that may be difficult to reverse. Especially, since the response of biodiversity to environmental changes is not usually rapid enough and since the rates of contemporary diversity changes tend to be underestimated (Essl et al. 2015). In addition, the effects of climate change also contribute towards the processes of invasion (e.g. Engel et al. 2011). Unmonitored spread of eastern white pine may thus be considered as an escalating issue especially in areas where the conditions for its spread are particularly favourable. The spread of this species should therefore be monitored.

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5.9 Using National Forest Inventories to assess the factors driving invasion in forest ecosystems: the case of silver wattle and blackwood in north-western Spain

Laura Hernández, Isabel Cañellas and Ignacio Barbeito

Introduction

Our theoretical and practical knowledge of plant invasions has improved substantially during the last decade (Richardson et al. 2010). However, our capability to address further challenges has been limited by the lack of broad scale periodic surveys. In this context, the recent inclusion of non-native species data in periodic permanent sample units in National Forest Inventories (hereafter NFI) (Corona et al. 2011) can constitute a valuable tool for monitoring the broad-scale evolution of plant invasions in forest ecosystems (Hernández et al. 2014).

Periodic National Forest Inventories can constitute a valuable tool for monitoring the broad-scale evolution of plant invasions in forest ecosystems.

The spatial extent of an invasion is generally considered to be primarily driven by abiotic factors. Abiotic barriers such as climate or soil determine whether invasive species propagules survive and affect growth rates in the colonisation stage of the invasion (Teoharides and Dukes 2007). However, the degree of the invasion, defined as the amount of introduced species that has invaded a particular region or habitat outside its original range, is largely influenced by the characteristics of the receiver habitat such as species richness, forest structure, maturity, disturbances, human influence, etc. (Chytrý et al. 2008). Despite the emphasis placed on early successional traits and adaptation to disturbance of invasive species, there is also a large number of shade-tolerant, late-successional species, which have invasive characteristics once introduced in mature non-disturbed forest ecosystems. Furthermore, mature undisturbed forests are not as resistant to invasion as thought. There is evidence of the influence of native forest richness in the patterns of invasion. Previous work has found a positive relationship between biotic drivers such as native richness and non-native invasion degree (Levine and D'Antonio 1999).

The degree of the invasion is largely influenced by the characteristics of the receiver habitat such as species richness, forest structure, maturity, disturbances or human influence.

The need to consider forest structure and species composition, by means of a classification of forest types, to more completely understand the vulnerability of forest ecosystems to invasions is examined in this chapter. Differences in tree size and distribution patterns together with species richness may explain the demographic success of the introduced plant (Barbeito et al. 2009).

Our study used NFI data to examine the biotic and abiotic factors that lead to the establishment and success of two invasive Acacia species – silver wattle (*Acacia dealbata* Link) and blackwood (*Acacia melanoxylon* R.Br.) – in Galicia region, north-western Spain. A combination of bioclimatic and human factors mean that the proportion of non-native flora in this area of Spain (14 %) is higher than for the rest of Iberian Peninsula (12 %) (Sanz Elorza et al. 2004). The findings highlight the suitability of using forest monitoring networks, such as NFIs, which collect periodic information on forests composition, demography, structure, and management to shed light on the factors that influence a forest's susceptibility to invasion. These data can also be used to identify detailed demographic rates and spatio-temporal patterns of invasive plant spread as key targets for conservation strategies.

Silver wattle and blackwood as invaders

The genus *Acacia* (wattles) belongs to the family Fabaceae. There are almost 1 400 species of *Acacia* around the world, most of them native to Australia and to a lesser extent Africa, Asia, and Central and South America. Australian *Acacia* species have become highly invasive around the world, including Europe (Lorenzo et al. 2010). Silver wattle and blackwood threaten native habitats by competing with indigenous vegetation and replacing native communities with the subsequent reduction of their biodiversity. On invasion, they establish quickly in the new environment, causing changes in the structure and dynamics of the ecosystem. This invasive capacity is driven by their ability to thrive on low fertility soils, their high capacity for regeneration after disturbances by means of vegetative or sexual reproduction (Sheppard et al. 2006), their high growth rate, long-term soil-stored seed banks, and, generalist pollination and seed-dispersal patterns (Lorenzo et al. 2010). Furthermore, several studies have demonstrated the allelopathic characteristics of *Acacia* species on other plants (Lorenzo et al. 2010). The combinations of all these factors give wattles great colonising capacity, enabling them to dominate the colonised site.

> *Acacias invasive capacity is mainly driven by their high regeneration and growth rates, long-term soil-stored seed banks, generalist pollination and seed-dispersal patterns, and, allelopathic characteristics.*

Introduction history in Europe and north-western Spain

In Europe, there are eight *Acacia* species with invasive potential (Lorenzo et al. 2010), with silver wattle and blackwood being included in this list and being the most widespread in southern Europe. In their natural geographic range in south-eastern Australian and Tasmania, silver wattle, with a broader ecological tolerance, is common in dry and wet forests, heathy woodlands, grasslands and riparian ecosystems, while blackwood is more commonly found in temperate forests. In Europe, silver wattle and blackwood occupy several areas in very diverse habitats around the Mediterranean basin such as coastal dune and sand habitats, littoral zones, woodlands, early-stage woodlands and abandoned fields.

The residence time of an introduced species influences the degree of invasion, since the longer the species is present in a new territory, the greater the probability of propagules and new incidences of spread (Gassó et al. 2012). In this sense, with more than two centuries, silver wattle and blackwood present a mid-high residence time compared with other invasive species such as the century plant (*Agave americana* L.) (more than 500 years). Wattles were introduced into Europe in the mid-19th century, mainly as ornamental species (Sheppard et al. 2006, Lorenzo et al. 2010), but also to stabilise dunes, for timber production, and also for leather tanning.

> *The residence time of an introduced species influences the degree of invasion. Wattles were introduced into Europe in the mid-19th century.*

In north-western Spain, the earliest records of these species date back to 1808 (Areses 1953) where these two species were used as ornamentals in parks and gardens. Besides, as a nitrogen-fixing tree, blackwood was used as an auxiliary species to increase the productivity in blue gum (*Eucalyptus* spp.) plantations, which are quite common in the coastal area of the study region, while the silver wattle was used for stakes in vineyards and other crops and to stabilise slopes along railway tracks (Lorenzo et al. 2010). Despite the fact that blackwood is not listed in the Spanish Catalogue of Invasive Species (Sanz Elorza et al. 2004), both taxa are considered as invasive species in Galicia.

Methods

The results presented here are based on spatially explicit information from two consecutives cycles of the Spanish NFI performed in the Galicia region, north-western Spain with a time interval of 10 years (1998–2008). In the NFI cycles analysed, permanent plots were established systematically in the forested area at the intersections of a 1 km x 1 km grid. Field plots consist of four concentric circular areas with radii of 5, 10, 15 and 25 m. Depending on the diameter at breast height (dbh) of the tree species, different characteristics are measured within each plot such as dbh or height of trees with dbh > 7.5 cm and height > 1.30 m. Furthermore, other forest attributes and conditions are measured (tree and shrub species composition, density, canopy cover, recruitment, saplings; i.e. trees with a dbh between 2.5 cm and < 7.5 cm). Biotic and abiotic predictors at plot level collected from NFI databases were considered as independent variables used to analyse the association of stand structure and disturbance regime with the establishment of silver wattle and blackwood. Regarding the biotic factors, we included plot species abundance, species dominance, species density and some other indicators defining composition diversity: tree richness, shrub richness, Berger-Parker index (Berger and Parker 1970), diameter-size diversity (dbh deviation) and vertical-size diversity (height deviation). For abiotic factors silvicultural treatments were considered. Presence and cover of shrub species proposed as forest management bio-indicators for northern Spain (Atauri et al. 2004) (gorse, *Ulex europaeus* L.; bell heather, *Erica cinerea* L.; St Dabeoc's heath, *Daboecia cantabrica* (Huds.)

