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Invasions by alien plants in the Czech Republic: a quantitative assessment across habitats

Invaze nepůvodních rostlin v České republice: kvantitativní srovnání různých biotopů

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Occurrence of alien plant species in all the major habitats in the Czech Republic was analysed using a data set of 20,468 vegetation plots, classified into 32 habitats according to the EUNIS classification. The plots contain on average 9.0% archaeophytes and 2.3% neophytes; for neophytes, this proportion is much smaller than 26.8% reported for the total flora of the country. Most neophytes are found in a few habitats: only 5.6% of them were recorded in more than ten habitats. By contrast, archaeophytes, and especially native species, tend to occur in a broader range of habitats. Highest numbers of aliens were found on arable land, in annual synantropic vegetation, trampled habitats and anthropogenic tall-forb stands. These habitats contain on average 22–56% archaeophytes and 4.4–9.6% neophytes. Neophytes are also common in artificial broadleaved forestry plantations; they also tend to make up a high percentage of the cover in wet tall-forb stands, but are represented by fewer species there. Entirely or nearly free of aliens are plots located in raised bogs, alpine grasslands, alpine and subalpine scrub and natural coniferous woodlands. Correlations between the number of archaeophytes or neophytes and the number of native species, calculated with habitat mean values, were non-significant, but there was a positive correlation between the numbers of archaeophytes and neophytes. The ratio of archaeophytes to neophytes was high in semi-natural dry and mesic grasslands and low in disturbed habitats with woody vegetation, such as artificial broadleaved forestry plantations, forest clearings and riverine willow stands. When individual plots were compared separately within habitats, the relationships between the number of archaeophytes, neophytes and native species were mostly positive. This result does not support the hypothesis that species-rich communities are less invasible, at least at the scale of vegetation plots, i.e. 10^0–10^2 m^2.

Keywords: archaeophytes, EUNIS, habitat invasibility, level of invasion, neophytes, phytosociological database, species number, vegetation cover

Introduction

Invasions by alien plants (sensu Richardson et al. 2000, Pyšek et al. 2004a) are considered as one of the major threats to the diversity of natural ecosystems (Williamson 1996, Kowarik 2003, Weber 2003). However, there is considerable variation between habitats in the level of invasion (sensu Hierro et al. 2005), i.e. the number of alien species they harbour and proportion of the total number of species made up of aliens. Such differences are usually explained by (1) variation in match between the ecological requirements of alien species, evolved in their native range, and the available niches in the invaded area; (2) differences in inherent vulnerability of habitats to invasion due to varying competitive abilities of resident species, vegetation structure and disturbance; and (3) exposure of some habitats, such as roads, railways, river corridors or human settlements, to a stronger pressure of propagules of alien species (Lonsdale 1999).

Alien floras of temperate areas are well studied, which has resulted in compilations of detailed lists of alien plant species for several countries, namely the UK (Clement & Foster 1994, Ryves et al. 1996, Preston et al. 2002), Germany (Klotz et al. 2002), Switzerland (Wittenberg 2005), the Czech Republic (Pyšek et al. 2002a), Austria (Essl & Rabitsch 2002) and Hungary (Mihály & Botta-Dukát 2004). These lists classify alien species according to invasion status into casual and naturalized (see Richardson et al. 2000 and Pyšek et al. 2004a for definitions), and according to their residence time (Rejmánek 2000, Pyšek & Jarošík 2005) into archaeophytes (species that arrived before AD 1500, i.e. before the establishment of world trade and the import of goods from other continents) and neophytes (species introduced after that date). The latter distinction is important for the assessment of representation of alien species in different habitats, because both groups are known to have different habitat affinities (Pyšek et al. 2002b, 2004b, 2005, Deutschewitz et al. 2003, Kühn et al. 2003).

Despite the considerable progress in the cataloguing of alien plants, there are large gaps in the knowledge of the habitat affinities of individual alien species in particular areas, as well as of the level of invasion in different habitats. The published overviews of habitat preferences of alien species are either based on the expert estimates, which lack quantitative information on species abundance in different habitats (Clement & Foster 1994, Klotz et al. 2002, Pyšek et al. 2002a, Walter et al. 2005), or contain only a selection of species or habitats (Pyšek et al. 1998, Török et al. 2003). The development of electronic databases of vegetation plots (phytosociological relevés) in some countries (Ewald 2001, Hennekens & Schaminée 2001, Chytrý & Rafajová 2003) enables a quantitative assessment of the level to which different habitats are invaded. The databases contain lists of species with cover estimations from plots that range in size from units up to hundreds of m^2. The plots are usually located over a broad range of vegetation types in a given area. Combined with the list of alien plant species for the same area, these databases can provide quantitative estimates of the level of invasion of different habitats, relationships between the level of invasion and the number of native species, lists of the most common alien species within individual habitats and information on the habitat range of individual alien species. Kowarik (1995) provides an example of such a study, which used over 5000 vegetation plots to assess the level of invasion in a broad range of habitats in the city of Berlin.

