Abstract

The present thesis is based on six manuscripts, which consider various aspects of conservation biology and ecology of wood-inhabiting fungi. Paper I provides an analysis of the role of focal species in conservation biology, based on the assertion that focus on particular species or species groups represents a relevant but often tendentious and subjective way of making conservation biology work in practice. It is argued that different focal species concepts express different, often implicit subsets of normative arguments for biodiversity conservation. On this basis the relevance of wood-inhabiting fungi as focal species is discussed, and it is stated that there are few “hard” arguments for the conservation of rare wood-inhabiting fungi in nature. Accordingly, conservation initiatives aiming on conserving wood-inhabiting fungi are only relevant if based on ethical considerations appreciating nature and biodiversity to have intrinsic value. In this context wood-inhabiting fungi are interesting in several ways. They constitute a substantial part of forest biodiversity and play key roles for other organisms dependent on decaying wood. In addition the composition of wood-inhabiting fungal communities may reflect recent and past forest history, and there is some evidence that rich occurrences of particular species may point to high levels of dead wood and megatree continuity at the local to regional scale.

The remaining papers investigate the ecology of wood-inhabiting fungi with special emphasis on habitat preferences. In paper II the effects of exudates from uncolonized beech wood and beech wood previously colonized by a number of early decay agents is investigated with respect to mycelial growth in a range of late stage decay fungi. These were found to show very different and specific responses depending on treatment, and it is concluded that different early decay agents influence occupied wood chemically in specific ways, and that they thereby have pronounced effects on subsequent community development. In papers III-VI the habitat preferences of wood-inhabiting fungi are investigated on naturally decaying wood in a number of near natural deciduous forests, based on sporocarps inventories. The studies show that very substantial changes occur in the fungal species composition during the decay process, but also other habitat factors, i.e. tree species, climatic conditions, death cause, forest history, as well as the original position of the dead wood in the tree are identified to have marked effects on the fungal species composition on individual decaying trees. Tree dimensions, on the other hand, were only found to influence species composition to a limited extend, and it is suggested that tree death cause and the presence of certain early decay agents, which may depend on the presence of old trees, is more important to fungal diversity than tree size *per se*. Thus, certain heart rot agents seem to facilitate the development of decay communities supporting rare and red-listed successor species. The results are discussed in a conservation context. It is concluded that forests managed for timber production may support rich communities of wood-inhabiting fungi, if appropriate, but economically reasonable, measures are taken to increase dead wood levels. However, due to the highly skewed selection of dead wood habitat types present in managed forests (abundance of cut stumps and branches, scarcity of old-grown, natural dead trees) they are unable to protect all aspect of fungal diversity depending on dead wood.

…

“And agarics and fungi, with mildew and mould,
Started like mist from the wet ground cold;
Pale, fleshy, as if the decaying dead
With a spirit of growth had been animated!

Their moss rotted off them, flake by flake,
Till the thick stalk stuck like a murderer’s stake,
Where rags of loose flesh yet tremble on high,
Inspecting the winds that wader by”

…

(From “The Sensitive Plant”, P.B. Shelley 1792-1822)

“A tree (or woodland) without fungi is like a stage
without actors. For, throughout its life a tree generates
a mobile wooden framework upon and within which
literally countless fungi enact diverse ecological roles.
Whereas some fungi bring resources to the tree others
degrade and recycle its products”

*(From “Pollard and veteran tree management” A.D.M. Rayner
1996 in “The Tree as a Functional Community” ed. H.J. Read.)*

Preface

Wood-inhabiting fungi constitute a highly diverse group of organisms forming fascinatingly complex communities. By their contributions to wood decay, nutrient recycling and redistribution they are of essential importance to forest ecosystems. They open up the wood resource for a multitude of other wood-dwelling organisms and interact with these in all sorts of mutualistic, predatory, parasitic and competitive interactions, and are hence of crucial importance to forest biodiversity.

Since the early ages of human civilization and settled agriculture, forest cover has diminished. In Europe forest decline started early, spreading its way from the Mediterranean cultures to Fennoscandia during the last 5000 years. This development, which has been closely linked with the development of modern society, has been detrimental to many forest dwelling organisms. No other single forest habitat type has, to my knowledge, declined to a greater extent than decaying wood. Accordingly, wood-inhabiting organisms are among the most severely threatened organisms in the present European landscape. In recent decades the interest in biodiversity and its conservation has increased substantially in Europe and other parts of the World. This has increased the demand for knowledge about biodiversity, its prerequisites and potentials.

The primary aim of the present thesis is to provide such knowledge for wood-inhabiting fungi, paying special attention to their habitat preferences at local and regional scales. As conservation of biodiversity is a somewhat controversial issue, not least with respect to the potentially harmful wood-inhabiting fungi, I have also been engaged with understanding biodiversity conservation in a more normative context. The practical studies reported in this thesis, have been driven by curiosity for understanding ecological processes in decaying wood. All the way though I have, however, attempted to relate my project designs and results to the practical world. It is my sincere hope that my work thereby will facilitate conservation of biodiversity in managed as well as unmanaged forests.

The thesis is based on six manuscripts, which are presented in a certain order. The first manuscript is about focal species in conservation biology and represents my attempt to provide a conceptual framework for understanding conservation initiatives focussed on certain species or species groups. The remaining manuscripts represent investigations of habitat requirements in wood-inhabiting fungi, beginning with the single wood piece in paper II and ending at the regional scale in paper VI.

Tak! /Acknowledgements!

This PhD thesis would not have been a reality without help and contributions from colleagues, friends, family and sponsors. First of all I wish to thank the Danish Research Academy, Spy-Nat-Force and the Danish Forest and Landscape Research Institute for sponsoring my project. Secondly, I wish to thank Morten Christensen for being a very encouraging, patient and inspiring colleague throughout my PhD time - Sometimes you were more enthusiastic about the project than I was! Thank you also for good company during fieldwork, in sun, sleet and snow, and for being very helpful whenever I really needed it. Thanks also to my supervisors Jens Emborg and Andreas Brunner. Even though you both know as little about mycology as I know about forestry, I have enjoyed your company at PhD-meetings, seminars and not least at the Spy-Nat-Force excursions. Jens, I have appreciated your inspiring pep talks and your absolute confidence in me, and Andreas, I have really benefited from your scepticism and irony. You have convinced me that Germans can have humour! Thanks also to Erik Aude, Katrine Hahn and Rasmus Ejrnæs for being very nice colleagues in the field, at the office or by telephone and email. I am thankful for your inspiring views on ecology and biodiversity. Thanks to all other partners in Spy-Nat-Force. I think we have been a great team, even though my project is clearly marginal. I really have enjoyed our joint natural forest excursions and our inspiring meetings at Munkedamshuset. Thanks also to other colleagues at KVL and FSL, especially Niels Strange for opening up my eyes to economic optimisation, and to fellow Danish mycologists, especially Steen Elborne, Tobias Frøslev, Henning Knudsen, Thomas Læssøe, Christian Lange, Jens H. Petersen, Erik Rald, Søren Rosendahl and Jan Vesterholt for many good hours spent with fungi. In addition, I am very thankful to Nils Hallenberg, Seppo Huhtinen, Neven Matocec, Leif Örstadius and Ain Raitviir for generously helping me with the determination of various critical fungal specimens, and to Mikako Sasa and *Novozymes* for providing materials, equipment and expertise of crucial importance to the project. I am also greatly indebted to Thomas Læssøe for generously commenting on my thesis in its final draft version, and to Richard Bradshaw for correcting the English in the preface and acknowledgements.

A very big and very special “thank you!” to Lynne Boddy for opening up your lab at the Cardiff School of Biosciences for my anarchistic experiments, and for being extremely helpful with all kinds of mycological, linguistic and biological questions throughout my project. Your help has been essential to me! Thanks also to all PhD students and Post-Docs in Lynne’s lab for making me feel welcome in Cardiff. But special thanks to Paul Wald for the funniest time I have ever spent in a laboratory, and for many deep discussions over a good pint. I still wonder what position I would have preferred to hold in a hunter-gatherer community.

Tak til min kære viv Malene for din store tålmodighed med mig og mine svampe. Din opbakning har været mig til stor glæde. Tak til mine døtre Sofia og Silja, som ind imellem har savnet mit nærvær når svampene og de døde stammer tog overhånd. Tak til Lene, Ole, Gertrud og Olaf fordi I har troet på mig hele vejen igennem. Også en særlig tak til Claus, for i sin tid da jeg var en lille purk – men også siden – at have inspireret mig til at give mig i kast med naturforskningen.

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Thesis Wood-inhabiting Fungi in Danish Deciduous Forests - Diversity, Habitat Preferences and Conservation

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I. Heilmann-Clausen, J. Focal species for conservation – an annotated check list. *Manuscript under revision.*

II. Heilmann-Clausen, J. and Boddy, L. Inhibition and stimulation effects in communities of wood decay fungi: exudates from colonized wood influence growth by other species. *Submitted manuscript.*

III. Heilmann-Clausen, J. and Christensen, M. 2003. Fungal diversity on decaying beech logs – implications for sustainable forestry. *Biodiversity and Conservation* **12:** 953-973.

IV. Heilmann-Clausen, J., Aude, E. and Christensen, M. Cryptogam communities on decaying deciduous wood – does tree species diversity matter? *Submitted manuscript.*

V. Heilmann-Clausen, J. and Christensen, M. Does size matter? – Tree part and size preferences of red-listed fungi in Danish beech forests. *Submitted manuscript.*

VI. Heilmann-Clausen, J. and Christensen, M. Diversity patterns and community structure of wood-inhabiting macrofungi on beech in the Danish landscape. *Manuscript.*

Wood-inhabiting Fungi in Danish Deciduous Forests

- Diversity, Habitat Preferences and Conservation

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Wood-inhabiting Fungi in Danish Deciduous Forests

- Diversity, Habitat Preferences and Conservation

1. Introduction

Successful conservation of biodiversity in a managed landscape requires a throughout understanding of the habitat requirements of the species in focus. Some species, e.g. big mammals, may be able to survive even in highly managed forest landscapes if these are big, sparsely populated with humans, and rich in prey. Saproxylic mites, on the contrary, may require small, but strictly unmanaged plots to survive.

In Europe the habitat requirements of wood-inhabiting fungi have been studied rather intensively in boreal forests (e.g. Eriksson 1958; Strid 1975; Mathiassen 1993; Kauserud 1995; Niemelä et al. 1995; Renvall 1995; Pentillä & Kotiranta 1996; Høiland & Bendiksen 1997; Lindblad 1998; Kruys et al. 1999; Nordén et al. 1999; Sippola & Renvall 1999; Martikainen et al. 2000; Berglund & Jonsson 2001; Miettinen 2001; Stokland 2001; Snäll & Jonsson 2001).

In nemoral Europe comparable studies are few. Alan D.M. Rayner, Lynne Boddy and co-workers have provided a throughout investigation of competitive and ecological processes influencing fungal community development in decaying deciduous wood, as reviewed by Rayner & Boddy (1988), Boddy (1993, 2000, 2001). While these studies provides a very good fundament for understanding ecological processes in decaying wood, they give few data on habitat requirements of wood inhabiting fungi relevant in a conservation perspective.

In Germany a number of studies have focussed on fungal succession on cut stumps of deciduous trees (e.g. Kreisel 1961; Runge 1975, 1990; Andersson 1995, 1997), while Kreisel (2000) presents an investigation of wood inhabiting fungi on road-side trees. Several other studies from Central Europe have a highly fungistic (i.e. mycofloristic) approach (e.g. Grosse-Brauckmann 1999; Nuss 1999; Mayrhofer & Peitner 2001) and few studies provide more detailed information on habitat preferences of wood inhabiting fungi on naturally created dead wood fractions. Lange (1992) studied the succession of macrofungi on decaying beech logs in a Danish forest reserve, a subject which I have also had the change to study prior to the current project (Heilmann-Clausen 2001). More recently a similar study have been published from Belgium (Walleyn & Vanderkerkhove 2002). In the Netherlands Keizer & Arnolds (1990) studied host preferences of wood inhabiting aphyllophorales, while Nordén & Paltto (2001) investigated wood-inhabiting fungi of hazel woods in Southeastern Sweden, paying attention to the importance of stand age and other dead wood features. Finally, Berg et al. (2002) provides a rather general description of habitat features influencing the presence of red-listed fungi, including wood-inhabiting species, in woodland key habitats in Southern Sweden.

In summary, it can be stated that the total knowledge of habitat preferences of wood-inhabiting fungi in the European deciduous forest zone is still rather fragmentary and partly anecdotal, and that the current knowledge stage barely allow the initiation of meaningful conservation initiatives, apart from the very obvious demand for more dead wood. The main aim of the present thesis is to increase the knowledge in this respect. As conservation of biodiversity does not occur in a vacuum I have found it relevant also to discuss the overall relevance of conserving wood-inhabiting fungi.

The thesis is divided in two main parts. The first part is devoted to a general discussion on wood-inhabiting fungi as focal species in conservation, considering four different normative conservation baselines defined in paper I. The second part presents a synthesis of the main findings of the remaining papers, paying special attention to the conservation of wood-inhabiting fungi in managed forests and reserves.

1.1. Methodological aspects

The original project outline of the current project had a strong focus on basic science, especially interaction studies, but included also an ambitious plan of investigating the connection between sporocarps production of wood-inhabiting fungi on the wood surface and the distribution of mycelial individuals within wood. During the project time this focus shifted gradually towards studies with a more applied scope, under inspiration of my physical placement in a highly cross-disciplinary environment at KVL, broadly focussed on ecosystem management. As a result I completely omitted the use of molecular methods, and all field studies are based on sporocarp inventories. In order to increase reliability all sample trees were thoroughly inventoried for fungal sporocarps on three separate occasions.

This methodology may seem old-fashioned in a booming time for molecular techniques, especially since it has been suggested that the presence of sporocarps gives an unreliable impression of actual frequencies of mycelia in wood, as fungal mycelia may thrive in substrates for years without sporulation (e.g. Shigo 1967; Rayner & Boddy 1988; Vainio & Hantula 2000). This is probably in particular true for cord formers and other non-unit restricted fungi and for heart rot formers end endo-

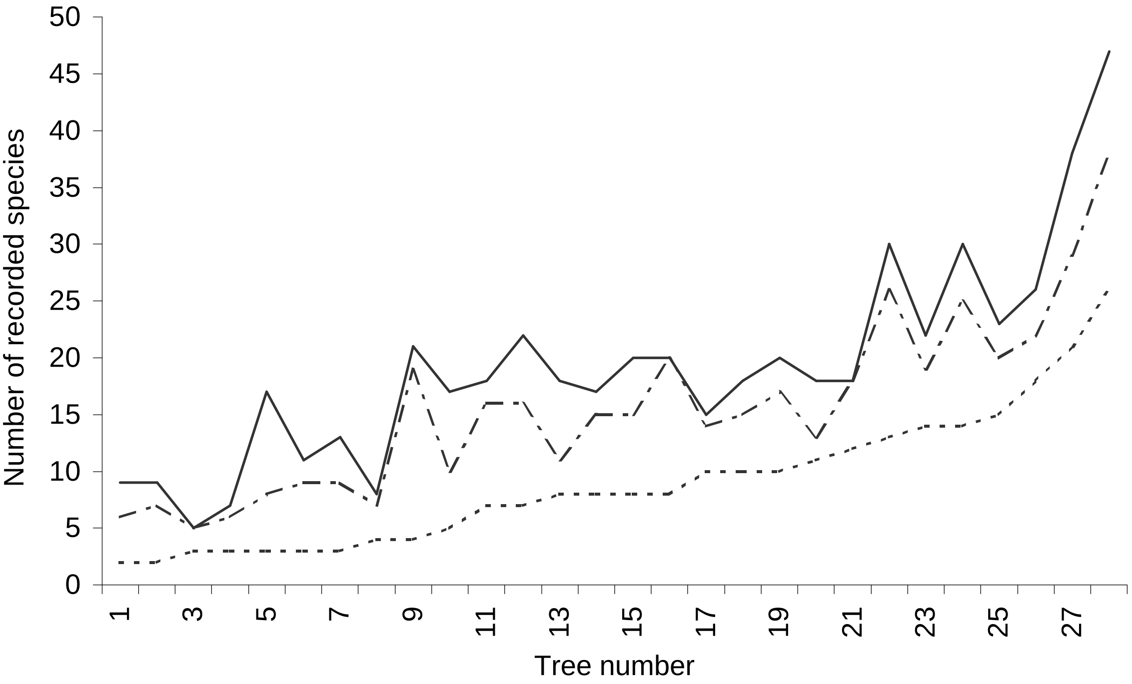

Fig. 1. The relation between number of sampling occasions and the cumulative number of fungal species recorded on 30 decaying trees in Draved Skov (Paper IV). The full line show recorded species numbers after three sampling occasions, while the dotted lines show species numbers after one and two sampling occasions, respectively. The trees are sorted according to the recorded species richness at the first sampling occasion.

phytes infecting living trees and persisting vegetatively in these for decades (see subsection 2.1.2.). It is possible that actual frequencies of many such species are greatly underestimated, and species considered to be very rare and restricted to old growth stands may in fact appear to be widely distributed even in managed forests. At present there are, however, very sparse data to support that this should be the case. Few attempts have been made to compare the presence of mycelia within wood with the presence of sporocarps at the wood surface. Johannesson & Stenlid (1999) and Gustafsson et al. (2002) found higher species numbers of wood-inhabiting fungi using molecular methods, compared to the results from sporocarps inventories. In both cases sporocarps were only inventoried once, and at least some of the molecularly defined species were microfungi, which makes it difficult directly to compare the relevance of the different methodologies. As shown in Fig. 1 one occasion of sporocarps inventory is clearly inappropriate in order to achieve a realistic impression of the fungal species richness on decaying wood, and though microfungi are interesting from an ecological point of view, they must, at the present knowledge stage, be considered rather irrelevant in a conservation perspective. From a more theoretical point of view it should be emphasized that wood-inhabiting fungi in general, and red-listed polypores and agarics in particular, as far as we know, depend solely on the production of sporocarps for dispersal (Heilmann-Clausen 2001). A decrease in sporocarp production is accordingly correlated with a decrease in dispersal ability, and the presence of sporocarps is thus a highly relevant measure for such species in a conservation perspective.