K. Koch; ling, *Calluna vulgaris* (L.) Hull.) were also considered in the analysis as a proxy for historical disturbance. For these analyses we selected the NFI plots with presence of silver wattle and blackwood in the studied region (Figure 123).

Based on aforementioned stand variables and forest management indicators collected from NFI databases, the plots can be classified as pure or mixed, managed or unmanaged stands. We used the Spanish Forest Map definition of pure and mixed stands: pure plots were defined as those where 70 % or more of the plot basal area belonging to a single species. The NFI reports the silvicultural treatments that have been performed in each of the plots; differentiating regeneration methods and stand improvement treatments. We used both indicator categories (stand variables and silvicultural factors) to classify invaded forests as follows:

- Native mixed forest (M_Native): Atlantic broadleaf mixed forest;
- Transitional-stage mixed forest (M_TranStage) – mixed conifer-broadleaf forests resulting from natural colonisation by native species of originally monospecific plantations which have not been intensively managed for timber production for an extensive period;
- Mixed plantation (M_Manage) – mixed conifer-broadleaf, conifer or broadleaf currently managed;
- Pure native forest (P_Native) – pedunculated oak (*Quercus robur* L.) forests;
- Pure conifer plantation (P_ConPlant) – fast-growing maritime pine (*Pinus pinaster* L.) plantation with short rotation and high harvest intensity;
- Pure broadleaf plantation (P_BroadPlant) – fast-growing blue gum (*Eucalyptus globulus* Labill.) plantations for wood pulp or fibreboard with short rotation and high harvest intensity.

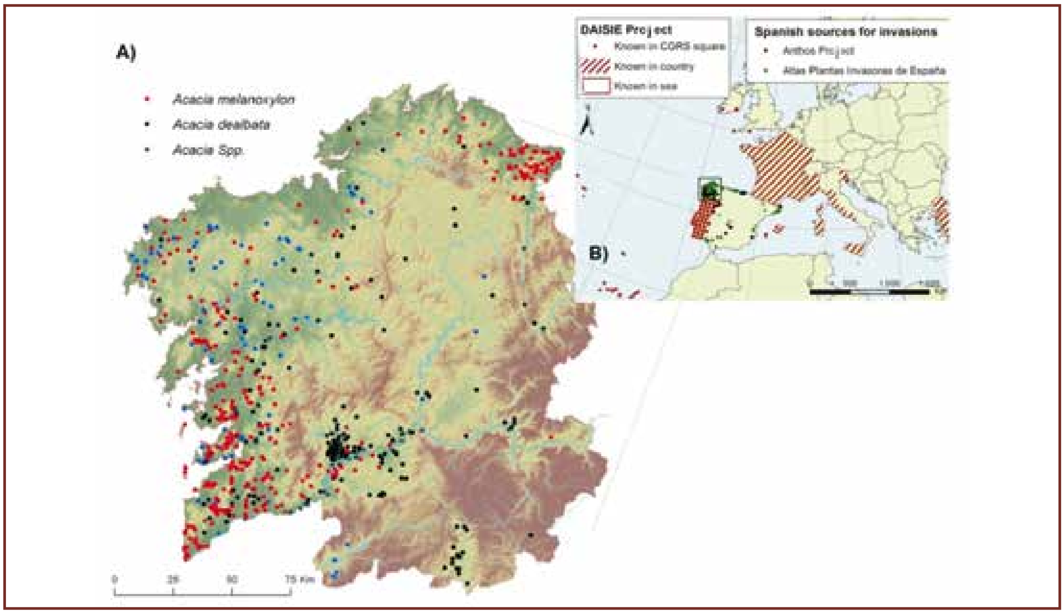

Figure 123. A) Current known distribution of silver wattle and blackwood in north-western Spain from Spanish NFI plots; and B) Europe (sources: Sanz Elorza et al. 2004, Anthos 2012, DAISIE 2009).

Evolution of wattles spread in forest ecosystems of north-western Spain

The comparison of the information derived from the plots in which *Acacia* species were present in the two sequential NFI allowed identification of their development and spread during the last decades in the forest ecosystems of northwestern Spain. The percentage of forested area occupied by blackwood and silver wattle reached 3.15 % and 2.36 % in 2008, exhibiting mid-high invasion annual rates of invasion (proportion of total area invaded per year) of 0.1 % and 0.083 % respectively. This spread was concomitant with an increase in growing stock and density, doubling in all the cases the preceding values although displaying different traits. Whereas blackwood is increasing its dominance in forests where it was present through increments in growing stock, silver wattle displays a greater increase in density. This pattern is also observed in the regeneration stratum where both species tend to dominate. The previous trends observed in combination with the reduction in plant cover richness and soil seed bank diversity reported in the region indicate an increasing homogenisation of the different habitats where the two species are present. Although this rise in dominance is general for all forest types where wattles were present, a significant increase is observed in forest ecosystems with mid-high disturbance degree (forest management, fires or land use change) such as *Eucalyptus* spp. plantations, mixed conifer-broadleaf and broadleaf forests. Furthermore, as was previously predicted (Gassó et al. 2012), the results revealed an early stage of invasion of both species in the study region, highlighting the potential of the species to continue spreading. This fact, together with the high frequency of disturbances such as fire, may be critical in determining the configuration of future forest landscapes in the region.

▶ *In north-western Spain, both silver wattle and blackwood are spreading rapidly, becoming the dominant tree species across large forest areas.*

Mixture drives wattle establishment

Our results suggest a higher recruitment success in the mixed transitional stage stands and plantations for blackwood. The natural regeneration of silver wattle shows preferences for establishment in all types of mixed stands (Figure 124). This finding supports the hypothesis of the positively correlation of species richness with invasion (Levine and D'Antonio 1999). The results of a random forest analysis indicated that diameter size deviation was the most important factor driving the establishment of the two species, followed by shrub species presence (proxy for disturbance), and species richness (results not shown). Stands with a different diameter size deviation may result from greater heterogeneity in the age of stand, species richness, the number of ecological niches, as well as forest management practices (partial cuttings) or some types of disturbances, while the diversity in the vertical structure is related to the species composition and the existence of different tree and shrub layers that can also provide the forest with a greater diversity of ecological niches.

▶ *Forest structural and compositional features play an important role in determining the establishment of wattles in the hosted forests.*