In this paper, we combine the data from the Czech National Phytosociological Database (Chytrý & Rafajová 2003) with the Catalogue of Alien Plants of the Czech Republic (Pyšek et al. 2002a) in order to obtain basic statistical information on the level of invasion of major habitats in the Czech Republic. We specifically address the folowing questions: (1) Which alien species have the broadest habitat range? (2) What is the level of invasion of the different habitats? (3) What is the relative representation of archaeophytes, neophytes and native species in particular habitats? (4) Is there a relationship between the level of invasion and species richness of native vegetation?

Study area

Czech Republic is a central-European country with an area of 78,864 km^2 and 10.3 million inhabitants. Its geographical location in the centre of the continent and the intensive movement of people and goods over several millenia have contributed to the introduction of many species (Pyšek et al. 2002a, 2003b). The landscape is intensively used and considerably fragmented due to the long-term effect of human activities: large undisturbed areas of landscape are virtually missing (Pyšek & Prach 2003). About one third of the flora of this country consists of alien species (Pyšek et al. 2002a), which were well studied over the last several decades (Hejný et al. 1973) and receive considerable attention at present too (Mihulka et al. 2003, Šída 2003, Petřík 2003, Kubát & Jehlík 2003, Mandák et al. 2004). At the same time, there is a long tradition of phytosociological research, which resulted in the compilation of syntaxonomical lists of plant communities (Moravec et al. 1995), vegetation maps (Neuhäuslová et al. 1998), habitat classifications (Chytrý et al. 2001) and electronic databases of vegetation plots (Chytrý & Rafajová 2003). Current research, based on the phytosociological tradition, focuses on revising the classification of vegetation using large electronic data sets, which cover various types of natural vegetation (Kočí 2001, Knollová & Chytrý 2004), semi-natural vegetation (Havlová et al. 2004) and synanthropic vegetation (Lososová 2004).

Materials and methods

A data set of vegetation plot records (relevés) from the Czech National Phytosociological Database was used (Chytrý & Rafajová 2003). Each plot contained a list of plant species with their cover-abundances recorded on the Braun-Blanquet or Domin scale (van der Maarel 1979) and basic information on geographical location, habitat characteristics and vegetation structure.

Individual plots were assigned to 32 habitats based on the EUNIS habitat classification (Davies & Moss 2003, available at http://eunis.finsiel.ro/eunis/; see also Rodwell et al. 2002), which is a standard classification of European habitats. Generally, Level 2 habitats of the EUNIS hierarchy were used, but also Level 3 habitats were accepted in a few cases where Level 2 habitats contained subtypes that are known to be rather different in terms of the extent to which they become invaded. In one case, two habitat types at Level 2 were merged as many plots could not be unequivocally assigned to only one of them. As there is no clear match between the anthropogenic habitats within EUNIS and the traditionally recognized phytosociological types of ruderal vegetation, we interpreted EUNIS habitat type J6 (Waste deposits) as including all types of annual ruderal vegetation, even those found in other habitats than waste deposits. By contrast, perennial types of ruderal vegetation were assigned to habitat type E5.6 (Anthropogenic forb-rich habitats) even if they occurred on waste deposits. The habitat types used are listed in Table 1, along with the corresponding phytosociological classes and alliances.

Of 65,730 plots contained in the database in July 2004, some were deleted because they: (1) could not be unequivocally assigned to one or other of the habitat types; (2) lacked an accurate geographic location; (3) were of extreme size with respect to plot sizes commonly used for particular vegetation types (Chytrý & Otýpková 2003), i.e. < 50 m^2 or > 500 m^2 for woodland habitats, < 10 m^2 or > 100 m^2 for scrub, < 4 m^2 or > 100 m^2 for grassland, wetland and aquatic habitats, and < 1 m^2 or > 50 m^2 for low-growing vegetation

Table 1. – List of EUNIS habitat types used in this study and corresponding phytosociological syntaxa. Habitat J6 was interpreted as annual vegetation in ruderal sites.