Molecular methods has increased our knowledge considerable on the ecology of wood-inhabiting fungi, especially in relation to population structures and infection strategies, and I do not doubt that as molecular methodologies are refined their potential for practical applications will increase. For studies on habitat preferences I do, however, still find sporocarp inventories most suitable, since they offer a non-destructive and highly extensive sampling methodology. In the present project I and co-workers sampled almost 400 decaying trees and made more than 6000 individual species records representing more than 500 identified macrofungal species. I am convinced that this would have been impossible using molecular methods.

2. Wood-inhabiting fungi, biodiversity and conservation

Conservation biology represents an applied and extended branch of ecology, which is engaged with the conservation and management of biodiversity. Biodiversity is a highly complex issue, relevant on all hierarchical levels in the biological world, from the individual genome to the entire biosphere (Fig. 2), and of crucial importance also to society. It is broadly accepted that means to reduce this complexity are necessary in order to make conservation biology work in practice. Focus on particular species, or species groups, is a widely accepted way of achieving this complexity reduction. Paper I represents an attempt to review the role of focal species in conservation biology. I claim in the paper, that the reduction of complexity embodied in focal species tends to be tendentious, rather than objective, and that different focal species concepts express different, often implicit subsets of normative arguments for biodiversity conservation. The same is arguable often the case for broader approaches connected with conservation biology, e.g. concepts such as “ecosystem management”, “adaptive management” and “near-natural forestry”. The current

PhD is no exception, and I have found it adequate to introduce my thesis with a discussion of wood-inhabiting fungi as focal species in conservation biology. It is my hope that this will make the normative prepositions involved with my work evident. The chapter is divided in three sections. In the first the relevance of different conservation baselines are reviewed with respect to wood-inhabiting fungi. The second represents an attempt to describe the fate of wood-inhabiting fungi in the modern landscape, while the third section reviews some practical attempt to introduce wood-inhabiting fungi in conservation biology

2.1. Why conserve fungi?

Paper I suggests four different conservation "baselines" to prevail in conservation biology emphasising biodiversity, biological integrity and aesthetic qualities respectively. Of these the biodiversity baseline is the most trivial, simply aiming on maximizing the amount of biodiversity conserved. It is motivated by the ethic equality argument that

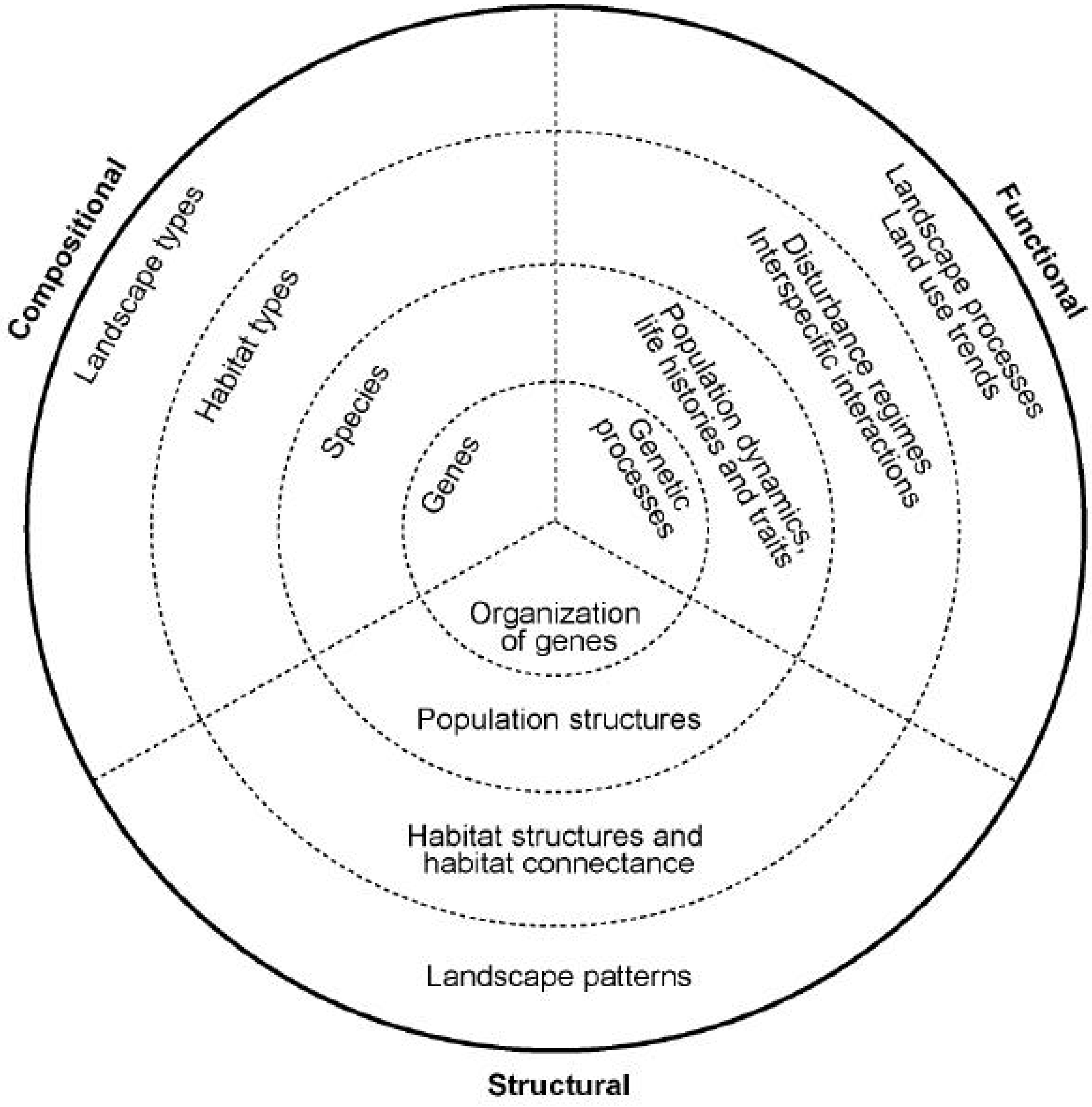

Fig. 2.Slicing the biodiversity pie. The division lines are dashed to emphasize that the different levels are interconnected. Adapted and modified from Noss (1990)

all species have equal rights to exist, but is also linked with instrumental usability arguments, pointing to biodiversity as a potential source for new crops, genes, drugs, enzymes etc. useful to humans. The biological integrity baseline focuses on the context in which biodiversity exists, i.e. the composition of biotic communities in an ecological, temporal and spatial context. It is motivated by the ethic ecocentric argument that natural or wild ecosystems, devoid of human influence have intrinsic value, and points to such ecosystems as potential inspiration sources for the development of sustainable management practices, working with rather than against nature. The ecosystem health baseline is based on the metaphor of ecosystem health, which implies the occurrence of stability and sustainability in ecosystem processes and functions interesting for humans, i.e. primary production, decomposition etc., irrespective of actual species composition. It is motivated by the ethic homocentric consideration that humans are the natural center in the world and that biodiversity is only relevant to the extend that it sustains human life on earth. Finally, the aesthetic baseline expresses the humanistic ethic consideration that nature has intrinsic value, but primarily by its radiation of human values, not least beauty.

In paper I the conservation baselines are discussed in a general ecological and normative context. The aims of the present section is to discuss the relevance of the suggested conservation baselines in a specific context, namely in relation to the conservation of wood-inhabiting fungi.

2.1.1. The magnitude of fungal biodiversity

If the biodiversity baseline for conservation is followed, species richness is of central importance. The magnitude of fungal biodiversity has been debated, but the estimate of 1.5 million species provided by Hawksworth (1991; 2001) is broadly accepted as realistic, though both higher and lower estimates have been put forward (e.g. Huhndorf & Lodge 1997; Fröhlich & Hyde 1999; Arnold et al. 2001). In every case, it is well supported that fungal species numbers by far outnumbers global estimates for diversity within the kingdom *Plantae*, while the kingdom *Animalia* is more species rich. The fraction of fungal species richness depending on decaying wood is not known with certainty. Siitonen (2001) estimated 1500 macrofungal species (excluding lichens) to depend on dead wood in Finland and comparable estimates has been given for Denmark (Heilmann-Clausen & Christensen 2001a; Rald 2001). The total number of macrofungi occurring in Denmark is in the vicinity of 5000 species (Møller 1997), so it can be estimated that about one fourth of these depend on dead wood habitats. Accordingly, it can be stated that wood-inhabiting fungi contributes considerably to the overall species diversity of forests, but also that dead wood is a highly important substrate to fungal diversity.

In the present project more than 500 macrofungi were recorded, and even single trees were found to support high species diversity. On several trees sporocarps of more than 40 species were recorded, with a maximum of 76 species recorded on a single decaying beech tree (paper III). Agarics appear to be the most species rich morphological group on deciduous wood in Danish forests, but also corticoid basidiomycetes are highly diverse (Fig. 3). Lower, but still significant species numbers are found among polypores, discomycetes and stromatic pyrenomycetes. The latter group include several highly frequent species with very persistent sporocarps, including *Eutypa spinosa, Kretzschmaria deusta* and *Xylaria hypoxylon* which appear to be among the dominant species on decaying beech trees in semi-natural forests in Denmark (Fig. 4).

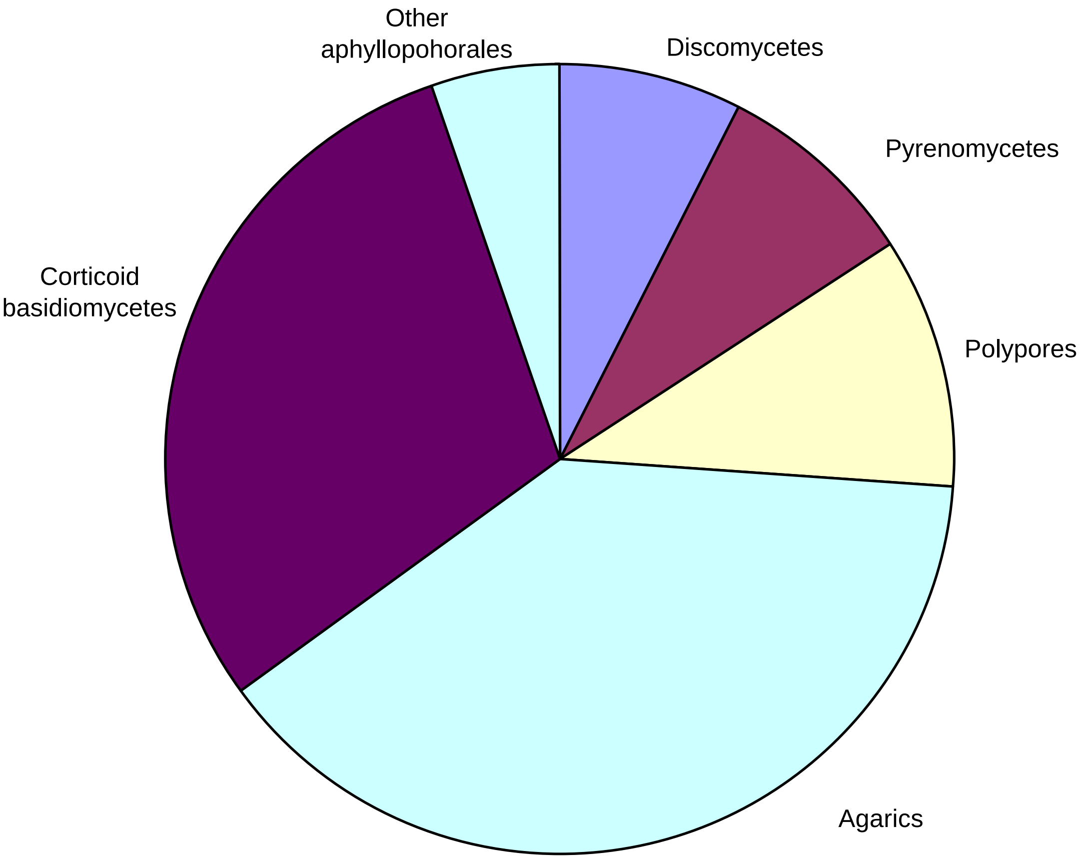

Fig. 3. Distribution on morphological groups of the 277 macrofungal species recorded in paper III. Heterobasidiomycetes with resupinate sporocarps are included in the corticoid basidiomycetes.

The importance of dead wood for microfungal diversity is less understood, but microfungi are ubiquitous in dead wood. In a study from Canada, Lumley et al. (2000) isolated a high number of poorly known and very rarely identified microfungi: Of 49 identified species seven were new to North America. Sporocarp based studies of wood-inhabiting pyrenomycetes (of which many can be classified as microfungi, due to very small sporocarps) show the same tendencies. In a study from Puerto Rico, Huhndorf & Lodge (1997) identified 157 different distinct species in just 396 collections, but only 47 mainly stromatic species could be assigned to a previously described species. Even in temperate Europe non-stromatic wood-inhabiting pyrenomycetes are poorly known, though it is recognized that the group is highly diverse. In a study from the forest reserve Suserup Skov, one of the main localities of the present thesis, Madsen & Johansen (1994) recorded 68 pyrenomycete species on 42 decaying beech trees, of which 24 non-stromatic species did not fit with any well-known species, described in the available literature. Theses results show that microfungal communities of dead wood are highly undersampled, and indicate that microfungi may constitute an important part of the fungal diversity in decaying wood.

The biodiversity baseline is based on both ethical considerations (all species have the right to exist), and usability arguments, claiming biodiversity to be an important and potentially life saving

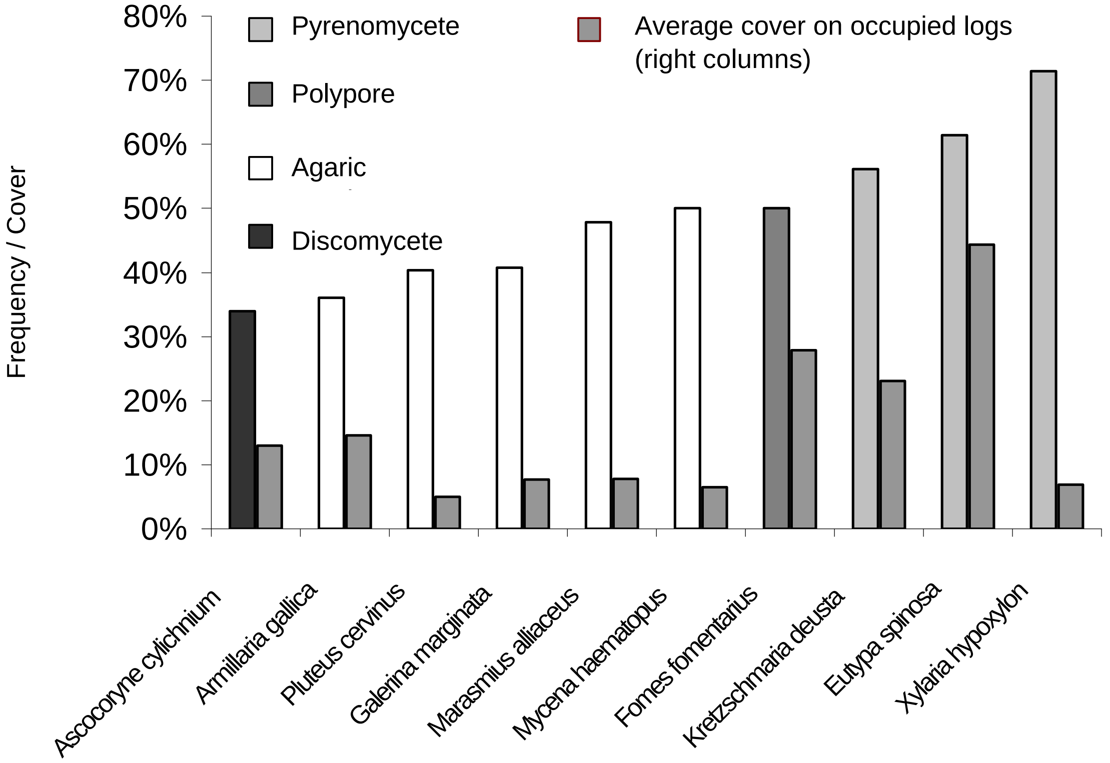

Fig.4. The frequency of the ten most common species on 281 decaying beech trees studied in study VI. Average cover percentages derive from a smaller sample of trees (n=71) on which the sporocarps were mapped in a 50 x 50 cm grit along the basal 5 metres of the log.

resource providing new drugs and other biotechnical products. Wood-inhabiting fungi are increasingly focused on in the latter respect. They have appeared to be a very good source for useful enzymes, and, inspired by traditional Chinese medicine, research on “medicinal mushrooms,” of which the majority investigated so far are wood-inhabiting, has increased immensely. Even a new scientific journal, “International Journal of Medicinal Mushrooms” has seen the day of light. Despite these developments, I find that usability arguments should be used with caution with respect to conservation of wood-inhabiting fungi in nature. First of all the immense biodiversity in this group makes it an impossible task to screen all species and their embedded genetic variation for useful resources, and there are few arguments that rare and declining species should be more relevant sources for useful substances, compared to more common species that will persist, even if no conservation efforts are undertaken. Secondly, if rare species nevertheless appear to provide special potentials, it would probably be much cheaper to conserve a selection of natural strains of declining species under laboratory conditions, rather than preserving their natural habitats.