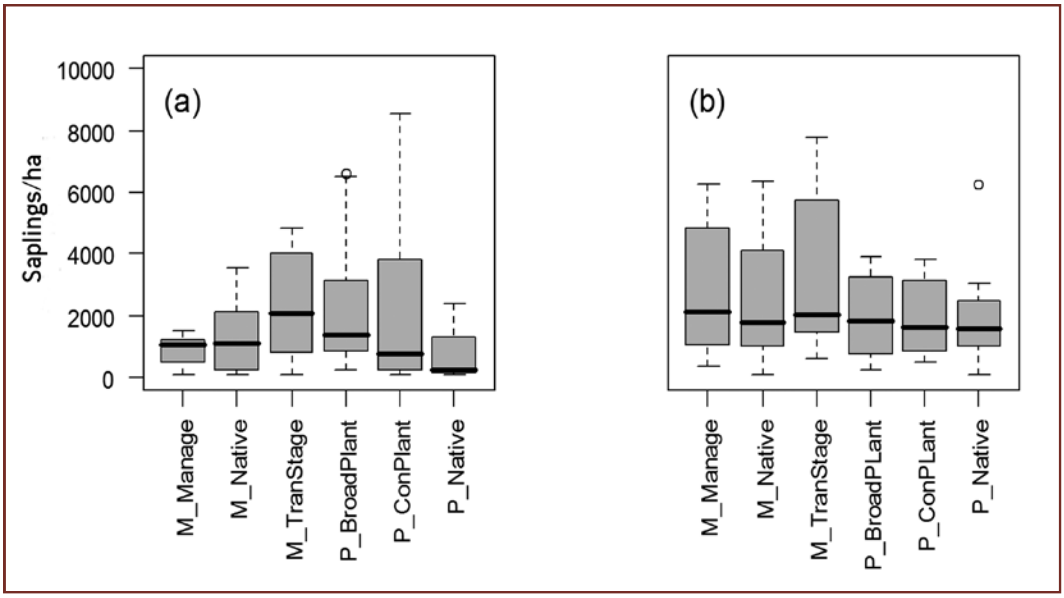

Figure 124. Density of established regeneration (saplings/ha) for (a) blackwood and (b) silver wattle in stands with different mixtures and disturbance regime in northern Spain. Forest types include: (i) Native mixed forest (M_Native); (ii) Transitional-stage mixed forest (M_TranStage (iii) Mixed plantation (M_Manage); (iv) Pure native forest (P_Native): pedunculate oak forests; (v) Pure conifer plantation (P_ConPlant); (vi) Pure broadleaf plantation (P_BroadPlant).

Potential management strategies

A thorough understanding of the factors driving the invasion and the changes in the biotic and abiotic components of the ecosystems can be used for control and restoration efforts (Le Maitre et al. 2011). Currently, there are maps of invasion risk at European level (EEA 2015) but their scale and precision severely restrict their usefulness for practical environmental management strategies. In the future, it will be possible to use the accurate results from NFIs (current distribution of the species in the georeferenced plots and connectivity distance between populations) along with other information (such as potential climatic niche) to derive accurate maps of the risk of plant invasion at different scales. This will enable more efficient planning and management of biological invasions at the regional level.

▶ *The accurate maps of the risk of plant invasion derived from NFIs information will enable more efficient planning and management of biological invasions at different scales.*

In order to control the risk of silver wattle and blackwood invasions to new areas it is also important to avoid disturbances (e.g. fires) that encourage their spread (Hernández et al. 2014). Silvicultural measures such as reducing dense canopy cover or preventing the accumulation of seed banks by limiting seed production through biological control (Richardson and Kluge 2008) have been advocated. Although information concerning management after establishment is scarce (see Souza-Alonso et al. 2013, Wilson et al. 2011), once populations of wattle are established, mechanical or chemical tools and biological treatments can be used to stop their spread. Silver wattle and blackwood seedlings are capable of rapid growth, but a high percentage of seedlings do not survive to saplings, so, in order to use resources effectively, control interventions should target vigorous seedlings (Wilson et al. 2011). This can include direct control through hand pulling, grazing, application of foliar herbicides, or ploughing. Adult plants can also be killed (e.g. through ring barking), but because they resprout, applications of a herbicide such as triclopyr (Souza-Alonso et al. 2013) or glyphosate treatment of stumps and additional follow-up treatments to kill regrowth are often necessary to make the eradication effective. Finally, biocontrol agents can be introduced to target vegetative growth or as seed-feeding. Some biological agents have been already released in South Africa with promising results (Wilson et al. 2011).

Conclusions

The expansion of silver wattle and blackwood populations in Europe is favoured by several biological characteristics which make these species successful invaders. In northwestern Spain, both silver wattle and blackwood are spreading rapidly, becoming the dominant tree species across large areas of forest in this part of Spain. Their ranges are mainly constrained by environmental factors and the connectivity between populations. Additionally, disturbance events such as fires and forest structural and compositional features (conifer/broadleaf; mixed/pure; and their structural diversity) seem to play an important role in determining the establishment of silver wattle and blackwood in different forest types. Since mixed forests are generally more structurally diverse, we argue that non-native species invasions in forests can be a function of, not only tree species diversity, but also of stand structural characteristics, which can be very variable for a given forest type. This case study highlights the suitability of using the data obtained in broad-scale periodic forest surveys, such as NFIs, to monitor plant invasion, as well as their potential to contribute in the future to the necessary practical and theoretical understanding of biological invasions in forests.

> ▶ *Non-native species invasions in forests are partly a function of stand structural characteristics which can be very variable for a given forest type.*

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5.10 Management of invasive tree species in the Donau-Auen National Park, Austria

Verena Quadt, Gerald Oitzinger and Karoline Zsak

The Danube is the second longest river in Europe with a total length of 2 850 km out of which 350 km run through Austria. Within the last two centuries, several river regulations and the establishment of dams for the purpose of flood protection, navigation and energy have modified and narrowed the original riverbed as well as the area of the natural flood plains. Such landscape alterations resulted in only two free flowing sections of the river in Austria, i.e. the steep slope of Wachau Valley and a part of the Donau-Auen National Park.

> *The Donau-Auen National Park is home to 838 plant and more than 200 vertebrate species and is located in free-flowing areas of the Danube, the second longest river in Europe.*

The upstream areas of the Danube – Obere Lobau – fulfil important recreation functions for the counties of Greater Vienna and Lower Austria, whereas the area of Untere Lobau further downstream form an ecological hotspot with several bodies of standing water. The dam located downstream from the National Park has, besides flood protection and recreation purposes (e.g. Danube Cycle Route), the roles of a refuge for threatened species of semi-dry grasslands – including orchids such as *Ophrys* spp., *Orchis militaris* L. and *Neotinea ustulata* L. (Manzano 2000) – and a migration corridor. The species diversity is very rich as 838 plant and more than 200 vertebrate species are found within the area of the National Park (Drescher and Magnes 2002). The riparian forest is categorised as either hard broadleaved riparian forest, which seldom floods (tree species commonly occurring are e.g. elms (*Ulmus* spp.), oaks (*Quercus* spp.), ash (*Fraxinus excelsior* L.) as well as various wild fruit tree species), and soft broadleaved riparian forest that experiences frequent flooding where the tree species commonly found are white willow (*Salix alba* L.), purple willow (*Salix purpurea* L.), alders (*Alnus* spp.), white poplar (*Populus alba* L.), and black poplar (*Populus nigra* L.) (National Park Donau-Auen 2016). In addition, although located within the National Park, the Danube is a major European waterway still fulfilling a significant transport function (Rak and Bergmann 2013).

An inventory of the National Park from 2008/2009 showed an increase of area dominated by two invasive introduced tree species: tree of heaven (*Ailanthus altissima* (Mill.) Swingle) and ash-leaved maple (*Acer negundo* L.). The proportion of natural regeneration and mature individuals of these tree species increased by 13 % and 15 %, respectively, within the last decade. Therefore, several strategies for eradication of these two invasive tree species were discussed: i.e. ‘no intervention’ method (complying with the protection strategy of the National Park) and the application of eradication methods in order to eliminate or reduce the occurrence of the invasive species. Because a policy of ‘no intervention’ would lead to species and habitat loss, a plan was drawn up to allow temporary management to encourage the chances for native species (Hochbichler et al. 2012).

Figure 125. Map of the Donau-Auen National Park showing the location of forests, meadows and wetlands (National Park Donau-Auen 2016).

> *The expansion of tree of heaven, ash-leaved maple and black locust in the Donau-Auen National Park led to the initiation of one of the biggest 'eradication projects' of invasive tree species in central Europe.*

The results of the inventory with regards to the expansion of tree of heaven and ash-leaved maple together with the spread of another introduced tree species, black locust (*Robinia pseudoacacia* L.), gave rise to the project 'Management of invasive neophytes in the Donau-Auen National Park' (2012–2014). This project was initiated with the aim to develop a suitable management approach to eradicate introduced tree species and to elaborate on already existing strategies used to control introduced invasive tree species (Oitzinger et al. 2015). The feasibility of different management operations used to control introduced tree species in the protected zones of the National Park where no management is usually allowed was also addressed.

The main questions that the project sought to answer were:

- How long does it take for the tree species to die after girdling?
- What is the mortality rate of the tested stems?
- Do the tested tree species form sprouts below the girdling zone?
- How long do sprouts originating from girdled trees survive?
- How will the tree vegetation develop on these stands following the eradication of the introduced tree species?

The project was rather complex including various experiments; Table 25 represents an example of experimental design of one of the project experiments where girdling was tested. In this particular experiment, 35 plots of different sizes (200–800 m^2) were established in order to evaluate measures used to eradicate tree of heaven and ash-leaved maple; natural regeneration has been continuously observed on half of the plots since the initiation of the project. Further detail on the project and methodology used in its individual parts can be found in Oitzinger et al. (2015).

Table 25. An example of an experimental design of one of the experiments where the girdling took was conducted in August and September 2013 (ToH = tree of heaven, AM = ash-leaved maple and BL = black locust).

Plot no.	Tree species	Year of girdling	No. of introduced trees/ha in the tree layer	Height dominant tree layer (m)	Age dominant stand in 2013	Dead wood (%) in 2013	Sample plot size (m^2)
2	ToH	Winter 2012	1996	18	20	20	486
4	ToH	Winter 2014	2587	20	21	20	286
6	ToH	Winter 2014	667	20	40	20	225
7	ToH	Winter 2014	511	25	66	15	352
8	ToH	Winter 2014	391	25	81	20	460
9	ToH	plot mulched	0	18	24	15	400
10	ToH	Winter 2014	1300	15	24	10	400
11	ToH	Winter 2014	1189	25	46	15	841
13	ToH	Winter 2010	500	30	46	20	400
14	ToH	Winter 2011	1175	25	40	15	400
17	ToH	Winter 2012	1389	20	31	20	540
18	ToH	Winter 2012	2060	15	26	40	432
19	ToH	Winter 2012	659	25	56	10	425
21	ToH	Winter 2013	451	25	56	15	576
22	ToH	Winter 2014	1120	25	40	15	250
23	ToH	Winter 2014	1016	20	31	5	512
24	ToH	Winter 2014	1238	25	20	10	420
25	ToH	Winter 2013	1689	22	26	20	450
26	ToH	Winter 2014	1366	25	40	10	432
28	AM	Winter 2010	140	30	46	10	500
29	AM	Winter 2013	467	27	24	25	300
30	AM	Winter 2011	650	15	40	10	400
31	AM	Winter 2011	593	18	20	20	455
32	AM	Winter 2011	480	20	60	70	625
33	AM	Winter 2011	336	30	46	20	803
35	AM	Winter 2014	1100	15	26	30	200
36	AM	Winter 2014	2667	10	10	5	150
38	AM	Winter 2012	267	20	26	30	486
39	AM	Winter 2012	1053	23	36	40	418
40	AM	Winter 2012	223	30	40	40	672
43	AM	Winter 2014	183	20	41	10	600
47	AM	Winter 2014	3000	10	10	5	480
48	AM	Winter 2014	379	30	46	20	448
50	BL	Winter 2014	1056	20	41	20	625
51	BL	reference plot	467	20	30	15	450

Figure 126. Eradication measures in the Donau-Auen National Park: a) girdling of ash-leaved maple (photo: ÖBf) and b) the mechanical removal of introduced tree species (photo: F. Kovacs).

The results of the project showed that girdling is an effective method for controlling the tree of heaven, with the mortality of mature trees reaching 60 % and 90 % half a year and one year after girdling was applied, respectively (Figure 126a). Although girdling could also be used to control ash-leaved maple, mortality rates of more than 90 % were only achieved after three years (Figure 126b).

One of the key aspects in eradicating invasive tree species is to suppress its natural regeneration and to halt the seed production; in the case of ash-leaved maple, it is important to prune female trees as they tend to produce large quantities of seeds in the years following the girdling operation.

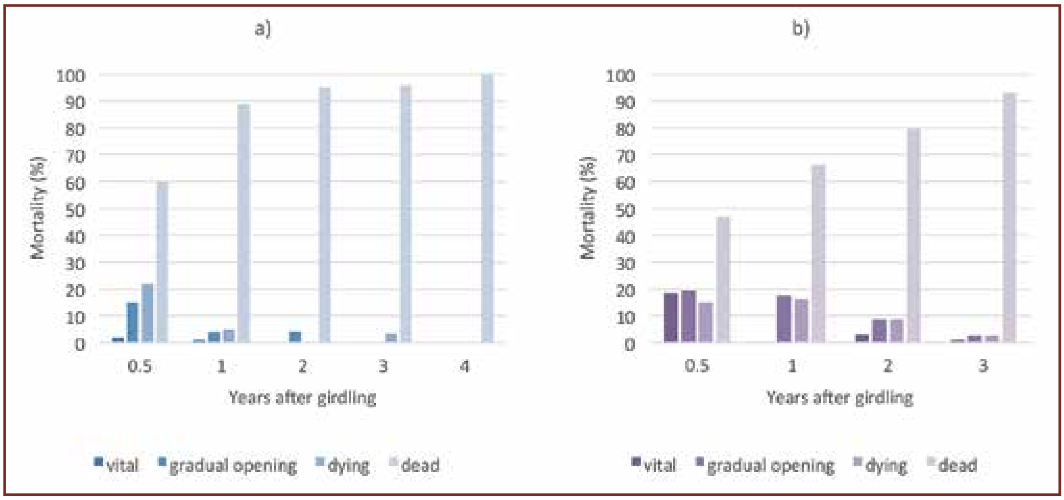

Figure 127: Mortality rates (proportion of dead trees following the girdling application) for the tree of heaven (a) and ash-leaved maple (b).

The vitality of adventitious sprouts also varied amongst the tree species tested; 55 % of the adventitious sprouts of the tree of heaven with dead or dying crowns were still vital in the year after girdling was applied. However, all sprouts died four years after the girdling was carried out (Figure 128). A different trend concerning the vitality of ash-leaved maple sprouts was observed; one year after the girdling was applied, 60 % of the adventitious sprouts were found to be dead with all adventitious sprouts dying four years after girdling.

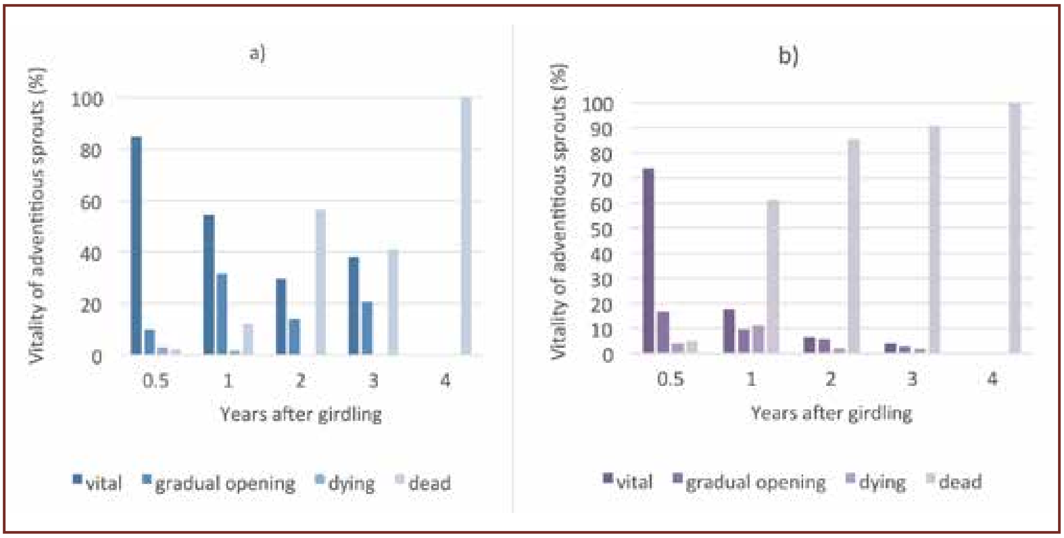

Figure 128. Vitality of the adventitious sprouts following girdling for a) tree of heaven and b) ash-leaved maple.