2.1.2. Ecosystem health and functional diversity

Following the ecosystem health baseline wood-inhabiting fungi are interesting due to their contribution to ecosystem functioning. From this point of view wood-inhabiting fungi play two very different key roles in forest ecosystems. They have a “negative” role as pathogens, and a “positive” role due to their key functions for wood decay and nutrient recycling.

The potential of pathogenesis is mainly found within two ecological fungal groups, which I will here grossly define as heart rot agents and latent invaders, respectively. Heart rot agents have the ability to establish themselves in living trees, through wounds, via root connections linking to attacked trees and stumps, or in some species due to active pathogenesis. After establishment, heart rot agents have the ability to cause extensive decay in the standing tree. In some fungal/tree species combinations only the true heartwood is decayed, but many heart rot agents have the potential of penetrating from the dead heartwood into the living sapwood, which is killed and decayed. Some tree species, e.g. beech, have no true heartwood but posses a lower number of living cells in the inner part of the trunk, and it may seem inappropriate to talk about heart rot agents in such cases. Nevertheless, I prefer to keep the term also in such cases for fungi causing decay primarily from the core of the tree and outwards. Depending on the main position of infection heart rot agents can be classified as causing root rot, butt rot or top rot (Rayner & Boddy 1988). Especially the two first mentioned groups includes several economic important pathogens, e.g. *Heterobasidion annosum* and *Armillaria* spp., but in Danish beech stands the most important pathogen appear to be the top rot agent *Fomes fomentarius.* Most heart rot agents are basidiomycetes, and especially species forming sporocarps of the polypore type are well represented.

Latent invaders are fungi with a capacity for establishment in vital sapwood. Some appear to have a truly endophytic life stage, meaning that they are actively growing in functional sapwood (Carroll 1994). However, many wood-inhabiting species seem to be present in living cells in a dormant stage, as latent propagules, which are activated if the water contents of occupied cells decreases, e.g. due to tree death or drought stress (Boddy 2001). The ecological significance of latent invaders has been much discussed. Endophytes present in leaves have been suggested to act as an extended defence mechanism towards herbivores and pathogenic fungi, but it is somewhat uncertain whether any wood-inhabiting endophytes maintain such functions (Carrol 1994). Pathogenesis is described for several fungi, which following my broad definition can be classified as latent invaders. The Dutch elm decease, caused by *Ophisotoma ulmi* and close relatives, can be seen as an example involving strong pathogenic abilities. Less aggressive examples are canker-forming species such as *Biscogniaxia nummularia* and *Eutypa spinosa*, which mainly develop in severely drought stressed beech trees, implying that pathogenic abilities are weak (Hendry et al. 1998). The latent presence of such species may primarily represent a strategy of resource capture, an attempt to be a step ahead in establishing extensive mycelia following tree death. Most known latent invaders are ascomycetes, including macromycete genera such as *Ascocoryne, Eutypa, Daldinia, Diatrype* and *Hypoxylon*, but also some basidiomycete examples, e.g. *Vuilleminia comedens* and *Stereum gausapatum* have been described (Boddy 2001).

Heart rot agents and many latent invaders are able to decay dead wood, and may survive in occupied wood many years after tree death. They thus function both as pathogens and as actors in the process of nutrient recycling, and can jointly be classified as primary decay agents. Many other wood-inhabiting fungi are only or mostly able to establish in dead wood, subsequent to primary decay agents, or in dead wood domains where such species has not been able to establish viable mycelia. In the latter case ruderal, opportunistic species may establish and cause primary decay, but in most cases fungi encountering dead wood need to replace already established latent invaders or heart rot agents, and can thus be classified as secondary decay agents. Secondary decay agents may arrive as spores or as mycelia. Species relying primarily on the spore dispersal has be denoted as unit restricted, while species adapted to vegetative, mycelial spread has be classified as non-unit restricted (Rayner & Boddy 1988). Attached dead branches, support highly specialised communities of spore dispersed secondary decay agents, mainly corticoid basidiomycetes (e.g. Griffith & Boddy 1990; Boddy 2001), which may cause extensive decay before branches finally break off.

On the forest floor spore dispersed secondary decay agents are challenged by non-unit restricted species able to spread via vegetative growth in soil and litter. A number of basidiomycetes form mycelial cords and are well adapted to a foraging strategy, searching the forest floor for available wood resources. Studies have shown that such cord forming species are abundant at least in temperate deciduous forests and it is probable that they play an important role in nutrient redistribution in the forest floor (Boddy 1993). Another important group of non-unit restricted fungi in dead wood are ectomycorrhizal fungi, which recent studies have proven to be an integrate part of the biota in extensively decayed wood (Tedersoo et al. 2003). The function of ectomycorrhizal fungi in dead wood is not known with certainty. Some species may have enzymatic capacities allowing them to take direct part in the degradation of dead wood remnants, while other species has been shown to be able to acquire nutrients from the mycelia of saprotrophic fungi (Lindahl et al. 1999: Leake et al. 2001). In every case the widespread presence of ectomycorrhizal fungi in decayed wood closes the ring of nutrient recycling and show that living trees may obtain nutrients almost directly from the dead wood of their ancestors.

The above, highly generalized review of ecological strategies among wood-inhabiting fungi provides a basal framework for understanding fungal community development in decaying wood. However, several strategies are not considered, e.g. mycoparasitic fungi, nematode trapping fungi and fungi feeding on bacteria, which appear to occur abundantly in decaying wood (e.g. Barron 1988; Pfister 1997; Boddy 2000). If also the remarkable species numbers of wood-inhabiting fungi are considered (see the previous subsection) it is clear that wood decay is a highly complex process. The good question following a functionalistic, ecosystem health approach for conservation, is now whether all these species and strategies are necessary – Or in other words; does high fungal diversity imply a more efficient process of decay and a more sustainable recycling of nutrients from dead wood and back into living plant tissues? I don't know of studies trying to answer this question, but my best guess is that a relatively low number of wood-inhabiting fungi, supplemented by a few selected bacteria, arthropod and annelida species would suffice for a very efficient nutrient cycling. In order to retain stability in a fluctuating environment, the number of species should probably be increased, but I feel convinced that the very high saproxylic diversity recorded in this and other projects are not required for the retaining of ecosystem health. Accordingly, I find ecosystem health arguments invalid in relation to conservation initiatives aimed on protecting endangered wood associated biota. And, oppositely, I feel convinced that well-planned conservation initiatives aimed on protecting wood inhabiting fungi are no serious treat to ecosystem health in nemoral deciduous forests. Even if the amounts of probagules of heart rot agents and other potential pathogens may rise following such initiatives, productive trees are normally highly resistant to attacks from such species. It is even possible that a more natural balance in the species composition of wood inhabiting fungi may decrease the importance of the currently most important pathogens, e.g. *Heterobasidium annosum* s.lato. which seem to have increased due to forestry activities in several parts of Europe.

2.1.3. Biological integrity

Within the concept of biological integrity organisms are valuated according to their ability to point to ecosystem integrity, which implies the presence of a species composition, diversity, and functional organization comparable to that of natural habitats within the actual region. Following the biological integrity baseline such ecosystems are perceived to have intrinsic value, but are also seen as systems of potential inspirational value for the development of sustainable management practices. This is based on the idea that ecosystems developed through hundred of millions of years are more "wise" than the much younger conscious human brain.

Following this way of thinking wood-inhabiting fungi are highly relevant focal species for conservation. They depend on a substrate that has decreased immensely in many parts of the world. At least in a European context I can recall no other forest habitat type, supportive of species rich communities, which have decreased more in abundance since human cultivation increased. At the same time, fungi are the principal agents of wood decay, and thereby they are of crucial importance for all other saproxylic organisms, e.g. insects and micro-arthropods. Interspecific relations between wood-inhabiting fungi and insects are well documented. Several papers have shown that different polypore species support different insect communities, both in occupied wood (Kaila et al. 1994) and decaying sporocarps (Økland 1995; Jonsell et al. 1999; Komonen 2001), and it has been documented that host recognition in some cases is mediated by specific fungal volatiles (e.g. Fäldt et al. 1999; Guevara et al. 2000; Belmain et al 2002). Also for bats and woodpeckers, the activity of specific decay fungi has proven to be of critical importance (Huss et al. 2002; Parsons et al. 2003). Due to this multitude of species-specific interactions involving fungal species it is evident that even small changes in fungal community structure in decaying wood are likely to influence the overall composition of saproxylic communities.

2.1.4. Public relations

Following the aesthetical baseline, conservation value is determined by the ability of an organism to express "human" values, e.g. devotion, beauty, cooperation, intelligence, strength and joy. Clearly these requirements disqualify wood-inhabiting fungi as relevant focal species for many people in the western world, which traditionally tend to perceive fungi as representative of darkness, decay and death. This perception is not static, however, and if ecological insight increase in society, fungi are more likely to be positively appreciated. The Rio summit in 1992 have generally increased the awareness of the natural heritage, even in heavily cultivated regions, and higher levels of education may enhance the understanding of natural systems. Recycling of waste has become acknowledged as a crucial necessity for a sustainable future. Gathering of fungi for eating has increased in Western Europe in the last century, and cultivation of edible fungi, including wood-inhabiting species such as the Oyster cap *(Pleurotus ostreatus)* and Shii Take *(Lentinula edodes)*, has boomed. Finally, wood-inhabiting fungi are increasingly utilised in the biotechnical sciences as important sources for useful enzymes and drugs.

All these recent developments are likely to benefit the public relations of fungi, and wood-inhabiting fungi certainly have the potential to radiate “human” values. They perfectly illustrate the principles of recycling, and their many mutualistic and parasitic interactions with other organisms makes them highly nontrivial for everybody interested in interactions, also outside the strictly biological world. If these aspects are adequately communicated in society there is little doubt that the general perception of fungi will change. At least it is my hope that the beauty and morphological complexity expressed in wood fungal sporocarps in the future will be appreciated as beautiful, pointing to recycling and cooperation rather than just decadence and death.

2.1.5. Summary - baseline of the current project

In conclusion I find that there are no “hard” arguments for conserving wood-inhabiting fungi. I am convinced that ecosystem health can be maintained without the currently declining wood inhabiting fungi, and doubt that the retaining of such species in natural populations are a prerequisite for saving humanity through the discovery of new drugs or enzymes. Further, I think that most people will enjoy their forest walks equally well even if substantial changes occur in fungal community structure. It is possible that a few will regret the loss of beautiful *Hericium* species, but more visitors will probably be provoked if dead wood amounts are increased along their favourite forest strolls. Accordingly, conservation of wood-inhabiting fungi only makes sense, if we with the words of Simberloff (1999) are “committed to the value of biodiversity in its own right, and not as a means to some other function”. Appreciation of the potential use-value and functional importance of wood-inhabiting fungi should only provide supplementary arguments.

This ascertainment leaves the biodiversity and biological integrity baselines as valid fundaments for conservation initiatives. As most wood-inhabiting fungi have rather narrow habitat requirements, the easiest way of increasing wood fungal biodiversity is to increase the diversity of dead wood habitat types. Host selectivity is widespread among wood-inhabiting fungi, and there is no doubt that the introduction of exotic tree species in Danish gardens and forests has increased the overall species richness of wood-inhabiting fungi considerably. In fact I will guess that this increase equals or even exceeds the loss of species due to deforestation and forest management during the last 3000 years. Therefore it could be argued that wood fungal diversity is doing well in Danish forests, which could lead to the suggestion that we should introduce even more exotic tree species to increase biodiversity. On a broader geographical scale these arguments are clearly not valid. Fungal species introduced with introduced tree species are likely to be common in the natural home range of the host tree, and their spread to new regions is unlikely to be important for their survival as species in a global perspective. On the other hand, they may potentially replace existing populations of fungal species with a long local history in the area of introduction. This is especially the case if introduced host tree species are used extensively and to the detriment of native host trees (see subsection 2.2.3).

Accordingly, I find that big care should be taken when applying the biodiversity baseline in a conservation perspective, and it is no secret that I personally support the biological integrity baseline for conservation. This is in particular true with respect to the conservation of biodiversity in reserves. Biodiversity reserves should to my opinion help to protect the overall diversity of life. In an increasingly cultivated world, natural and “wild” ecosystems represent the extreme contrast to all cultural influence. Introduction of new species or other human activities may increase the biodiversity of such systems, but this will invariably make these systems more similar to other ecosystems, and hence decrease diversity on the wider scale. There may be many other arguments than biodiversity conservation involved with reserve selection, such as preservation of ground water resources, cultural landscapes, important genetic resources or simply curiosity – *let's see what happens to this system if we relinquish the bridles.* This is fair, but I find it unfair to state that such reserves necessarily benefits the attempts to protect biodiversity.

In managed forest biological integrity should to my opinion be incorporated to a wider extend than at present. Again, introduced species may “dilute” native biodiversity although overall species richness is not affected, and such effects may even influence community structure in unmanaged reserves, because of the good dispersal abilities of many forest organisms, e.g. fungi. These aspects are considered in more detail in the next section. Of course managed forests should also, and importantly, satisfy the legible arguments involved in the ecosystem health baseline, e.g. an economic sustainable timber production, and provide beauty, experiences and stress release for forest visitors. However, if the choice is between two equally productive and valuable tree species, very good arguments should be provided if the exotic tree species are preferred to the detriment of its native equivalent.

2.2. Fungi and landscape integrity

In the present section I will attempt to describe the fate of wood-inhabiting fungi in the modern European landscape, in a context of biological integrity. As an introduction some basal aspects of the life cycle of wood-inhabiting fungi, critical for understanding these as actors in forests and landscapes, are presented.

Decaying wood is a temporal habitat and wood-inhabiting fungi accordingly need to be able to disperse themselves or their offspring between individual dead wood habitat units. This process can be broken down in three key phases, a) dispersal from the old disappearing wood habitat patch, b) establishment in a new suitable habitat patch, and c) competition and resource acquisition in the new resource patch allowing the production of new dispersal units. Each phase involves bottlenecks, of which several are poorly understood.

Interspecific interaction involving wood-inhabiting fungi has been studied intensively, especially since the 1980'ies (for reviews see Rayner & Boddy 1988, Boddy 2000), and the basic competitive principles structuring fungal community structure in wood are rather well understood, at least with respect to early decay phases. Similarly, dispersal ecology and population structures have been the subject of several recent research projects (e.g. Kirby et al. 1990; Worral 1994; Högberg et al. 1995; Vasiliauskas et al. 1998; Høgberg & Stenlid 1999; Nordén 2000; Edman & Jonsson 2001; Hallenberg & Küffer 2001; Johannesson et al. 2001; Gustafsson 2002; Kauserud & Schumacher 2002, 2003), of which several have focussed on threatened species. These studies provide a basal framework for understanding fungal dispersal at forest as well as landscape scale, though some aspects e.g. the overall importance of arthropod vectors is still poorly understood.