The majority of stem sprouts of tree of heaven and ash-leaved maple died within 1–3 years following the treatment application and are therefore considered manageable; however, tree of heaven continues to produce root sprouts following girdling and these may continue to grow if not treated.

It is important to note that the root sprouting is stimulated when the tree of heaven is girdled as the root sprouts were observed appearing especially in the ground vegetation and shrub layers. In one plot the proportion of tree of heaven in the ground vegetation layer doubled from 40 % to 80 %, and in another it increased from 3 % to 85 %. In another plot, the proportion of tree of heaven in the shrub layer increased from 15 % to 26 %. However, the opposite was recorded for ash-leaved maples as their root sprouts were almost absent from the shrub layer with a substantial decrease; i.e. from 32 % average cover before treatment (2013) to 3 % average cover after treatment (2014). The remarkable difference between the reported root sprouting of the two introduced species may be explained by the browsing pressure since red deer shows a preference for ash-leaved maple.

Another experiment (focusing on black locust within the National Park) looked at the species composition of natural regeneration following different treatments: clearcutting or girdling of black locust. The species composition after treatment is presented in Figure 129 (detail on methodology to be found in Oitzinger et al. 2015). The proportion of natural regeneration of ash-leaved maple in plot that received clearcut was more than 35 %.

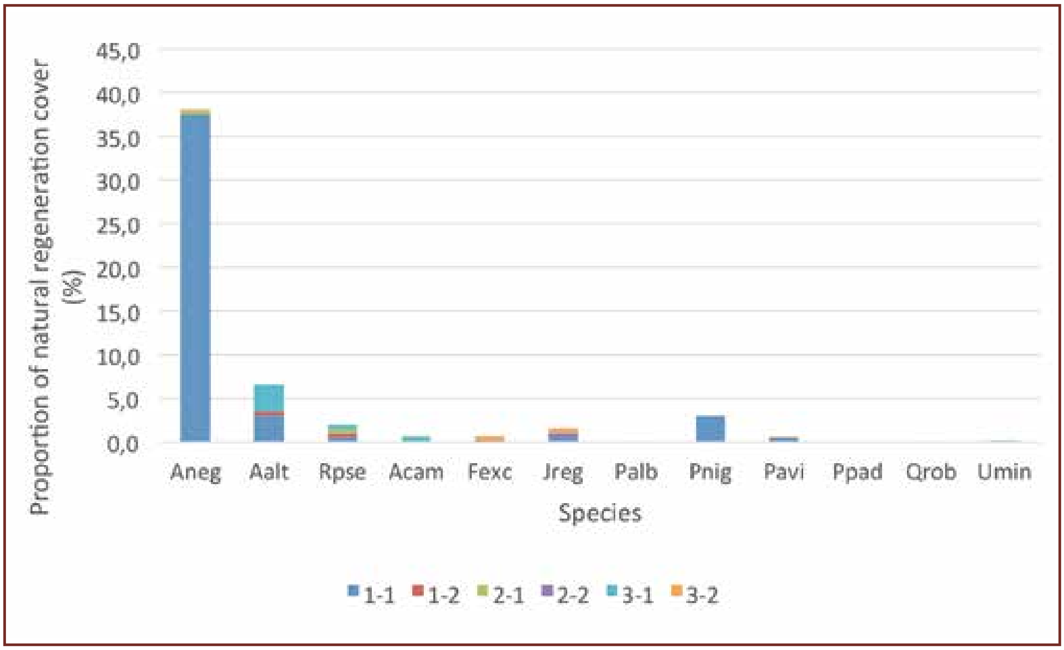

Figure 129. Proportion of natural regeneration of different tree species in an experiment where the species composition following treatments (girdling or clearcut) in 2014 was observed. Coding on the graph as follows: Aneg = *Acer negundo*, Aalt = *Ailanthus altissima*, Rpse = *Robinia pseudoacacia*, Acam = *Acer campestre*, Fexc = *Fraxinus excelsior*, Jreg = *Juglans regia*, Palb = *Populus alba*, Pnig = *Populus nigra*, Pavi = *Prunus avium*, Ppad = *Prunus padus*, Qrob = *Quercus robur*, Umin = *Ulmus minor*.

One advantage of applying girdling as a method to eradicate invasive tree species, as opposed to using clearcut, is that a substantial proportion of deadwood remains in the stand and the forest stand structure is maintained. Deadwood is a key component of forest ecosystem and it is therefore important to support it, especially in protected parts of the National Park. Clearcuts also favour the spread of ruderal vegetation, and therefore other invasive plant species such as giant goldenrod (*Solidago gigantea* L.) may be encouraged, which also suggests unsuitability of clearcut as an eradication measure due to steering the ecosystem dynamics towards an undesired direction. Furthermore, the light conditions following clearcut are favourable for the growth of black locust sprouts, and therefore clearcutting is not recommended for sites where black locust is already present.

The costs of eradication measures are important when controlling the spread of invasive tree species. In the case of the project described here, the costs for mapping and girdling were calculated to be €1.80 per tree, which is about €170–270 per hectare (Hochbichler et al. 2012). These values could be considered as baseline for estimating the cost of further girdling measures in riparian forests in order to eradicate introduced and/or invasive tree species. It is important to note, however, that the costs for girdling were actually higher than expected since the work was carried out by experienced professional technical staff rather than by seasonal workers. From a legal point of view, when planning girdling measures in stands of invasive tree species younger than 60 years, national law always has to be consulted, and if necessary, special permission has to be obtained.

The recommendations based on the project results indicate that clearcuts should not be applied on large areas where invasive tree species are widespread as such interventions cause substantial disruptions to the stand structure and will require long-term and rigorous post-treatment. A more appropriate approach (stand level) that complies with a philosophy of minimal intervention consists of the application of measures that target individual introduced trees (e.g. girdling) in order to suppress them, and therefore allow for natural regeneration of native tree species. An obvious advantage of such treatment is that the need of further interventions appears to be relatively low.

The project showed that a successful transition from stands dominated by invasive species to stands where such species represent only a minor component (or are absent altogether) is possible, but it requires substantial effort and considerable financial resources. Attention should also be paid to species that have been considered invasive elsewhere, but are not yet present within the Donau-Auen National Park. If such species should appear in the National Park, control measures should be used in timely manner in order to prevent their establishment. Monitoring of the permanent plots set up as a part of this extensive eradication project will be continued in order to gain representative results concerning the methods and the success over a longer period. The consecutive treatments (e.g. girdling and root sprout removal) will also be continued to ensure that these invasive tree species are eradicated from the area of the National Park.

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Synthesis and Conclusions

Frank Krumm and Lucie Vítková

Beside climatic changes, invasive species are currently considered one of the biggest threats to biodiversity. When scientists, practitioners and society discuss about intentional or unintentional introduction of species, the major concerns are usually about losing control of species that do not belong in certain natural ecosystems. The ease of travel and the nature of global economy have been the major drivers of species introductions; this is unlikely to change as there do not appear to be any realistic scenarios that would reduce activities related to travelling and trade, which could consequently result in a decreased number of the new introductions.

Species invasions are believed to be natural processes and are considered to be a part of natural dynamics, similarly to extinctions. What is different due to human activities is, however, the rate of introductions and consequently also the rate of invasions, which is confirmed by prehistoric records and by invasion processes that can be demonstrated on isolated islands such as Hawaii or the Galapagos. Apart from the impacts on biodiversity, there are undesired effects of invading species, at least from a human perspective, such as that on human health or in terms of monetary values. In addition, ecological ethics plays an important role as it helps us to understand how certain movements came about and how particular terms have developed over time as well as how different parts of society can influence the perceptions on and interpretations of specific topics.

One of the main findings after getting a deeper insight in different topics with regards to introduced and invasive tree species across Europe, and beyond, is to better understand and classify historical processes. Our climate has been changing and so has the natural species composition. Ice ages and inter-glacial periods have, in a meantime, been better understood with species migrations being supported with sound scientific evidence. Chapter 1.1 addresses these natural pathways of introductions and shows how the ecosystems altered in the past. It is important to keep in mind that changes are a part of individual ecosystems and are also an inseparable part of ecosystem's dynamic development with paleological records, developing methods and novel means of analyses offering more insights into the natural migration routes of species.

5 000–6 000 years ago, humans came into play and have rapidly developed ever since; while using and managing land with increasing intensity, humans also migrated and expanded the trade of various goods. Since such activities started altering the ecosystem, biological invasions interacted in various ways with land use changes and disturbance regimes have been increasingly altered. The frequency of disturbances, but also the disturbance types, has changed also promoting species invasions. However, the interaction between land use change and invasion is not as simple since both introduced plants and animals can alter the disturbance regime of the sites they invade.

European tree species richness was substantially enriched after the Americas were discovered in the 15th century. Consequently, foresters and other land managers started introducing species into European forests from the New World as well as from other parts of the globe (chapter 1.2).Aesthetics became increasingly important and estate gardens, parks and arboreta were created forming an important element for recreation, education and inspiration. Although native species were used for ornamental purposes, utilising species of non-native origin became a common practice due to their (not only) unusual appearance. Some species introduced for ornamental purposes escaped from designated areas causing substantial problems in the forests.

The era of industrial revolution brought increasing demands for timber, which led to serious deforestation of native forest in Europe; in order to restore the forest cover, species of non-native origin were used in some European countries. Since the 1980s, the nature conservation in Europe has dynamically evolved, among other reasons, as a consequence of pollution and forest dieback. The awareness of the fact that nature is endangered by human actions has grown and the changes to ecosystems and the damage to underlying natural processes often leading to the loss of biodiversity have been widely discussed and the presence of introduced tree species has also been considered as an important factor. Such discussion also became political requiring accurate terminology; although the terms related to the introduction of species and invasion biology varied considerably often leading to misunderstandings.

Understanding historical developments and political movements may influence the way certain perceptions are shaped (chapter 2.1), which consequently influences the use of specific terms. In order to better understand certain terms and their different interpretations, it is therefore crucial to bear in mind political as well as societal developments.

Old-growth forests or wilderness are considered as something good or moral and words such as ‘invasion’ or ‘neophyte’ attract negative societal perceptions. Since human ethics determines human behaviour, which is often shaped by subjectivity, the question whether a species should be declared as invasive is a matter of applying suitable scientific approach (chapter 2.2). Although frameworks were developed to support realistic assessments, objective evaluation if a species is invasive in its biological sense, or if it is just perceived as negative by society as it is non-native, still remains a challenge.

Environmental conditions vary across and the question if species has invasive character can also change over time. Although risk assessments analysing whether tree species establishes and can become invasive have advanced, future developments on how invasive species develop under a changing climate and ongoing land use changes are not easily foreseen (chapter 2.3). Although discussion based on scientific facts are sometimes challenged, people’s perceptions matter and vary among different actors as they are often driven by economics and/or emotions. This makes the situation complicated; nonetheless, variation appears to be a challenging precondition to transparent communication and appropriate moderation among different stakeholders (chapter 2.4).

Mutualists may have a strong impact on species due to the changes created by associated/ other species’ arrival or when native species adapt to the presence of introduced species. Soil mutualists, such as mycorrhizal fungi have the potential to strongly influence tree invasions once they co-invade (chapter 2.5). Co-invasion represents potential influences that are currently not completely understood since indirect processes and corresponding interactions have not yet been entirely comprehended. This is one of the crucial questions that needs to be answered objectively by science; nonetheless, it is not easy to resolve the many unanswered questions in relation to introduced and invasive tree species as developments are rapid and factors such as climatic and land use changes needs to be more accurately defined in order to get a clearer picture. However, it is important to bear in mind that land use changes interact with climatic changes, which may also promote tree species invasions, scientific support for which is also still needed. The science supporting the invasion ecology has been well developed in some parts of the world where introduced species have played an important role in the landscape for longer periods of time. South Africa can be considered as an example as introduced tree species substantially altered local ecosystems and subsequent invasions created irreversible changes to the local ecosystems (chapter 2.6).

Management of introduced and invasive tree species needs to be supported with scientific evidence and suitable risk evaluations in order to be able to come across various challenges related to forest management. This includes theoretical concepts on how to assess potential impacts of invasive species. Chapter 3.1 addresses several approaches assessing the magnitudes of such impacts; since propagule pressure and species traits of particular species drive the impacts they have on the environment, scoring systems thus assist in evaluating the need for action and consequent investments aimed at active control or management approach.

Although the establishment of lists containing invasive species may aid the early management actions, it is certainly not an easy task to put one together, especially in heavily populated and heterogeneous area such as Europe. The European Union established a list with species considered to be invasive that are not allowed to be grown in Europe. Such initiatives are necessary as monitoring is an essential prerequisite for suitable management and control measures providing foundation for establishment of suitable legal framework. However, such lists often create concerns and are under constant discussion (chapter 3.2) with nature conservation and forestry representing the classic conflict within the landscape management (chapter 3.3) This may, however, be attributed to different interpretations of research results, or to studies conducted by different institutions, sometimes financed by different parties. Although such factors form inevitable part of the above-mentioned discussion, they often prevent constructive developments. Heterogeneous geography, history and cultures as well as diverse political and societal landscapes yet increase the complexity. In order to provide reasonable resolutions, transparent communication amongst different stakeholders is the precondition of successful implementation of certain rules.

Insights into practical management of introduced and invasive tree species are important as they can demonstrate various management experiences that were either successful or somehow failed to reach their aims. It is important to share the lessons learnt as they can form foundation for future decision-making (such insights are presented in chapters 3.4–3.8). Eradication of invasive species is the usual strategy used to protect habitats of high conservation values. The management of National Parks usually aims to eradicate introduced species from their areas with even the use of glyphosate being allowed to be applied in some places in order to protect native species composition. The chapters 3.4 and 3.5 represent examples of introduced and invasive species in National Parks; the former presents several options of active management applied in Italian National Park as invasive tree species have been negative affecting protected areas with the latter presenting the status of the introduced tree species within Polish National Parks where only minor eradication measures have been done due to, so far, relatively low, but growing, proportion of introduced species.

Suitable silvicultural strategies are key component of successful forest management and they may need to be altered so that they suit the purpose of managing forests where introduced and invasive tree species are present. Different silvicultural options used in forests in northern Italy where introduced and invasive tree species are present can be used as one such example (chapter 3.6) as Italy is one of the major recipients of invasive species in general.

The occurrence of introduced tree and shrub species in relation to the extent of planted and coppiced forests is addressed in chapter 3.7; as this is a specific issue in Italy, where vast areas of forests are managed under varieties of coppice system, which over time created areas of high conservation value, some of which have been designated as Natura 2000 sites. The shrub layer in forests directly influences the natural regeneration and the competition caused by shrub layer is therefore necessary to be considered by forest managers. One of such examples can be demonstrated on the Asian knotweeds (chapter 3.8). There are other shrub species, such as butterfly bush (Buddleja davidii L.) that often escapes from gardens into forest where it also hinders natural regeneration and therefore affects forest stand dynamics.