The real black box, which remains to be opened concerns the establishment process, from the arrival of a viable fungal spore at a dead wood habitat to the establishment of a competitive mycelium. This process involves several important steps, including breaking of spore dormancy, germination, establishment of a primary mycelium, and at least in most basidiomycetes, diploidisation following the arrival of a new spore of an appropriate compatible mating type. Some of these steps are individually well studied, but for most wood-inhabiting fungi little or nothing is known on the conditions necessary for the establishment of a primary, competitive mycelium. Most wood-inhabiting fungi, including very rare species, produce spores that germinate willingly on agar under laboratory conditions, and some, e.g. *Hericium* spp. may even produce sporocarps on agar in a Petri dish (pers. obs.). Edman et al. (2002) calculated, based on spore trapping experiments, that an average sized spruce log in northern Sweden receives not less than 500 spores of the near threatened polypore *Fomitopsis rosea* every 24 hours, yet the species occur with a rather low frequency on spruce logs in the area. The species has been shown to have good competitive abilities (Holmér & Stenlid 1997) and therefore the establishment phase seem to be the most critical phase for this species. Probably conditions allowing establishment occurs very rarely, compared to the overall amounts of dead wood present in the landscape. It is my clear impression that this phenomenon may be one of the main explanations for rarity and decline among wood-inhabiting fungi.

2.2.1. Habitat availability

The quantity of potential habitats for wood-inhabiting fungi has decreased immensely almost everywhere in Europe during the last centuries. In Denmark, for instance, the forest cover has declined from about 90% in prehistoric times to the present level of 13%. An absolute low was reached around 1800, where only about 4% of the land was forest covered (Fritzbøger 1994). The wast majority of contemporary forests have a long history of management, and in 1992 it was estimated that only about 8% of the Danish forest area (0.8% of the land area) descends directly from deciduous forests remaining around 1800, and only about 500 ha forest (0.01% of the land area) had a long, recorded history as non-intervention forests (Skov- og Naturstyrelsen 1994). Since then initiatives have been taken to increase naturalness in Danish forests. More than 5000 ha of forest have now been declared as strictly unmanaged reserves, and initiatives are undertaken, especially in the state forests, to apply near natural forestry methods, and to increase dead wood levels, wet areas etc. to the benefit of native biodiversity (Larsen et al. 2001). Nevertheless, it is obvious that saproxylic organisms have suffered from a marked decline since prehistoric times.

Based on general species-area relations, Sittonen (2001) calculated that the observed decrease in available coarse wood debris (cwd) habitats (90-98%) in Fennoscandia is likely to cause a species loss of at least 22-32% in the long run. A comparable estimate was given by Berglund & Jonsson (2001) based on extrapolations from actual field observations in a forest wetland mosaic in northern Sweden. The overall decline in cwd amounts in the landscapes of Central and Western Europe is not known with certainty, but does without doubt exceed the estimated 90-98% decline reported from Fennoscandia. The accomplishing species loss for saproxylic organisms is not known with any degree of certainty, but is most likely substantial, as reflected in many national European red-lists. (See subsection 2.3.1).

2.2.2. The fragmented landscape

The decrease in cwd amounts in the European landscape has not only lead to a decrease in the availability of suitable habitats for saproxylic organisms, but has also resulted in the fragmentation of suitable habitat patches. This is evident both at the local scale, where management in most forests has increased distances between individual wood units (especially for large diameter wood fractions) and at the regional scale, where remaining forests typically form more or less isolated patches in a matrix of farmland and urban areas. Even at the European scale fragmentation has occurred, and the most extensive forest areas, including the majority of cwd rich forest reserves, are restricted to mountainous, or otherwise cultivation hostile areas.

In this highly patchy landscape fungi can generally be defined as organisms with very good, but very imprecise dispersal abilities. Long-distance dispersal of wood-inhabiting fungi is generally mediated by tiny (c. 5-30 ?m in length) wind borne spores, which are produced in waste numbers. Although a major fraction of the liberated spores are settling within a very short distance from the sporocarp (e.g. Nordén & Larsson 2000), long distance dispersal (>300 km) of viable spores is possible and has been documented in many fungi, including wood-inhabiting species regarded as threatened (e.g. Hallenberg 1995; Nordén 2000; Küffer & Hallenberg 2000). This long distance dispersal is, however, highly haphazard, and wind-borne spores have no active means to locate and settle on adequate habitat patches, though variations in spore size and shape and the presence of protuberances may reflect adaptation to various establishment environments (Hallenberg & Parmasto 1998; Nordén et al. 1999; Nordén 2000).

In a few wood-inhabiting fungi, specific insect vectors are known to be an important means for dispersal at the regional scale (e.g. Rayner & Boddy 1988; Vasiliauaskas et al. 1998), and at the local scale, hyphal cords and small arthropods, e.g. mites and collembolans are additional dispersal agents (Rayner & Boddy 1988; Rolstad & Gjerde 2003). It has been suggested that arthropod vectors may be the most important means for dispersal in some species, e.g. *Ganoderma spp.*, which produce spores that apparently are adapted to passage through the gut of flies before germination (Tuno 1999).

Habitat fragmentation is likely to be most detrimental to species with poor adaptations to long distance dispersal, though effective vectors for local dispersal may counteract this tendency. At present there are few data to suggest that threatened species should be especially sensitive to fragmentation for this reason. On a more theoretical basis it has been suggested that poor dispersal ability is a predictable trait for species adapted to persistent and predictable habitat types with a random distribution pattern in the primeval landscape, while species depending on naturally patchy or temporally habitats can be assumed to have good dispersal abilities, and there is some evidence that this actually applies for saproxylic insects (e.g. Nilsson & Baranowski 1997). Thereby it can be speculated whether fungi depending on old living trees, presenting a very common and persistent habitat in primeval forests, are more likely to have poor ability for dispersal, compared to species living on decaying dead wood in the forest floor (a very common, but less persistent habitat), while species depending on highly patchy habitats, e.g. burned wood, can be predicted to have good abilities for long range dispersal.

2.2.3. The landscape of establishment

Apart from the decrease and fragmentation of cwd habitats a shift in general forest composition has occurred. In many parts of Europe, forestry has favoured conifers to the detriment of deciduous tree species. At the same time forest management has developed to be a more “clean” business focussed on the production of timber. In prehistoric forests trees of all sizes were present, including very old and partly damaged trees. Some traditional practices, especially forest grazing and pollarding allowed or even favoured such old trees due to their high mast or leaf production, but in modern production forests old or damaged trees are unwanted. For fungi adapted to colonization of living trees, e.g. heart-rot agents and latent invaders, the consequences of these landscape changes are a distinctly altered environment for establishment.

Most fungi able to colonize living trees are host selective, while strict host specificity is rare (e.g. Rayner & Boddy 1988; Ryvarden & Gilbertson 1993-1994). It as been shown that host extractives may facilitate spore germination and stimulate hyphal growth in associated heart rot agenst and latent invaders, but mostly in a non-specific manner (e.g. Hrib & Rypácek 1981; Chapela et al. 1991; Hendry et al. 1993; Boddy 2001). Thus, the wood of a specific tree species represents a selective environment for arriving fungal propagules. Many species are able to establish, but host selective specialists have a competitive advantage. The same principle is most likely applicable for different types of entrances for fungal propagules within the single tree, e.g. different wound types, characterized by different biochemical and microclimatic conditions, as well as for different cwd microhabitats on the forest floor.

Accordingly, an altered balance between tree species or a selective reduction in specific wound types, characteristic of old trees, changes the competitive balance of the establishment landscape. For declining establishment habitats the fraction of spores representing selective species are likely to decrease, to the benefit of generalist species and species selective for increasing habitat types. Thus, the decline of certain cwd microhabitats does not only lead to a decline in available habitat patches for selective species, but does, in addition, imply that non selective species are likely to arrive first or with such a majority of propagules, that the selective species are likely to be unsuccessful.

2.2.4. The competitive landscape

Different fungal species express widely different functional strategies. Some species show distinct ruderal traits and have low competitive ability but high growth and reproduction rates. Other species posses strong competitive abilities and are less dependent on a fast reproduction rate or may use vegetative dispersal by cords to reach new habitat patches. Finally species may be stress tolerant, meaning that they are adapted to slow growth and persistence in a stressful environment where interspecific competition is limited.

For vascular plants it has been shown that stress tolerant species are declining in landscapes characterized by intensive human use, while species with ruderal or competitive traits increase (Grime 2002). Among forest plants there is a similar trend so that a majority of "ancient forest species" are stress tolerant, while competitive strategies prevail among remaining forest plants with less strict habitat requirements (Hermy et al. 1999). In both cases the sensitivity of the stress tolerant species seems to relate to increasing nutrient inputs and more frequent disturbances, while habitat fragmentation is an additional factor influencing ancient forest species. It is interesting to ask whether the same factors affect wood-inhabiting fungi.

Little is known on the effects of increased nitrogen deposition on wood-inhabiting fungal communities, though high nitrogen availability is known to inhibit wood decay in some species (Rayner & Boddy 1988). Nevertheless, nitrogen is required by wood-inhabiting fungi, like in all other organisms, and it is reasonable to assume that species able to benefit from increased nitrogen levels have a competitive advantage with increased nitrogen deposition. As nitrogen amounts increases most in soil, humus and litter, while wood interiors are likely to retain relatively low nitrogen contents,

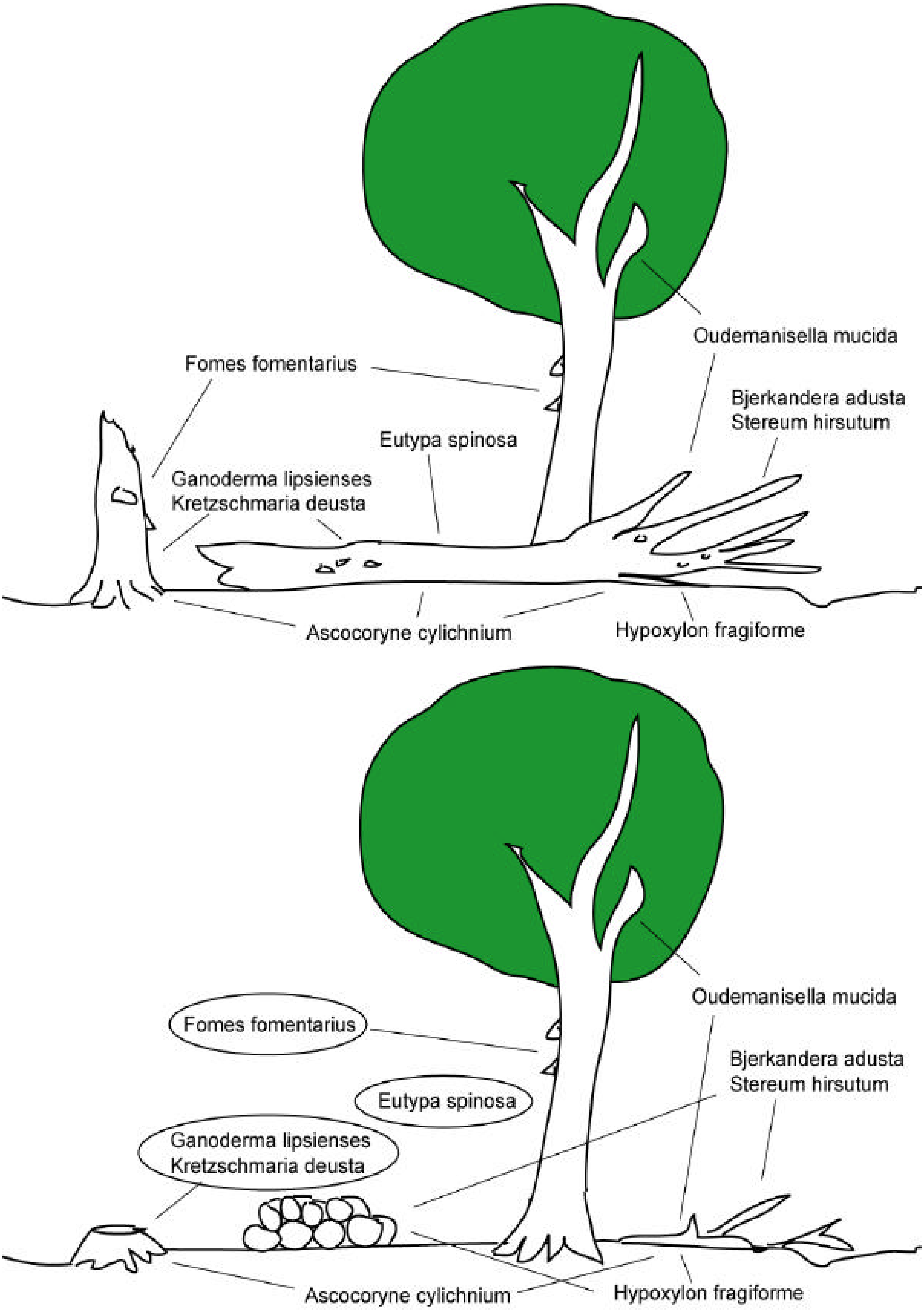

Fig. 5. Occurrence of common primary decay agents in the natural forest (top) and their supposed situation in a managed forest (bottom). While some species continue to have many niches in the managed forests, other species experience a habitat loss (encircled). Especially Eutypa spinosa have very difficult conditions for sporulation.

it can be speculated that species able to derive nitrogen from the soil and humus pool, e.g. competitive cordforming basidiomycetes are likely to increase under increased nitrogen deposition, to the detriment of unit restricted species, unable to derive nutrients from external sources.

For wood-inhabiting fungi forestry act as a disturbance agent in several ways. Clear-cutting, thinning and draining may cause a more stressful microclimatic regime in forest interiors, benefiting species adapted to survival in dry wood (Miettinen 2002). Another important effect relate to the way dead wood is created in managed forests, and to changes in the balance between different tree species, tree types and cwd fractions, as discussed in the previous subsection. In managed forests most cwd is created after cutting, e.g. as cut stumps or non-merchantable logging waste. Cut surfaces are more likely to represent "open" resources, uninfected by decay fungi, compared to cwd produced in unmanaged forests (cf. Boddy 2001). Trees (and branches etc.) may die for many natural reasons, but fungal attack is commonly involved. Even though splintered wood may expose uninfected open resources in unmanaged forests, the relative fractions of "closed" resources, i.e. fungi-infected heartwood and unbroken, bark-covered log and branch parts are much higher than in typical managed forests. Accordingly, managed forests can be assumed to favour ruderal and ruderal-competitive opportunistic species, to the detriment of stress tolerant heart rot agents and some latent invaders, specialized in infecting living trees. Latent invaders associated with twigs and smaller branches probably are unaffected, since this habitat type has decreased relatively little due to forestry.

2.2.5. Summary

In summary, the modern European landscape represents highly altered conditions for wood-inhabiting fungi. Habitat decline has affected population sizes in all species negatively, with the exception of species selective or specific for introduced host trees. Habitat fragmentation has been a supplementary negative factor, but especially species with poor abilities for long-range dispersal have, arguably, suffered. Most wood-inhabiting fungi has the potential for long range dispersal by wind borne spores, but even small differences between species in the relative efficiency of long range spore dispersal may have shifted the competitive balance between species. Finally, an altered balance between establishment habitats has changed the competitive balance to the disadvantage of species depending on specific, strongly declining habitat types, while species associated with less declining or increasing establishment habitats has gained a competitive advantage. In general terms, this, most probably, has been to the benefit of ruderal and ruderal-competitive species, while some groups of stress-tolerant species has declined. In more specific terms, specialised heart rot agents and successor species depending on their specific rot are likely to have suffered the most dramatic decline. The same may be the case for species selectively associated with hosts that has decreased strongly, e.g. *Tilia*. On the other hand species associated with twigs, small branches, cut stumps and logging waste, including abandoned stacks of firewood, has been less affected or have even increased (Fig. 5).

2.3. Practical applications of wood-inhabiting fungi as focal species in conservation biology

Compared to most other macroscopic organism groups fungi have received limited attention in the conservation literature (Fig. 6), which probably reflect their rather bad public relations (see subsection 2.1.4), and lack of knowledge among conservation biologists. Wood-inhabiting fungi are no exception, but in the last decade a number of papers focussing on these organisms and their role in conservation biology have appeared. With remarkable few exceptions, these papers derive from Fennoscandia and Eastern Europe, where the relationship between humans and fungi traditionally has been more positive than generally in the Western World. Most studies have been fungistic (i.e. myco-floristic), or have focussed on the habitat requirements, community structure and dispersal abilities of wood-inhabiting fungi in a conservation perspective. While several of these papers are considered in other parts of the present thesis, I will in this section shortly review attempts to apply wood-inhabiting fungi actively in conservation biology. These applications seem to fall within three approaches. Thus, wood-inhabiting fungi are prominent members of several European red-lists, they have been included in attempts to develop biodiversity surrogates and have been proposed as indicators in a context of biological integrity.

2.3.1. Red-list

The aim of red-lists is to “provide an explicit, objective … classification of species according to their extinction risk” (IUCN 2001). Earlier, red-lists were compiled following a diversity of national and regional approaches, but international criteria have been formulated by the World Conservation Union (IUCN 2001), and are know being widely applied throughout the world. In regional applications of these criteria it is specified that only native species should be considered (e.g. Gärdenfors et al. 2001). Thereby the IUCN criteria for red-listing show clear reference to the biological integrity conservation baseline.

Many wood-inhabiting fungi are assumed to be declining, and hence severely threatened locally

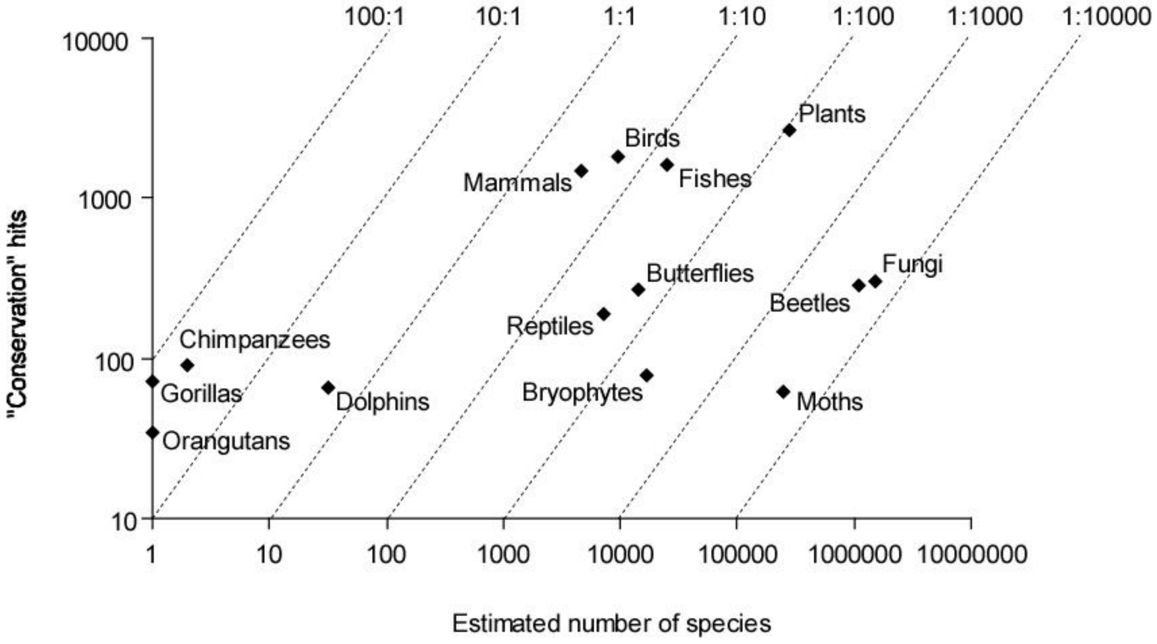

Fig. 6. The relation between estimated species numbers and conservation hits in the article database offered by “Web of Science” for selected organism groups. Dashed lines indicate different ratios between estimated species numbers and data base hits, derived from simple searches combining the organism group term with the term “conservation” using the “and” operator. The searches were restricted to articles published since 1990. For references on estimated species numbers see paper I.

or regionally in Europe, and are, accordingly, substantial members of several national and regional red data books (e.g. Kotiranta & Niemelä 1996; Bendiksen et al. 1997; Stoltze & Pihl 1997; Gärdenfors 2000). Recently, the "European Council for the Conservation of Fungi" has lobbied for the inclusion 33 fungal species, including 10 wood-inhabiting, in Appendix 1 of the Bern Convention, as European priority species. Even though most other macroscopic organisms groups are included here, this attempt has as yet been unsuccessful.

Of the 878 fungi listed in the Danish red-list (Stoltze & Pihl 1997), 249 (29 %) are wood-inhabiting, including 15 species regarded as extinct (Rald 2000), and very similar figures have been given for Sweden (Rydin et al. 1997). In Fennoscandia red-listed wood-inhabiting fungi are increasingly used as focal species in order to evaluate the effect of conservation initiatives (Berg et al. 2002) or to assess the negative impacts of forestry (Stokland et al. 1997; Kruys et al.1999; Sippola & Renvall 1999; Siitonen et al. 2001; Stokland 2001). Also in the present project this approach is followed consistently in papers III-VI.

2.3.2. Biodiversity surrogates

Species richness surrogates have been suggested in a number of variants (see paper I). Their main intention is to provide statistically sound indication of local or network species richness, typically with the aim to guide selection of sites for inclusion in reserve networks. In the present context I will pay attention to the coincidence and complementarity approaches. The former is based on the assumption that richness in one taxonomical group may reflect richness in other groups, so that a well known and easily surveyed group, e.g. birds or higher plants, can be used as surrogate of the diversity in less easily surveyed groups. The complementarity approach, on the other hand, assumes that complementarity or species turnover in one taxonomical group across a number of sites reflect complementarity or turnover in other groups. Again the typical aim is to fasciliate the design of reserve networks protective also for less known species groups.

Attempts to investigate species richness coincidence patterns involving wood-inhabiting fungi are sparse. Jonsson & Jonsell (1999) and Berglund & Jonsson (2001) found few and mostly inconsistent significant correlations in species diversity of vascular plants, lichens, bryophytes, wood fungi and beetles in boreal spruce forests in northern Sweden. In both cases the general lack of coincidence was suggested to reflect different habitat requirements among groups. Thus, many beetles prefer warm, sun-exposed substrates, bryophytes depend on a stable, humid environment, wood-inhabiting fungi depend on cwd amounts and diversity, while lichen diversity tend to be especially high on old living trees, especially Aspens.

Also Virolainen et al. (2000) reported that species richness of polypores were affected by other factors that those affecting species richness of higher plants, beetles and heteroptera in boreal old growth forests of Finland and Sweden. Accordingly, a complementary site selection based on polypores was inadequate in order to capture the most species rich or complementary sites for the other organism groups studied – and *vice versa.* Rather similar results were reported by Sætersdal et al. (2003) from western Norway, who found that a complementary site selection based on vascular plants had a low success rate in capturing the most complementary sites for polypores, compared to the situation for bryophytes, lichens, spiders, carabids, staphylinids and snails. For all groups species composition was significantly related to a general vegetation gradient from deciduous forests to oligotrophic pine forests, but the correlation was weakest for polypores. Sætersdal et al. (2003) further reported that polypores exhibited the highest species change (beta diversity) between samples, but the lowest species richness (alpha diversity) per sample. This corresponds well with a study from northern Sweden (Berglund & Jonsson 2003), which showed wood-inhabiting fungal communities to be poor in frequent and rich in locally rare species, compared to communities of vascular plants, bryophyte and crustose lichens. For wood-inhabiting fungi this type of community pattern seems to be a common feature, as discussed in paper IV. A possible explanation is the very high habitat diversity provided by decaying wood combined with a good, but highly random potential for long-range dispersal among fungi.

To sum up, wood-inhabiting fungi appear to have a limited potential as biodiversity surrogates, and at the same time species diversity in other organism groups appear to be poorly suited as an indicator of species diversity in wood-inhabiting fungal communities. This reflect that diversity of wood-inhabiting fungi at site level are influenced by factors, especially cwd amounts and cwd microhabitat diversity, which have little importance for most other forest organisms, with the important exception of other organism strictly dependent on decaying wood (i.e. saproxylic organisms).

2.3.3. Indicators of biological integrity

Several papers (e.g. Høiland & Bendiksen 1991; Karström 1992; Kotiranta & Niemelä 1996; Bredesen et al. 1997; Parmasto & Parmasto 1997; Heilmann-Clausen & Christensen 2000b; Norstedt et al. 2001) have suggested wood-inhabiting fungi as indicators of old growth or pristine forests of high conservation value or, following the definition given in paper I, of forests showing high biological integrity. Recently this application has been seriously questioned (Nordén & Appelquist 2001; Rolstad et al. 2002), based on the obvious potential of fungi for long distance dispersal (see subsection 2.2.2). Nordén & Appelquist (2001) thus noted that many wood-inhabiting fungi are likely to depend on a rich supply of microhabitats rather than the presence of long local forest continuity.

This view is without doubt true and relevant with respect to local forest continuity, but the situation may be different if regional trends in forest continuity, especially dead wood and mega-tree continuity, are addressed. Population studies, utilizing genetic markers and observations on sporocarps distribution patterns at the landscape scale, have given some insight in the realised dispersal potential of rare wood-inhabiting fungi. Nordén (2000) found evidence of a very limited gene flow between populations of the rare wood-inhabiting fungus *Steccherinum robustius* separated by 330 to 640 km in Sweden, while another study (Högberg & Stenlid 1999) reported a somewhat isolated south Swedish population of the suggested old-growth indicator species *Fomitopsis rosea* to show signs of inbreeding (lower levels of heterozygoty, higher frequencies of infertile sporocarps) compared to “core”-populations in northern Sweden, Finland and Russia. These findings have been supported by recent spore trapping experiments (Gustafsson 2002), which have documented dramatic declining spore deposition rates for rare wood-inhabiting fungi along geographical gradients at various scales in Sweden. This decline is most distinct along a general gradient from Northern Sweden, characterized by high forest cover, a rather recent history of effective forest management and relatively high cwd levels, to Southern Sweden, where the forests are fragmented and has a longer and more intensive history of management. At the local scale spore deposition rates were found to correlate significantly with the fraction of old growth forest in the vicinity (r. 3 km). In a somewhat related study from Norway (Sverdrup-Thygeson & Lindenmayer 2003) it was found that the incidence and frequency of the proposed old growth indicator species *Phellinus nigrolimitatus* increased with increasing fractions of old forest within the 80 ha area surrounding the plots, while local forest continuity of the 40 x 40 m inventory plots were of less importance.

These studies indicate that carefully selected wood-inhabiting fungi may indeed have the potential to indicate old growth or dead wood continuity at the regional scale, although their good dispersal abilities may disqualify them at the very local scale. This potential may increase as one moves southwards in Europe, where the history and magnitude of forest fragmentation and wood retrieval is much more dramatic than the case in Fennoscandia. As yet no studies has been performed to investigate the population structure and realised dispersal of any rare wood-inhabiting fungi in central or western Europe, and while such studies are badly needed I found it most likely that the presence of particular wood fungal communities with high diversity of heart rot agents, and specialised late stage agarics may be superior indicators of local to regional dead wood continuity in many European regions.

2.3.4. Summary

It is important to appreciate that different focal species approaches have different potentials that should not be intermingled. For instance, integrity indicators may be unsuitable as indicators for species rich communities, while biodiversity surrogates on the contrary may point to species rich communities lacking integrity. I am not surprised that Sverdrup-Thygeson (2001) found that four wood-inhabiting fungi, suggested as old-growth indicators, were unable to predict species richness and presence of red-listed beetles associated with sporocarps of the common polypore *Fomitopsis pinicola.* It is highly probable that such insects are influenced by other habitat factors, e.g. special microclimatic conditions, than those influencing the distribution of rare wood-inhabiting fungi at landscape scale. Similarly, I do not find that the results of Ohlson et al. (1997) disqualifies wood inhabiting fungi as indicators of biological integrity, even though they found the presence of suggested indicator species at the very local scale (1-6 ha plots) to correlate with actual dead wood amounts rather than absolute forest continuity, deduced from forest fire chronologies covering 300-2500 years. Considering the effective dispersal of wood inhabiting fungi at this scale, and the kind of disturbance implied by forest fires it would indeed be strange if the opposite result were found.

In general I find it highly relevant to focus on red-listed wood-inhabiting fungi in a conservation perspective. Red-lists have the potential of tracking the efficiency of a national or regional conservation scheme, and may point to valuable localities requiring special protection. Due to their high numbers, red-listed species are, however, impractical and expensive to monitor, and this may seriously limit their use in practice. It may be more relevant to focus on smaller selections of indicator species. I am convinced that wood-inhabiting fungi may have a wider, and more applicable potential in this respect, as indicators of dead wood continuity at the local to regional scale. On the contrary, I find that the biodiversity surrogacy approach generally should be abandoned, at least in a European context, simply due to its inability to consider integrity. It is possible that hybrid approaches could be developed, e.g. by using the approach in relation to carefully selected species groups, e.g. care-demanding red-listed habitat specialists or suspected integrity indicators. In less understood regions, e.g. vanishing tropical rainforests, the concept may be more relevant in its present form, if the goal is to secure highly diverse areas before it is too late.

Apart from the focal species approaches discussed above it is quite obvious that some wood-inhabiting fungi function as keystone species, by influencing community structure and biodiversity to a bigger extend than their abundance predicts (cf. paper I). Especially primary decay agents may have such roles due to their importance for other organisms, e.g. hollow breeding vertebrates, saproxylic arthropods and selective or specific fungal successor species. From Fennoscandia there is growing evidence that some polypores act as keystone species (Niemelä et al. 1995; Komonen et al. 2000), and as discussed in subsection 3.1.3. the same may well be the case for some heart rot agents in beech forests. Future attempts to develop indicator schemes based on wood-inhabiting fungi should certainly consider such aspects.

3. Habitat factors, species diversity and conservation

The present chapter provides a synthesis of papers III-VI with respect to habitat preferences among wood-inhabiting fungi and the potential implications for practical conservation. The chapter is divided in two main sections.

The first section presents a review of different habitats factors found to influence species composition and diversity of fungi in decaying wood at various spatial scales. The second section attempts to synthesise the main conclusion from this review with the more general discussion of wood inhabiting fungi and landscape integrity provided in section 2.2. Finally, a few suggestions are given on future research that could help increase the knowledge on wood inhabiting fungi, their ecology, biodiversity and conservation.

3.1. Habitat factors, species diversity and community structure

Several habitat factors have previously been recognized to influence fungal community structure in decaying wood, including decay phase (e.g. Renvall 1995; Heilmann-Clausen 2001), tree dimensions (e.g. Bader et al. 1995), microclimatic conditions e.g. (Griffith & Boddy 1991), tree species (e.g. Keizer & Arnolds 1990), death cause (e.g. Renvall 1995; Niemelä et al. 1995), and forest management history (e.g. Sippola & Renvall 1999). These factors, and a few more, are considered below in individual subsections. Each subsection rely heavily on one or more of papers III-VI and references to the work of other researchers are mainly given if this is considered important for the synthesis of the results from several papers, or if new ideas are proposed. It should be noted that the covered fungal species group differ between the papers. Corticoid basidiomycetes and small discomycetes (apothecia < 10 mm) are only included in papers III and IV.

3.1.1. Cwd fractions

A living deciduous tree is composed of roots, trunk, branches, twigs and leaves. Each of these elements has a specific function in the living tree and is exposed to a unique set of environmental conditions. Many wood associated fungi are well adapted to establishment in living trees, as heart rot agents or latent invaders (Boddy 2001). For such fungi the different compositional elements of a tree represent widely different establishment niches, due to differences in bark thickness, microclimatic conditions, wounding incidence, host responses etc. Accordingly, different fungal communities are able to establish in different parts of a living trees. Especially roots and twigs attract special fungal communities (Rayner & Boddy 1988). After the death and fall of a tree differences between different tree parts are likely to remain to some degree, but most differences now relate to dimensions (see 3.1.2.), local microclimatic conditions (3.1.6.) or to the effects of the decay caused by the decay communities established before tree death (3.1.3.).

The importance of three different cwd fractions (standing snags, fallen logs and branches thicker than 10 cm) for fungal diversity on beech is analysed in paper V. The branch fraction was, despite a lower average wood volume, found to be richer in species than logs, and when equal volumes were compared the difference was found to be statistically highly significant. Snags were, both per unit and per m^3, found to be the most species poor cwd fraction. The high species richness of the branch fraction probably reflect that branches of a single tree consist of many, more or less separate units, and therefore are likely to cover a larger variation in environmental conditions and hence provides higher habitat diversity per m^3 compared to the log fraction. The low species richness on snags point to general unfavourable conditions for fungal sporulation, due to strongly fluctuating microclimatic conditions and common desiccation events during dry periods. Ultimately, standing snags will fall. It is my experience that such fallen snags often host rather specific fungal communities, including red-listed species, as also described by Renvall (1995) for *Pinus sylvestris* in northern Finland.

As a group red-listed species did not exhibit significantly different habitat preferences compared to non red-listed species. However, of the six most frequently observed red-listed species in the study, three showed significant or almost significant preferences for certain cwd fractions. Thus *Nemania chestersii* and *Micromphale brassicolens* appeared to prefer branches, while *Camarops tubulina* showed a preference for logs, indicating that preferences for certain cwd fractions is a common phenomena at the single species level.