Economics has been a major driver of species introductions done for the purpose of timber production. Although introduced and invasive tree species pose a challenge in terms of economics as various cost and revenues are generated, some opportunities also rise (chapter 4.1). Different conditions (social and environmental) across Europe create various scenarios that are necessary to be considered when evaluating the economic aspects, especially when multiple ecosystem services are taken into an account in rural economies where people are directly dependent on such species.

Numerous models focusing on future tree species distribution under changing climate have been available; although the level of uncertainty has been still relatively high, there is a clear trend predicting the shifts of native species' ranges in European forests. This has obviously brought the use of introduced trees species into equation since some of the native one, and commercially important ones, will be unable to cope with the changing climate. Such shift has been affecting species competition (chapter 4.2) with questions such as 'What happens under drier conditions and higher temperature?' or 'How plastic are certain species?' and 'Where is the tipping point before a species gets locally extinct?' requiring accurate answers in order to maintain resilient forests. Although these questions are of major interest, experiments providing reliable data to support their answers require long-term and large-scale experimental design. In addition, as hotter and drier future is expected (chapter 4.3), main ecosystem services that introduced as well as native tree species provide will be affected and this will require a joint effort of multiple stakeholders as well as interdisciplinary research addressing various causes and consequences. Such efforts will also have to take into an account pests and diseases as pathogens of introduced tree species and the prospects for biocontrol will be a challenge in future (chapter 4.4).

Large forest areas were cleared within the last centuries with considerable changes being experienced across Europe. Air pollution, increased CO2 concentrations and acid rain have been identified as having major impacts on forests within the last 50 years. Although forests have recovered from these severe impacts, the intensification of land management, land use changes and climatic changes seem to have had negative consequences on species diversity in forests. Hence, the loss of biodiversity has been commonly discussed (not only) in relation to introduced tree species (chapter 4.6) as it has created substantial perturbations on forest ecosystems. The competitive potential of many introduced species on the one hand, but also interactions between arthropod communities and the introduced tree species should be taken into consideration as insects form an important component of biological diversity within our forests (chapter 4.5).

Natural disturbances are another important ecosystem driver as their type, frequency, intensity and scale has shaped our landscape. Since more extreme events, but also further changes in land management, influencing disturbance regimes, are expected in the future, species invasions may be provided with good conditions for spread, which can be demonstrated by e.g. extreme storm events or fires (the latter demonstrated in chapter 4.7).

Several introduced tree species to Europe have been the centre of discussion and research for some time, which is a reason why country- and species-specific case studies were included in this publication (5.1, 5.4–5.9). More specific case studies, dealing with case studies on regional scale are presented in chapters 5.2, 5.3 and 5.10. The former addresses the forest management of Douglas fir in Freiburg City Forest (south-western Germany) whose aim is to produce high quality timber but also fulfil the aim of the recreation function. Chapter 5.3 evaluates natural regeneration of Douglas fir and chapter 5.10 is an example of protected area where invasive species of non-native origin are present and where substantial efforts have been made to eradicate such species bearing in mind protection function of valuable riparian habitats.

Conclusions

The present publication shows that the situation among introduced species is not black and white presenting us with a lot of grey areas. “A forest pest is not always a forest pest” is one of the key messages in chapter 2.4 and it clearly indicates that it is not always straightforward to determine whether certain species will become an issue or it will be ‘problem free’. The chapters, and in particular the case studies, support the position that it often depends on the management objectives and in particular circumstances, whether a species is considered as problematic or not. However, it is clear that there are circumstances where introduced tree species can harm the environment. In order to maintain resources for future generations, measures to manage invasive introduced species are needed.

However, on the other hand, as a result of introduction and cultivation, certain introduced species (e.g. black locust or Douglas fir) have not only made a significant contribution to income from forests, but have also become part of the European landscape and nature; some introduced species have become a part of the cultural and historical heritage. Social trends are depicted in discussions and political situations are also reflected in human perceptions – society, which is constantly growing worldwide, forces other demographic changes and consequently also land use changes. The broad society is decoupling of land use processes. Subsequent changes in land use induce drastic consequences for land management and consequently, the perception on natural processes are changing constantly and vary among the different stakeholders. Therefore, it is not easy to define terms and establish criteria that all actors can agree with as emotions strongly influence the discussion.

There has been available evidence for introduced species becoming invasive causing severe threats to biodiversity, human health, timber production, etc. The need to (re)act and manage in certain way is given if any ecosystem services are somehow negatively affected or endangered by introduced or invasive species. We can learn how introduced species can harm local biodiversity, alter fire regimes or influence water cycles from experience in Europe as well as in other parts of the world. Protection functions the ecosystems have can be affected and the costs to control invasive species may increase tremendously due to the rapid growth of certain invasive species. Unfamiliar situations where introduced and invasive tree species dominate come about and time is therefore needed in order to gain experience and knowledge to be able to appropriately respond to such situations. On the other hand, a suitable use of introduced species in the right circumstances can make an important contribution to economic, social and environmental services.

Since we use natural resources and we a part of nature, some of the changes we make to the environment ought to be considered as acceptable - at least to certain extent. This is mainly due to having have to adequately support our survival, which is one of the major drivers of the changes we made to natural ecosystems. A species dominating its environment is one of the subjects addressed in this book, and yet, we, humans, are the most 'invasive' of species as we have altered our environment in an incredibly short time and in ways that cannot be reversed in certain cases. One of the great challenges of our time is therefore, how to deal with the consequences of trade and travel and statements such as: "Do we need a new nature?" (Josef H. Reichholf, German environmentalist and scientist) given in "The New Wild: Why invasive species will be nature's salvation" by Fred Pearce) try to increase awareness and stimulate the discussion. Some examples of tree species introductions show that ecosystems can be substantially altered with whole species populations sometimes disappearing. Shifts in species ranges and species compositions are also part of naturally occurring processes – but how far can we accept humans to alter these processes? Natural and human induced disturbances will occur in the future and global trade will be intensified as opposed to limited; both of these factors shall be accepted. In the case of natural disturbances that affect forest ecosystems, voices are getting louder calling to allow certain natural development as many processes and species are, to certain extent, linked.

There has been a growing pressure to use natural resources; this has also been one of the reasons for considering introduced tree species as an option for the future, if risk assessment approves and if all necessary conditions for growing an introduced tree species are fulfilled - though, this may be rather difficult. Some introduced species with invasive character have the potential to change ecosystems in a way that multi-purpose forestry cannot fulfil its major tasks anymore and this has to be kept in mind if there is an intention to use any species of non-native origin. Protective functions, such as water catchments or protection against natural hazards like fires and avalanches, but also the production of valuable timber and provision of recreational opportunities, should remain the main objectives in a close-to-nature forest management as a basis for integrative forest management.

Key messages

- Policy must provide frames at different scales that allow distinguishing between different scenarios, environments and objectives. Although, this has been addressed by European Union and relevant legislations and Black Lists issued, such efforts should reflect the local conditions such as climatic and environmental differences.

- It is important to understand the natural history prior to human influence as well as the effects humans have had; the migration of species is a natural process and is a precondition for adaptive capacities of natural ecosystems. The example of the migration of silver fir, for instance, shows how adaptive a species can be, and that influencing co-factors, such as the presence or absence of deer and wolves can affect ecosystem functions drastically. Attributing changes to single factors and the presence or absence of single species often provides a misleading picture.
- Communication between generations is also important and it is therefore necessary to educate our children about the value of our forest as they are an inseparable part of the environment that we live in. It is necessary to enhance various aspects of environmental education in the teaching curriculum since early school classes also include the topic of species introductions and invasions as well as the ways such species develop and shape our environment. As part of the In-Tree project (that gave rise to this book), workshops on the topic of introduced tree species were conducted for children of various ages (10–17) (see Box 27).