Forestry activities deliberately remove certain wood fractions; especially logs and larger branches, while twigs and stumps (especially cut stumps) are left for natural decay. Managed forests thereby present a smaller, but also very different selection of microhabitats for saproxylic organisms compared to unmanaged forest. The present project gives no direct data on the effects on wood associated fungi, but an investigation from Finland (Sippola & Renvall 1999), shows that the effects may be pronounced. Sippola & Renvall (1999) found that cwd created as logging waste attracted species (especially the corticoid species *Phlebiopsis gigantea* and *Stereum sanguinolentum*) that were observed very infrequently on natural cwd, while natural cwd, on the other hand, supported several species that was not recorded on logging waste at all (most distinctly the polypores *Fomes fomentarius* and *Skeletocutis lenis*). Accordingly, the study support that forestry may alter the species composition of wood-inhabiting fungi, not only by hindering establishment of species with strict habitat requirements, but also by favouring ruderal species that are rather infrequent in natural forests (cf. subsection 2.2.4.).

3.1.2. Dimensions

Cwd dimensions (typically as original tree diameter) are often argued to be a key factor for the presence of rare wood-inhabiting fungi (e.g. Bader et al. 1995; Renvall 1995; Høiland and Bendiksen 1996; Bredesen et al. 1997; Kruys et al. 1999; Sippola and Renvall 1999). Two explanations are commonly given for this assumption. Firstly, large logs are argued to provide more stable and favourable microclimatic conditions for fungal growth. Secondly their slower decay rate is assumed to make the establishment and continued existence of rare, slow-growing specialists more probable (Bader et al. 1995; Renvall 1995; Høiland and Bendiksen 1996; Grove et al. 2002). These two explanations can hardly both be correct. It is well documented that small diameter cwd generally decays faster than large diameter cwd (Rayner & Boddy 1988; Mackensen & Bauhus 1999; Tarasov & Birdsey 2001), but in stead of pointing to favourable conditions for fungal growth this indicates that large logs provides a stressful environment for fungal growth. This stress may relate to poor aeration and elevated CO_2 levels within large logs, either as a consequence of a long distance to free air or due to periods with very high moisture levels. Increased amounts of durable heartwood may be an additional factor for tree species possessing true heartwood, e.g. conifers and *Quercus* spp.

The importance of tree dimensions for fungal diversity is analysed for beech in papers III and V, and is briefly considered in paper IV for a broader selection of deciduous hosts. In all studies species richness were found to increase with tree size, expressed by diameter at breast height (dbh), but differences were found mostly to reflect positive species-area relationships predicting species richness to increase with increasing habitat size (e.g. Begon et al., 1990). Tree dimensions were in no case found to have a major effect on community structure judging from ordination analyses. If trees are weighted by their wood volumes it can be shown that large trees actually tend to present lower sporocarp species richness per m^3 compared to small trees (Fig. 7). According to paper V this trend is evident also when bigger selections of trees are compared, and also when only red-listed species are considered. The explanation seems to be straightforward and simple: Small trees have a bigger surface area and may hence support more sporocarps per volume unit. Additionally, a selection of small trees involve many more separate wood units per volume unit compared to a selection of larger trees, and are accordingly likely to represent a bigger variation in edaphic conditions, microclimate, death causes and infection histories and

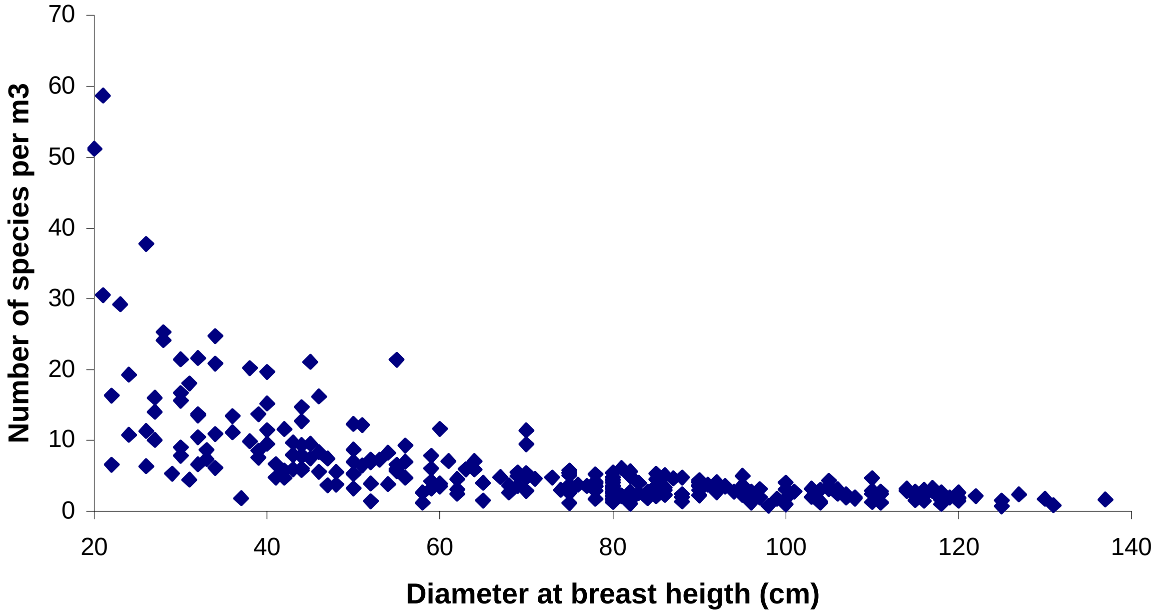

Fig. 7. The relation between tree size and fungal species numbers per m^3 wood considering 281 decaying beech trees studied in Paper VI.

hence a higher habitat diversity when equal volumes are compared.

In paper III the importance of dbh is analysed in a species-specific context, using logistic regression on fallen beech trees with a dbh exceeding 70 cm. Following this approach only a few species were found to show statistically significant preferences for large diameter trees. Most of these are common late stage saprophytes, including several cord-formers, which are frequent on cut stumps or buried wood even in managed forests, e.g. *Armillilaria gallica, Hydropus subalpinus, Lycoperdon pyriforme Megacollybia platyphylla, Pluteus cervinus* and *Physisporinus spp.* Only one red-listed species, the late stage agaric *Omphalina epichysium* did show a preference for large trees. In paper V the importance of tree size was investigated for red-listed species as a group and individually for the six most frequently observed red-listed species. Compared to paper III, the study is based on a bigger data material, covering a broader range of tree sizes. Nevertheless red-listed species did not as a group show a preference for large diameter trees, and only one species, the heart rot agent *Ischnoderma resinosum,* was found to show an almost significant preference for large dbh trees.

The preference of several common stump and buried wood associated species for large trees, gives some support for the suggestion of Bader et al. (1995) and Renvall (1995), that large logs, due to their more stable microclimatic conditions sustain different fungal communities than smaller logs. Also cut stumps and buried wood are characterised by stable microclimatic conditions, compared to most other wood types. On the other hand, the general lack of preference of red-listed species for large diameter trees fail to confirm the hypothesis that this water holding capacity of large logs is important for a substantial part of the rare species observed in the current project. Thus, the current project does not support the view that large diameter trees *per se* are more valuable for saproxylic biodiversity compared to smaller trees, a fact which is discussed also in the following subsection.

In a forestry context it is, however, important to note that smaller cwd fractions generally decay much faster than large logs and hence represent a habitat for cwd-associated organisms for a considerably shorter period. Tarasov & Birdsey (2001) found cwd fractions with d. <15-25 cm to decay about double as fast as cwd fractions with d. > 15-25 cm, for a range of tree species in western Russia, and similar figures were reported by Mackensen & Bauhus (1999) from Tasmania. Thus maintenance of a specified amount of cwd per area unit requires the average annual amount of wood left for decay to be bigger, if small cwd fractions are prioritised. This may be impractical in practice, and may easily lead to continuity breaks in local cwd amounts over time and hence impose negative effects on species requiring a stable, local representation of cwd in all stages of decay (cf. Stokland 2001).

3.1.3. Death cause and decay history

When a tree dies it is typically infected with a wide diversity of fungal individuals (Boddy 2001), of which many are able to decay wood. Some may even, directly or indirectly, be responsible for tree death. It has long been recognized that different fungal species influence their environment in different ways (e.g. Shigo 1967; Chapela et al. 1988, Boddy et al. 1989, Boddy 2000), and thus it is obvious that the initial fungal community structure of a death tree may influence the subsequent establishment of other saproxylic organisms, due to mutualistic, parasitic or other interspecific interactions, or as a result of species specific substrate modifications.

The importance of tree death cause and decay history as factors for fungal diversity in beech wood is considered in papers II, III and V. Paper II presents an experimental investigation of the impact of exudates from sterilised wood colonized by four different early stage decay agents on the growth rates in a range of late stage wood decayers. Wood previously decayed by *Stereum hirsutum* resulted in reduced extension rate, delayed growth or total inhibition in a majority of the tested species. It is suggested that this effect is due to the liberation of secondary metabolites produced by the fungus as part of a defensive strategy. A single species was, however, stimulated in the presence of wood decayed by *Stereum* indicating that this defence can be overcome. Exudates from wood decayed by *Fomes fomentarius* stimulated the growth rate in several species, while wood decayed by *Eutypa spinosa* and *Trametes versicolor* caused more variable responses, depending on test species. It is suggested that the wood exudates responsible for the reported effects may function as infochemicals, influencing microbial community development in wood.

In papers III and V it was, based on two different data sets, found that trees broken at the root neck were more likely to host red-listed species, compared to uprooted trees. Paper III presents a detailed analysis of this finding. The study shows that trees broken at the root neck host a number of selective species. Three of these, viz. *Ganoderma lipsiensis, Ischnoderma resinosum* and *Xylaria polymorpha* are known or suspected butt rot agents, which all are able to form extensive decay columns in occupied logs. It is, accordingly, suggested that the mentioned species are directly responsible for the root neck breakage, by causing butt rot, and that they subsequently creates a decay environment favouring the occurrence of red-listed species. Two additional heart rot agents, *Camarops polysperma* and *Polyporus squamosus,* were over-represented on trees with high (>2) numbers of red-listed species, and may play a similar role. Like the three above-mentioned species they occurred with a low to moderate frequency on the studied logs, being far outnumbered by *Eutypa spinosa, Fomes fomentarius* and *Kretzschmaria deusta,* which are the dominant primary decayers on beech logs in Denmark (Fig. 4). This connection between low to moderately frequent primary decayers and high numbers of red-listed species is remarkable and suggests that some of these low-frequent heart rot agents may function as keystone species for saproxylic biodiversity.

Niemelä et al. (1995) and Renvall (1995) have addressed the importance of early decay agents and death cause for fungal community structure in a boreal context, and Renvall (1995) described in great detail several different “successional pathways” in coniferous wood initiated by certain primary decayers or a specific death cause. Also for saproxylic insects, early decay agents, especially polypores, have been found to host species-specific communities (e.g. Kaila et al. 1994; Økland 1995; Komonen 2001; Yee et al. 2001). It is thus reasonable to ascertain successional pathways as an important structuring factor for biodiversity in decaying wood, and accordingly tree death cause is not a trivial issue in a conservation context. In paper V this finding is discussed in some detail. It is suggested that a high tree age generally promotes the establishment of specialised heart rot agents, which subsequently may open up specific decay pathways supporting red-listed species. Accordingly, the hypothesis is proposed that a high tree age is more important for the fungal diversity than tree size *per se* - at least in an Atlantic climate, as prevailing in Denmark.

In a conservation perspective selection of sites presenting a high diversity of primary decayers may be optimal, while stands with impoverished communities of primary decayers, e.g. after centuries of management may prove to have a limited potential for short-term conservation of saproxylic diversity. In a management perspective it can similarly be recommended to select logs representing a diversity of primary decayers for natural decay. If trees are artificially killed in order to improve biodiversity different methods of killing could be used, in order to open up different decay pathways.

3.1.4. Decay phase

It has long been recognized that significant changes occur in wood during the process of decay, and several authors have provided general descriptions of the associated microbial community development (e.g. Shigo 1967; Rayner & Webber 1984; Rayner & Boddy 1988; Boddy 2001; Heilmann-Clausen 2001). First of all the community structure changes from being open, when unoccupied wood domains are still available for colonizing, to a closed community structure were colonizing is only possible for species able to replace (or invade) already established individuals. Accordingly, competitive abilities are increasingly import as decay proceeds. Secondly the quality of the wood resource changes considerably during wood decay. These changes are structural, chemical, microclimatic and biotic, and may favour species preferring or tolerating high arthropod activity, species tolerating fluctuations in humidity, as well as specialist species able to decay residual products from the principal ligno-cellulose decomposition.

The relation between decay phase and fungal community structure and diversity is considered in papers III, IV and VI. The results are very consistent and show decay phase to be the dominant structuring factor in all communities studied and is reflected in a pronounced shift in the importance of various ecological species groups during decay. Latent invaders and unspecialised opportunists prevail in early decay stages, but are soon replaced by more competitive and fast decaying secondary invaders. These again are replaced by highly competitive cord-forming basidiomycetes and late stage agarics, especially members of the genera *Mycena*, *Pluteus* and *Psathyrella.* Also bryophyte associated species and formers of ectomycorrhiza show late optima. Most heart rot agents produces sporocarps during a considerable part of the decay period, but most with a peak in rather early decay phases.

Species richness was in all studies found to peak on intermediately decayed trees. This peak probably reflects an increase in the number of niches as wood decay proceeds, as suggested by Renvall (1995). While some parts of a log may decay rapidly, other parts may remain relatively little decayed (cf. Pyle & Brown 1999), allowing the co-occurrence of both early and late stage decay fungi in intermediately decayed logs. In addition, increasing micro- and mesofauna activity may increase the number of niches in decayed wood.

In the two beech wood studies (papers III & VI) red-listed species were found to show a highly distinct preference for trees in intermediate to late decay phases, while newly dead trees were found rarely to host sporocarps of red-listed species. While this probably to some extend reflect a lack of absolute correlation in mycelial presence and sporocarps production, e.g. in heart rot agents, it shows that red-listed species as a group have a short “window of opportunity” for spore dispersal. As shown in Fig. 8, simulated gaps in the supply of dead wood decreased red-listed species richness (as sporocarps) to a bigger extent than the case for non red-listed species. Thus, there is some evidence that dead wood supply gaps of more than 10 years may change competitive balances in the disfavour of red-listed species at stand scale in beech forest.

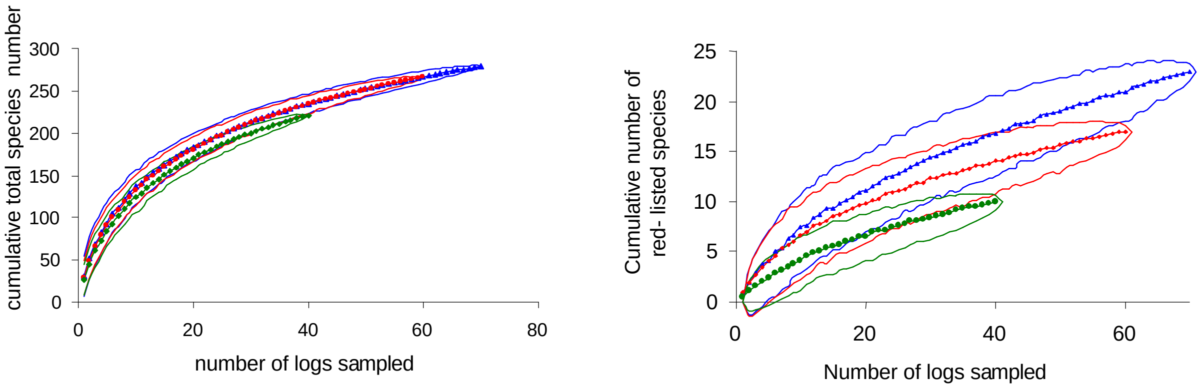

Fig. 8. The effects of simulated dead wood supply gaps created by omitting one or more age classes from the dataset analysed in Paper III. The effects are visualized by cumulative species richness curves. While total species richness is little influenced by such simulated supply gaps (figure to the left) red-listed species appear to be distinctly more sensitive (figure to the right). The supply gaps selected are those that resulted in the strongest decrease in cumulative species richness for each group.

3.1.5. Tree species

Just as different tree parts represent different establishment environments, the wood of different tree species has different properties affecting the establishment of wood-inhabiting fungi. Some differences relate to the general chemical and structural properties of the wood, e.g. pH, presence of antibiotics, bark and wood morphology (Rayner & Hedges 1982; Rayner & Boddy 1988), while other differences relate to the intimate interactions between living host tissue and fungi able to infect living sapwood (Chapela et al. 1991; Hendry et al. 1993).

The importance of tree species diversity for the diversity of wood-inhabiting fungi is the main topic of paper IV. The study shows clear differen-

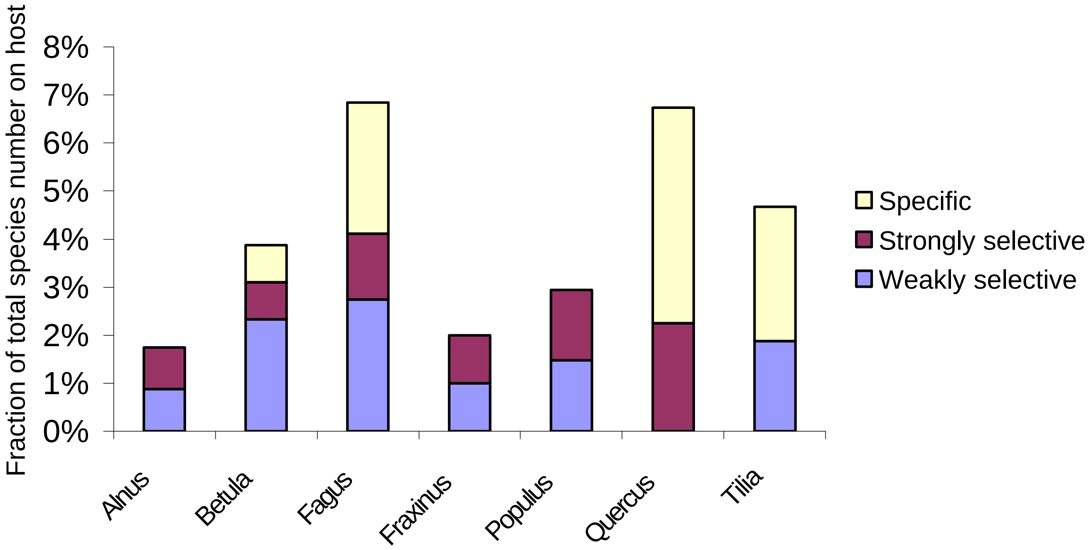

Fig. 9. Host selectivity and specificity patterns for wood-inhabiting fungi recorded on decaying deciduous wood in Draved Skov (Paper IV). Species were defined as "specific" if occurring on at least 33.3% of the trees in one species and being absent from other hosts. Species occurring on 25-33.3% of the trees in one species and being absent from other hosts were similarly denoted as "strongly selective", as were species with a large majority of occurrences (= 75%) restricted to a single host. Finally, species with at least five occurrences and a majority (= 50%) restricted to a single host were classified as "weakly selective".

tiation in species composition between the seven studied deciduous tree species *(Alnus glutinosa, Betula pubescens, Fagus sylvatica, Fraxinus excelsior, Populus tremula, Quercus robur* and *Tilia cordata)* at the study site. All tree species were found to support selective or specific species (Fig. 9), but especially *Fagus*, *Quercus* and *Tilia* were found to possess distinctive mycotas.

The heartwood of *Quercus robur* is well know for its high durability, owing partly to high contents of tannic acids, and this most likely is the main explanation for the distinctiveness of the associated mycota. In contrast, wood of *Fagus* and *Tilia* do not appear to have unique properties, which could explain the distinctive mycotas hosted by these species. The percentage of specific and selective species is by far highest among polypores and pyrenomycetes, while, in contrast, very few corticoid fungi, agarics and bryophytes showed any selectivity patterns (Fig. 10). These clear differences certainly reflect differences in dominating ecological strategies among these groups. Fungal species interacting with live hosts, i.e. endophytes and heart rot agents are well represented among pyrenomycetes and polypores, while comparably few agarics, corticoid species and no bryophytes are known to do so. Apparently, *Fagus* and *Tilia* host more fungal species adapted to interact species-specifically with living hosts, compared to the other include tree species. This is interesting as *Tilia*, together with *Quercus*, were the most widespread tree species in the region until c. 500 BC, while *Fagus* for the last 2000 years have had this dominant position. Theoretically, a dominant host is likely to have a stronger selective pressure on the accomplishing species pool, compared to a less common host, with respect both to novel establishment of species via long-range dispersal, and to adaptations in regional populations of resident species. The results support this theory to apply in the

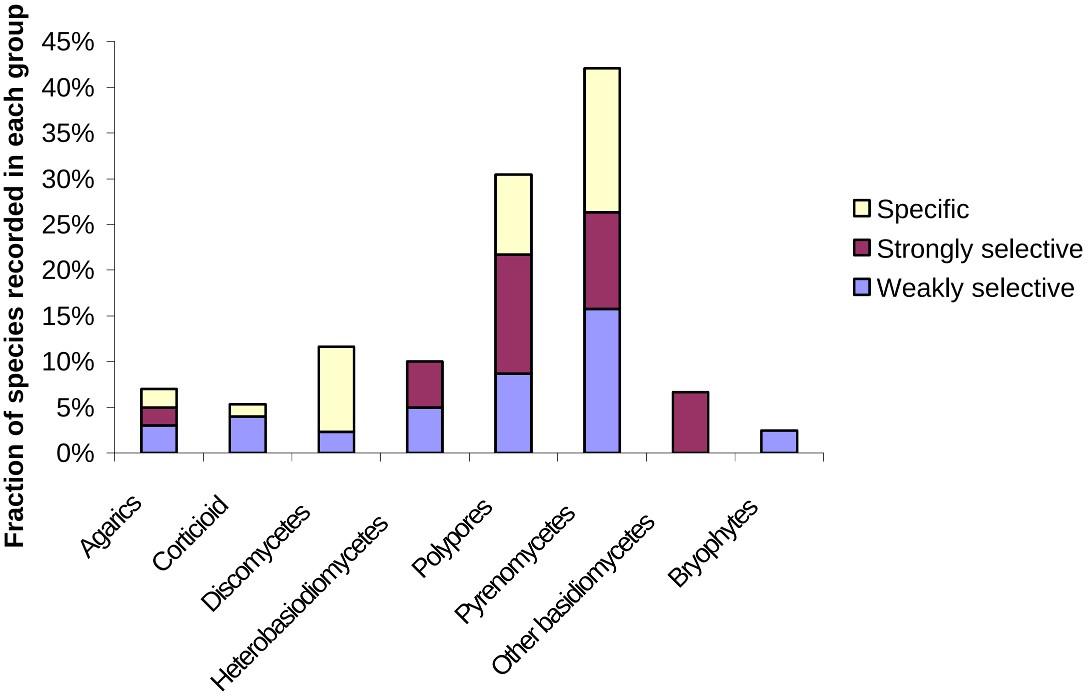

Fig. 10. Host selectivity and specificity patterns for wood-inhabiting fungi belonging to various morphological groups on wood of seven deciduous tree species in Draved Skov (Paper IV). Definitions of selective and specific species as in Fig. 9.

current case, and suggest that native dominant tree species contribute more to the overall species pool than less dominant or novel introduced hosts.

Species richness per tree was found to differ only slightly between the studied hosts. Most distinctly, *Quercus* was found to host significantly less species per tree than *Alnus, Betula* and *Populus*. As *Quercus* is far the most durable of the included tree species this difference may be instantaneous rather than absolute and it is not improbable that an individual decaying *Quercus* tree over its entire decay period may host as many fungal species as individuals of the other, faster decaying species. However, it is also possible that the very durable wood is a restrictive stress factor, lowering the overall species pool of wood-inhabiting fungi capable of infecting the species. With respect to overall species richness, the individual contributions to the species pools of the different tree species are important. Thereby *Fagus, Quercus* and *Tilia* can be stated to be the most important host trees for overall species richness. *Tilia cordata,* which has declined dramatically in the region may even be suggested to be a key-stone species for fungal diversity, as it appear to be more important for the actual species composition than its current frequency suggests.

In a management context, the clear differences in species composition between different deciduous hosts show that the development of sustainable forestry methods emphasising mixed stands of native tree species may benefit fungal diversity. Further it can be suggested that successful conservation of wood-inhabiting fungi at the landscape scale requires a balanced prioritising of forest types supporting a wide array of native tree species.

3.1.6. Climate

The effects of climatic conditions on fungal community development in wood have been studied rather intensively (see reviews in Rayner & Boddy 1988; Boddy 2001). The studies show that extreme, but realistic climatic conditions provide stressful conditions for fungal growth, while intermediate climatic regimes allow growth in most species. Low water contents hinder metabolic functioning, while high water contents impose poor aeration and hence restrict aerobic processes, including fungal wood decay. Similarly, low temperatures decrease the rate of metabolic activity, while high temperatures may be detrimental to enzyme functionality. However, different fungi have very different temperature optima and both thermophilic and psychrophilic wood decaying species have been found (Rayner & Boddy 1988). Similarly some fungi are known to remain active in very wet or dry wood, which is detrimental to growth in other species. Climatic variation occurs on several scales, within and across sites, and even within every single wood piece. In this subsection I will distinguish macroclimatic variation (between site variation) and microclimatic variation (within site variation). To some degree even “nanoclimatic” variation (within wood variation caused e.g. by occupying fungi or variations in surface moss cover), is considered.

In paper VI a highly distinct but complex community gradient was found to reflect the geographical position of the 14 study sites across Denmark. Even though soil type was identified as the most important variable structuring this gradient, it was found also to reflect macroclimatic variation. Most recorded pyrenomycetes thus had optima in the “upper” end of the community gradient, which correlated with a relatively continental climate, as expressed by low Lang’s Index scores (Annual precipitation/Average annual temperature). Several pyrenomycetes are known to be well adapted to drought stress, compared to basidiomycetes, and some species may even decrease wood water-contents actively, probably as part of a defensive combative strategy. Accordingly, it is argued that this species group may have a competitive advantage in relatively dry regions.

The effects of microclimatic variation is considered in papers III, IV and VI, in all cases based on subjective classifications and indirect variables, rather than direct monitoring of humidity and temperature, which would have been preferable, but extremely laborious considering the scale of the projects. Furthermore, the selections of studied trees were not aimed at securing a balanced representation of microclimatic extremes, meaning that no efforts were made to select trees embedded in swamps or fully exposed in clear cuts. Accordingly, the results should be taken with some caution, as indicative rather than conclusive.

In paper III, based on data from beech trees in the forest reserve Suserup Skov, a rather weak positive effect of soil contact were evident in the final model for overall species richness, which also included a positive effect of *Anemone nemorosa* cover on the forest floor surrounding the studied trees. In both cases the effects may relate to microclimatic conditions. A high degree of soil contact may increase general wood humidity and buffer fluctuations, but does also allow the widespread invasion of soil mycota, e.g. cord formers. Similarly a high *Anemone nemorosa* cover may, or may not indicate stable microclimatic conditions. In a gradient analysis of the same data set (Heilmann-Clausen 2001) it was found that a distinct but complex gradient integrating microclimatic stress and decay rate was associated with a pronounced shift in community structure, suggesting that the microclimatic regime has a bigger effect on fungal community structure and development than on the overall species richness in the data set.

About the same conclusion was reached in paper IV, based on data from deciduous wood in the generally moist forest reserve Draved Skov. In this study the degree of moss cover of the logs were found to be a key variable structuring the second most important community gradient, while a weak positive effect were recorded of soil moisture with respect to red-listed species incidence. Species with high scores along the moss cover gradient include several bark inhabiting *Mycena* species *(M. picta, pseudocorticola, speirea)* but also several species with very thin ephemeral corticoid sporocarps, e.g. *Jaapia ochroleuca, Stypella grilletii* and *Tulasnella eichleri*. The gradient was interpreted to reflect a stabilising effect of a high moss cover on the microclimatic or rather nanoclimatic conditions benefiting certain species with small sporocarps sensitive to desiccation. Likewise the positive relation between soil humidity and red-listed species incidence may reflect that some of the recorded red-listed fungi, of which a majority are corticoid species, may prefer humid conditions.

In study VI, including data from 14 different sites, moss cover were found to be an important variable explaining variations in species richness, but only as long as site variables were not included in the model. In the final complete model the variable contributes to a rather limited extend. Again a high moss cover may reflect beneficial nanoclimatic conditions for the formation of sporocarps, and may relate to high sporocarp species richness rather than to species richness at mycelial level. However, the effect may also relate to more substantial differences. Thus, Ódor & van Hees (2002) suggested that extensive presence of pyrenomycetes through wood desiccation may prevent the development of extensive moss communities. There is, in other words, the possibility that the extend of moss cover on the wood surface relates in part to the fungal community structure inhabiting the underlying wood.

In summary, the papers present few results directly relevant in a conservation perspective. However it seems reasonable to state that climatic extremes provide conditions for the development of stress tolerant fungal communities, which have poor competitive abilities under more intermediate conditions. Extensive drainage, lowering of ground water tables and the widespread use of clear-cutting has probably been detrimental to many wood-inhabiting fungi depending on a moist and stable microclimate. This does, however, not imply that highly stressed environments, e.g. exposed forest edges, are without value for the maintenance of fungal biodiversity. Conservation initiatives should aim on preserving dead wood in extreme as well as intermediate microclimatic environments, a fact which should be considered both in the selection of forest reserves and when wood is left for decay in managed forests.

3.1.7. Soil type

Soil chemistry and soil type is well known as a key factor structuring plant communities as well as the occurrence of terrestrial fungi, but little is known on the effects on wood-inhabiting fungi. It is quite obvious that non-unit restricted fungi, e.g. cord formers may be directly influenced by soil conditions, as they typically grow through soil or humus to reach new wood resources. It is more uncertain whether also unit-restricted wood decay fungi are influenced. Wood chemistry and structure (e.g. year ring widths) is to some extend influenced by soil chemistry, but it is uncertain whether the resulting differences are significant to the associated mycota.

The importance of soil type for wood-inhabiting fungi is considered in papers IV and VI. In paper VI a very distinct community gradient were identified to reflect a landscape gradient in which soil type was a significant component. Trees situated on chalk rich soils supported a number of cord formers and litter saprotrophs, e.g. *Kavinia himantia, Marasmius wynnei* and *Micromphale brassicolens* which are known to prefer calcareous soils. Also some wood-inhabiting species including several *Mycena* and *Pluteus* species had optima on clay or chalk rich soils, pointing to preferences for a high pH if not the concurrent climatic gradient (see the previous subsection) is responsible. On the other hand, most ectomycorrhizal species had optima on nutrient poor sandy soils, which may suggest that decaying wood represents an important source for nutrients, and hence an interesting domain for ectomyccorhizal fungi, on nutrient poor soils especially. Additionally, the ability of dead wood to retain humidity in dry periods may make it a preferred substratum for fructification on sandy soils, with low water capacity, compared to clayey soils with higher water capacity.

In paper IV the within site effects of soil conditions were investigated, but only rather weak effects were found. Interesting is the negative relation between soil C-contents and the incidence of red-listed fungal species, and the simultaneous positive relation to soil moisture, showing trees situated on humid mineral soil to have the biggest chance of hosting red-listed species. Most of the recorded red-listed species in this study are corticoid fungi, which often form sporocarps with close soil-contact, or have parts of their mycelia embedded in adjacent soil. It seems obvious that such species have variable optima with respect to soil properties and we suggested that the positive association of red-listed fungi with humid, mineral soil may relate to special adaptations to such soils among a majority of the recorded red-listed corticoid basidiomycetes. Soil C-contents were also found to influence fungal community structure in more general terms. Thus, several ectomycorrhizal species, e.g. *Clavulina cristata, Inocybe petiginosa, Tomentella subtestacea* and *T. stuposa* were found to prefer mineral soils poor in carbon, while most cord-forming corticoid fungi, e.g. *Phanerochaete filamentosa, P. velutina, Trechispora cohaerens* and *T. stevensonii* showed a preference for humic soils.

In summary the two studies show that soil conditions influence fungal community structure on decaying wood to some extend. Clear effects are visible with respect to cord-forming and ectomycorrhizal species, but it remains questionable whether unit restricted wood-inhabiting fungi are significantly affected. In a conservation perspective, soil conditions can be stated to be of rather limited importance for the biodiversity of wood-inhabiting fungi. However, strongly calcareous soils are known to support several very rare wood-inhabiting species, e.g. *Discina spp., Polyporus melanopus* and some ectomycorrhizal corticoid species (Hansen & Knudsen 1992; 1997; 2000). Also several rare wood-inhabiting agarics, e.g. members of the genera *Pluteus* and *Psathyrella* may, according to study VI, prefer rich soils.

3.1.8. Continuity and connectivity

Continuity and connectivity are two facets of the same issue, as continuity concerns temporal aspects, and connectivity concerns spatial aspects of habitat presence. Lack of continuity may be detrimental to immobile species with poor dispersal abilities. Lack of connectivity, on the other hand, may be critical to area-demanding species, e.g. moderately mobile species depending on temporal, patchy habitats. Nilsson et al. (1995) distinguished four types of forest continuity, viz. a) tree or shade continuity, b) megatree continuity, c) dead wood continuity and, in the presence of both megatree and dead wood continuity, d) functional primeval forest continuity. For wood-inhabiting fungi both dead wood continuity and megatree continuity can be assumed to influence community structure, though it has been argued that the potential for long distance dispersal make them less affected by continuity breaks (temporally or spatially) than most other forest organisms (see subsection 2.3.3.). Megatree and dead wood continuity is very difficult to document more than a century back, making it complicated to assess the impact of continuity breaks for current biodiversity patterns. Connectivity, on the other hand, is rather easy to study, but it is often complicated to access the actual importance for biodiversity, exactly because the contributions from continuity or discontinuity in most cases are difficult to access and separate.