Box 27.

´Introduced species can cause serious problems in ecosystems. Raising awareness about the issue already in school can help to alleviate the problem. Ecology is part of the German school curriculum, and in this context it is a relevant topic that leaves room for critical ethical debate, which is a good tool to help students form their own opinion. Combining the scientific view with a more effective artistic approach as a teaching tool helps visualise the problems related to invasive species. At our school students created very different outputs after a short introductory presentation, which shows that a creative process is stimulated by this topic that works with students of all ages.´

Annette Schuck, vice director of the Angell school, Freiburg, Germany

- Climate change is driving natural changes in ecosystems but also the frequency and severity of disturbances, which are an underlying factor (largely unpredictable) interacting with other ones. Accepting change may be a good way to cope with the situation as invasions of certain species are difficult to prevent with the predictions being rather uncertain. However, this is critical as there is a need to secure future with respect to food, security and culture. It seems risky to leave this uncontrolled as there are too many questions that remain open.
- A variety of sectors (e.g. forestry, agriculture, horticulture and landscape management) as well as the broader society, land owners and managers, are affected by tree species introductions but also by species invasions. Adaptive management approaches that provide management actions suited to local conditions are thus necessary.
- International collaboration and joint projects resulting in suitable risk assessments are a way forward to account for potential threats also helping to analyse the impacts of already existing introduced and invasive species.
- Finally, national administrations should also enhance and allow for communication across sectors. Certain approaches may be applied in one sector, but if stakeholders in other sectors (e.g. landscape planners, infrastructure planners and horticulturists) do not apply these measures, the impact of these measures will be much less pro-

nounced than it could have otherwise been. Close to human settlements, there are many examples of non-native species (intentionally introduced for ornamental purposes) that escaped from parks and gardens and that became a problem for the surrounding forests and the corresponding forest functions. This is an issue for forest owners and managers and can increase forest management costs dramatically.

In order to answer the question posed by Josef Reichholf: "Do we need a new nature?", it is important to understand basic ecological principles. In addition, we need to ensure sustainable use of our resources in order to provide security for future generations. In order to do this, we need the best possible comprehension of the processes taking place in our environment and suitable and innovative solutions to the challenges of using our resources sustainably. We also need to ensure adaptive capacity of our natural and managed ecosystems in order to maintain biodiversity and minimise the threats that reduce biodiversity.

Glossary

This glossary was compiled with the help of the contributing authors to ensure consistency with their working definitions, which may result in the below-mentioned definitions to differ from other sources.

Abiotic: agent shaping particular ecosystem not derived from living organisms.

Alfa biodiversity: species diversity of a specific site (i.e. local species pool).

Achene: dry one-seeded fruit that does not open to release the seed.

Acidophilic: thriving in relatively acid soils.

Allelopathic/allelopathy: chemical inhibition of one species by another where the inhibitory chemical is released into the environment where it affects the development and growth of the neighbouring individuals.

Archaeophyte: species which is non-native to a certain geographical region introduced prior to 1492 (Christopher Columbus' arrival in the New World).

Axillary panicles: arrangement of flowers on the top of the stalk where the flower cluster is irregularly branched.

Basal area: cross-sectional area of a tree measured at the breast height (1.3 m above ground).

Beta biodiversity: species diversity amongst different sites (or habitats).

Biocoenosis: an association of different organisms forming a closely integrated community.

Biotic: living agent shaping particular ecosystem.

Dehiscence: spontaneous opening of a plant fruit at its maturity for the purpose of releasing its contents.

Detritivore: organism that uses organic waste as a food source.

Edaphic: produced or influence by soil.

Epicormic growth: shoot growing from an epicormic bud that is located underneath the bark of a tree's stem or branch.

Epinasty: increased growth of the upper surface of a plant part (e.g. leaf) resulting in a downward bending of the plant part; i.e. the leaf drops from a horizontal to a more vertical position.

Gamma diversity: species diversity at a landscape level (i.e. regional species pool).

Guild: group of species of the same trophic level that utilise the same resources.

Heliophilous: plant requiring or tolerating a high level of direct sunlight.

Mesic: type of habitat with a moderate or well-balanced supply of moisture.

Mulching: layer of organic residues placed on the surface of cultivated soil.

Mycoherbicide: herbicide based on a fungus that produces toxic compounds that dissolve the cell walls of targeted plants.

Neophyte: species which is non-native to a certain geographical region introduced after 1492 (Christopher Columbus' arrival in the New World).

Propagule pressure: number of species introduced or released into a specific location region (to which they are not native), some of which will go on to establish a self-sustaining population while will not.

Ramet: clonal colony of genetically identical individuals reproduced vegetatively, not sexually, from a single ancestor that have grown in a specific location.

Riparian: area/plant located/growing adjacent to a body of water.

Rhyzome: underground stem of horizontal growth which puts out lateral shoots and adventitious roots.

Saprophytic: organism living on dead or decomposing matter.

Saproxylic: organisms (usually insects) that depend on dead or dying wood during certain part of their life cycle.

Thermophilic: warmth-loving species.

Xeric: species growing in a dry environment or environment containing little moisture.

In-Tree **project partners:**

Universität Potsdam

CzechGlobe
Global Change Research Institute CAS

Faculty of Forestry and Wood Technology

ÖSTERREICHISCHE BUNDESFORSTE

Corpo Forestale dello Stato
Centro Nazionale per lo Studio e la Conservazione della Biodiversità Forestale "Bosco Fontana"
- Verona -

Bosgroep Zuid Nederland

coillte

DISAFA
Università degli studi di Torino

Faith Wilson
ECOLOGICAL CONSULTANT

TESAF
Dipartimento Territorio e Sistemi Agro-Forestali
Università di Padova

UNI FREIBURG

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Julius Kühn-Institut
Federal Research Centre for Cultivated Plants

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Dezernat für Umwelt, Jugend, Schule und Bildung
Forstamt
Freiburg
IM BREISGAU

GEORG-AUGUST-UNIVERSITÄT GÖTTINGEN

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UNIVERSITÀ DEGLI STUDI DI SASSARI

FVA
Forest Research Institute Baden-Württemberg

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BfN
Federal Agency for Nature Conservation

National Research Council of Italy

Centro Ecologia Aplicada

THÜNEN

UCD DUBLIN

UNIVERSITEIT GENT

MINISTERIO DE ECONOMÍA Y COMPETITIVIDAD

INIA
Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria

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In Focus – Managing Forests in Europe

In the context of forest and landscape management, the use of introduced tree species is an important and controversial topic. On one hand, the species can provide an opportunity for timber production and for adapting the species composition within forests so that forests can better cope with the changing climate while on the other hand, such species may cause biodiversity loss and/or disturbance to native ecosystems.

Introduced tree species in European forests – opportunities and challenges is a compilation of scientific and practical knowledge on introduced tree species in European forests and contains contributions from 89 authors from 18 countries.

The historical context of species introductions plays a key role in understanding the current as well as possible future distribution of tree species. There has been an intensive discussion on the interactions between the introduced tree species and their introduced environment, and also on the processes that may lead to the species becoming invasive within their introduced range. The risk of a species becoming invasive can be evaluated using suitable risk assessments that help us to predict the future behaviour of the species, and also the potential contributions of these species to ecosystem services provided by the forests where they occur. Therefore, the links between the introduced tree species and the key topics such as economics, climate change, pests and diseases and effects on biodiversity are also assessed in order to demonstrate the complexity of the issues pertaining to the introduction of tree species. Case studies of selected introduced tree species occurring in Europe are presented to demonstrate the necessity to manage ecosystems in order to fulfil certain goals; the case studies cover species-specific and site-specific experiences as sharing the application of suitable management practices is of particular interest.