In paper VI attempts are nevertheless made to access the importance of both dead wood continuity and habitat connectivity for wood-inhabiting fungi across 14 sites in the Danish landscape. The results are rather complex. Thus, average species richness per studied tree was found to decrease with increasing maximal living tree age and cwd continuity. The opposite trend was evident for red-listed species incidence, which increased with cwd continuity and connectivity, and with the number of years since last cutting. In the final logistic model for red-listed species incidence a simple geographical variable was, however, found to be best able to account for variations in the frequency of red-listed species between sites, thereby suggesting regional landscape trends to be important for the occurrence of these. The most north-westerly part of the study area, which showed the lowest red-listed species incidence, is at the limits of the natural range of beech in Europe, and has historically been rather sparse for beech forests. We therefore proposed that many of the recorded red-listed species may have difficulties in establishing and maintaining viable populations at the edge of the distribution area of their most important host tree. However, it cannot be excluded that lack of local or regional cwd continuity may be an equally important factor. The overall decline in overall species richness per tree with increasing forest age and cwd continuity, seem to reflect competitive exclusion of ruderal non-specialist species to the benefit of a lower number of stress tolerant or narrow niche specialists, especially heart rot agents, in mature forest communities (Fig. 11)

3.1.9. Summary

Papers III to VI provide considerable insight in habitat parameters influencing community structure and species richness of wood-inhabiting fungi in Danish deciduous forests, but most probably with relevance elsewhere Decay stage appears consistently to be the most important variable for understanding fungal community structure, while tree species, climatic conditions, death cause, dead wood continuity as well as the original position of the dead wood in the tree are supplementary key variables.

The effect of the latter variable and tree species does probably to a large extend relate to differences in the environment of establishment, imposed by variable microclimatic regimes and differences in host/fungus interactions depending on tree species and position in the tree. The effect of death cause is complex and deserves more studies, but it seems clear that different death causes may activate or involve different primary decay agents, which subsequently open up different decay pathways to the benefit of various communities of secondary decay agents. Some heart rot agents seem to permit the development of specialised communities

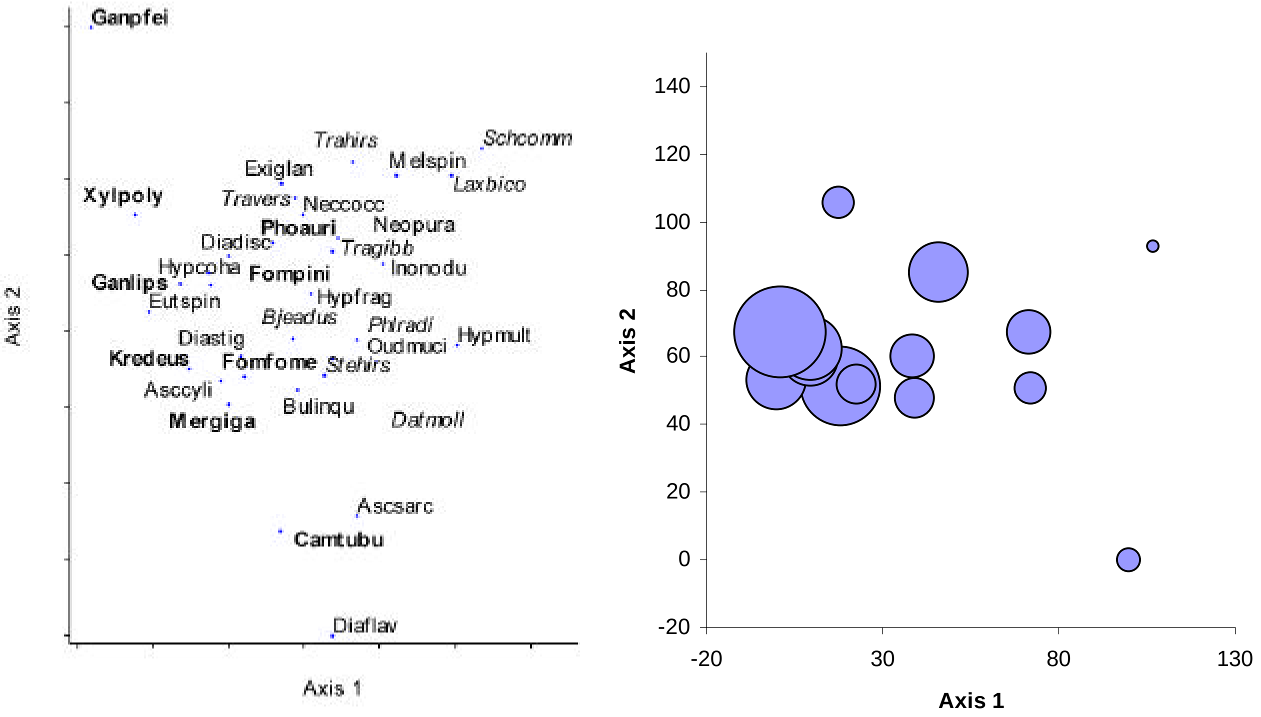

Fig. 11. DCA ordination of primary and early secondary decay agents based on frequency data from the 14 localities included in paper VI. To the left the distribution of species optima in the ordination space is shown. Heart rot agents (in bold face) and early secondary invaders (italics) show widely different optima. In the figure to the right different bubble sizes indicate the old cwd-ratio scores. The figures indicate a distinct tendency of heart rot to have optima in sites with long cwd continuity, while early secondary invaders show the opposite trend. For species abbreviations refer to Appendix 1 in paper VI

of secondary decay agents rich in red-listed species. It is proposed that tree death cause is more important for species composition and for the presence of rare species, than tree size *per se*. Thus, tree dimensions were only found to influence fungal community structure to a limited extend, and most species showing a preference for large diameter wood appeared to be common decayers of stumps and buried wood.

Cwd habitat continuity and connectivity were found to influence community structure in a complex manner. Species richness declined with cwd continuity and high tree age, while red-listed species incidence increased. These trends seem to reflect a general shift in the competitive environment in old growth forests benefiting stress tolerant latent invaders and heart rot formers on the detriment of common ruderal species. Also regional phytogeographic patterns appeared to influence fungal communities, as red-listed species incidence on decaying beech wood decreased in regions where this tree species has been marginal in a historic perspective. Finally, variations in soil type within and between sites was found to influence fungal community structure to some extend, and effects were most distinct for non-unit restricted species, e.g. cord formers and ectomycorrhizal species.

3.2. Conservation in practice

A basal distinction in conservation biology is between approaches favouring function-integration versus function-separation (Larsen et al. 2001). In the first case conservation is integrated as an element in a scenario of multiple use forestry, in the second case it is sought achieved by the selection of specific biodiversity conservation areas. The first scenario implicate several latent conflicts with respect to wood-inhabiting fungi, at least if timber production is involved.

Some wood-inhabiting fungi may imply a threat to forest health, because they have the potential to cause widespread attacks on the standing timber crop (Butin 1995). Recent studies have shown that the most important agent of decay in standing timber in Danish deciduous forest, the heart rot agent *Fomes fomentarius*, is of limited importance in this respect, as the species rarely attack trees in the productive age (Thomsen et al. 2001). Another conflict concerns the visual appearance of forests. Retaining of substantial cwd amounts in forests appear visually disturbing to some forest visitors and may be provocative to forest owners and managers, preferring forest to appear ordered and “clean”. To some extend decaying wood may even hinder forest operations and threaten the security of forest visitors. Finally, and most importantly, there is the obvious conflict between economic and ecological timber value. Maintenance of cwd-associated biodiversity requires that wood, representing a possible economic income, is left for natural decay. From an economic point of view it is sensible to leave the least economic valuable cwd fractions for decay. The interesting question, which will be addressed in the following subsection, is whether these fractions are adequate for biodiversity conservation.

3.2.1. Conservation in managed forests

The most low-priced wood fractions are cut stumps and twigs, which currently are the main wood fractions left for decay in Danish managed forests. Slightly more valuable are branches and malformed logs, which typically are manufactured as industrial wood or firewood. According to recent estimates, this fraction constitutes more than 20% of the standing volume in Danish beech forests, with a strong bias towards small diameter classes (Nils Strange, personal comm.). Finally more wellshaped logs constitute the biggest and most valuable wood fraction.

An obvious primary step in the conservation of wood associated organisms in managed forest, would be to increase the amounts of decaying wood, by leaving bigger fractions of the lowest priced of the currently manufactured wood fractions, i.e. branches and small trees resulting from logging and thinning. Permanent firewood collection and manufacturing free zones would be a very simple initiative to achieve this goal. Small cwd fractions seem to give good “value for money” with respect to biodiversity (Kruys and Jonsson, 1999; Schiegg, 2001; Paper V), and for a first sight this approach seem to unite economic and ecological considerations in an optimal way. As discussed in subsections 2.2.4., 3.1.1., and 3.1.8. it is, however, evident that the approach will be unfavourable to species depending on special infection sites characteristic of old trees, i.e. heart rot agents and for secondary decay agents depending on the decay created by such species. Accordingly, retaining of whole, old-grown trees for natural decay is a necessary supplement, if the goal is to conserve more substantial parts of the wood associated biodiversity in managed forests. Such biodiversity trees should be naturally dead, preferably following fungal attack caused by a diversity of heart rot agents. For several reasons such trees are very rare in managed forests at present. First of all trees are seldom allowed to grow to a high age, which is more or less a prerequisite for extensive attacks from heart rot agents. Secondly, if visible fungal attacks are encountered by foresters, attacked trees are often deliberately removed with a marginal or even negative economic gain. Initiatives to increase the frequency of old living and naturally dead trees in managed forests would be a big step forward. It is important to note that tree size and economic value seem to be of subordinate importance in a conservation perspective. Thus, slow-growing suppressed trees as well as low quality trees misshaped e.g. by marginal growth conditions may offer big biodiversity value. A simple, but valuable initiative could be to omit cutting from internal and external forest edges, along coastlines, lakes and forest streams. An alternative approach could be to rely more on natural thinning and to leave suppressed understory trees to a bigger extend than done presently. However, the biodiversity value of such suppressed, slow growing understory trees is yet to be assessed.

It is not possible to give any precise guidelines regarding the optimal density of retained biodiversity trees. Fungal communities are not, like bird communities, strongly density dependent, and the overwhelming species richness characterising wood fungal communities makes it very difficult to provide adequate estimates of required wood volumes necessary for the conservation, in a temporal perspective, of specified fractions of the overall wood fungal species pool. Even in unmanaged forests, species accumulation curves do not tend to saturate, due to a very high frequency of locally rare species (Fig. 12), and it seems evident that managed forests realistically are unable to support all aspects of biodiversity depending on decaying wood.

3.2.2. Conservation in forest reserves

Conservation of biodiversity associated with dead wood in strictly unmanaged forest reserves is for several reasons an obvious choice. Carefully selected reserves are more likely to preserve the integrity of saproxylic communities, and at the same time the conflicts embedded in the function-integrating approach are more or less prevented. On the other hand, the set aside of forests as reserves is costly, especially if private land are included. Therefore it is necessary with a careful prioritising when forest reserves are selected, considering economic as well as ecological aspects. The present project gives some clues in this respect. Most notably paper VI show that the incidence of red-listed species occurrence varies considerable between sites, even if dead tree size and other key variables are accounted for. Sites situated in the south-eastern part of Denmark towards the core of the beech distribution area were found to be richer in both beech specialists and red-listed species (see subsection 3.1.8.), and can hence be argued to provide bigger conservation value if the goal is to preserve the specific saproxylic communities associated with this host. Whether local or regional dead wood continuity plays a supplementary role is uncertain, but highly probable. Due to the potential role of primary decay agents, especially heart rot formers, as keystone species for saproxylic biodiversity (see subsection 3.1.3.), it can be argued that sites representing a high diversity of heart rot agents are optimal for biodiversity conservation.

A more general finding is that it is valuable for the conservation of fungal diversity at landscape scale to design reserve networks with the aim of representing different native forest types. Variation should be secured both with respect to tree species composition, soil type and prevailing microclimatic conditions. As fungi have good abilities for dispersal, at least over intermediate distances, small reserves may be valuable for wood-inhabiting fungi if situated in the vicinity of other, preferably bigger reserves. This is especially relevant, as there is often a negative correlation between cwd availability and locality site (e.g. Götmark & Thorell 2003).

3.2.3. Conclusion - on the roles of managed forests and reserves

At the end of the day, the prioritising of function-separation versus function-integration is a political and idealistic issue. Strictly unmanaged forest reserves have the potential of preserving integrate and "wild" saproxylic communities, and are apparently ideal for conservation of red-listed species, which are unlikely to maintain viable populations in managed forests, even if substantial steps for

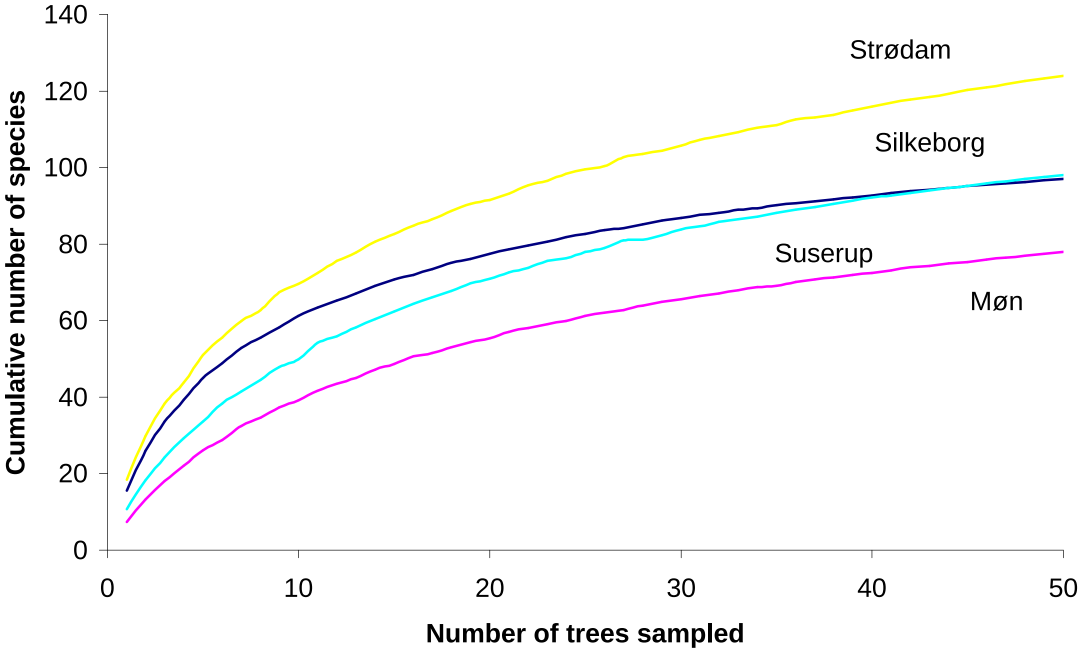

Fig. 12. Cumulative species richness curves for the four most intensively localities sampled in study VI.

increasing dead wood amounts are taken. However, function-integrating forests are likely to provide valuable stepping-stones for rare wood-inhabiting fungi, allowing their dispersal between reserves. Tightly managed forests and plantations of exotics are unlikely to play a similar role, and may even threaten integrity at landscape scale, due to their favouring of ruderal strategists and species selective for introduced tree species (see section 2.2.). Accordingly, an overall strategy of nature management in which function-integration is not a part requires that more and bigger reserves are selected if it has to be efficient with respect to conservation of fungal biodiversity.

3.3. Suggestions for future research

Though the knowledge on the diversity, ecology and conservation of wood-inhabiting fungi has increased considerably during the last decade many questions on the biology of wood inhabiting fungi remains open or only partly answered. With respect to conservation I consider the lack of insight in the establishment biology of rare species most critical, but studies on population structure of rare species in the European deciduous forest zone are also badly needed. With relation to spore dispersal, the knowledge on arthropods as vectors is still fragmentary. It could be interesting to know if many species produce spores that only germinate after gut passage. The general effects of different types of forestry on wood fungal diversity and community structure should also be investigated. For instance it could be examined to which degree the funga of non-native tree species differ from the funga of native tree species. Finally it would be highly relevant to investigate the relation between forest continuity (esp. dead wood and megatree continuity) at different spatial scales and the present diversity of wood inhabiting fungi, especially with relation to the presence of rare specialist species. Such studies could show if wood inhabiting fungi are suited as indicators of biological integrity at any scale, and indicate whether conservation of wood inhabiting fungi is to the benefit of other threatened aspects of forest biodiversity.

In a more general ecological context it would be highly interesting to go deeper into understanding the role of early decay agents for the subsequent community development in decaying wood. As part of such studies the importance of chemical recognition between individuals should be studied. Possibly, such studies may provide new insight in general ecological principles structuring microbial communities and may even have an applied aspect, as highly defensive chemical substances may have a potential as alternative wood protective agents.

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