EUNIS habitat type	Syntaxon
C1 Surface standing waters	*Lemnetea, Potametea* (except *Batrachion fluitantis*), *Isoëtion, Sphagno-Utricularion*
C2 Surface running waters	*Batrachion fluitantis, Montio-Cardaminetea*
C3 Littoral zone of inland surface waterbodies & D5 Sedge and reedbeds, normally without free-standing water	*Phragmito-Magnocaricetea* (except *Scirpion maritimi*), *Littorellion, Isoëto-Nanojuncetea, Bidentetea*
D1 Raised and blanket bogs	*Oxycocco-Sphagnetea*
D2 Valley mires, poor fens and transition mires	*Scheuchzerio-Caricetea* (except *Caricion davallianae*)
D4 Base-rich fens	*Caricion davallianae*
D6 Inland saline and brackish marshes and reedbeds	*Scirpion maritimi*
E1 Dry grasslands	*Festuco-Brometea, Koelerio-Corynephoretea, Festucetea vaginatae, Sedo-Scleranthetea*
E2 Mesic grasslands	*Arrhenatheretalia, Nardetalia* (except *Nardion*)
E3 Seasonally wet and wet grasslands	*Molinietalia* (except *Filipendulenion* and *Veronico-Lysimachion*)
E4 Alpine and subalpine grasslands	*Juncetea trifidi, Salicetea herbaceae, Nardion*
E5.2 Thermophile woodland fringes	*Trifolio-Geranietea*
E5.4 Moist or wet tall-herb and fern fringes and meadows	*Filipendulenion, Veronico-Lysimachion, Senecion fluviatilis, Petasition officinalis*
E5.5 Subalpine moist or wet tall-herb and fern habitats	*Mulgedio-Aconitetea*
E5.6 Anthropogenic forb-rich habitats	*Artemisietea, Lamio albi-Chenopodietalia, Agropyretea*
E6 Inland saline grass and herb-dominated habitats	*Crypsietea, Thero-Suaedetea, Thero-Salicornietea, Festuco-Puccinellietea, Loto-Trifolienion*
F2 Arctic, alpine and subalpine scrub habitats	*Pinion mugo, Betulo carpaticae-Alnetea*
F3 Temperate and mediterraneo-montane scrub habitats	*Rhamno-Prunetea*
F4 Temperate shrub heathland	*Calluno-Ulicetalia*
F9.1 Riverine and lakeshore [*Salix*] scrub	*Salicion triandrae, Salicion eleagno-daphnoidis*
F9.2 [*Salix*] carr and fen scrub	*Salicion cinereae*
G1 Broadleaved deciduous woodland	*Salicion albae, Alnion glutinosae, Querco-Fagetea, Quercetea robori-petraeae, Betulion pubescentis*
G1.C Highly artificial broadleaved deciduous forestry plantations	Plantations of *Robinia pseudacacia, Populus* ×*canadensis* and *Quercus rubra*
G3 Coniferous woodland	*Erico-Pinetea, Vaccinio-Piceetea* (except *Pinion mugo* and *Betulion pubescentis*), *Eriophoro vaginati-Pinetum mugo, Pino rotundatae-Sphagnetum*
G3.F Highly artificial coniferous plantations	Plantations of *Picea abies, Pinus sylvestris* and *Larix decidua*
G4 Mixed deciduous and coniferous woodland	*Fagion* (natural mixed forests of *Fagus sylvatica, Abies alba* and *Picea abies*) and artificial mixed stands of deciduous and coniferous trees
G5 Lines of trees, small anthropogenic woodlands, recently felled woodland, early-stage woodland and coppice	*Epilobietea*
H2 Screes	*Thlaspietea rotundifolii*
H3 Inland cliffs, rock pavements and outcrops	*Asplenietea, Parietarietea*
H5.6 Trampled areas	*Plantaginetea* except *Loto-Trifolienion*
I1 Arable land and market gardens	*Atriplici-Chenopodietalia, Secalietea*
J6 Waste deposits	*Sisymbrietalia, Eragrostietalia*

in stressed or disturbed habitats; (4) were recorded before 1970; this latter restriction was applied in order to focus the analysis on relatively recent patterns in the distribution of alien species. Although the plot records in the database provided a sample of all the major habitats and all regions within the country, they originated from various sources and were sampled for various purposes (Chytrý & Rafajová 2003), so that they cannot be considered as an objective statistical sample. To reduce the effect of local oversampling of some areas, we performed a stratified resampling of the database (Knollová et al. 2005), with strata defined by plot assignment to one of the 665 phytosociological associations recognized in the Czech Republic (Moravec et al. 1995). Assignments by the authors of individual records were used. The strata were combined with a geographical grid that divided the country into quadrangles of 1.25 longitudinal × 0.75 latitudinal minutes (approximately 1.5 × 1.4 km). If any intersection of a stratum and a quadrangle contained more than one plot, we selected one at random. The resulting data set contained 20,468 plots.

As the focus of this study was vascular plants, cryptogam records were deleted from the data set. All vascular plants were classified as archaeophytes (pre-AD 1500 aliens), neophytes (post-AD 1500 aliens), or native species according to Pyšek et al. (2002a). The only exception was *Arrhenatherum elatius*, which is classified as a neophyte by Pyšek et al. (2002a); due to the lack of clear evidence a more conservative approach was preferred and this species is treated as an archaeophyte in the current analysis.

For each vegetation plot, the number of species within each of these categories was counted and the total cover of the species within each category calculated. The total cover was calculated from species cover values as recorded on Braun-Blanquet or Domin scale, transformed into percentages according to van der Maarel (1979) and subsequently expressed as proportional numbers ranging from 0 to 1. The species cover values were summed for all the species belonging to each species group (archaeophytes, neophytes, or native) on the basis of random overlap of fixed covers. For example, the summed cover of two species x and y was calculated as $c_s = c_x + c_y \cdot (1 - c_x)$, where c_s was the summed cover, and c_x and c_y were covers of species x and y, respectively. The summed covers calculated in this way were always between 0 and 1. This calculation, as well as all other operations with species-by-sites matrices, were performed using the JUICE 6.3 program (Tichý 2002).

For the purpose of correlation and regression analysis, the number of species within each species group (archaeophytes, neophytes or native) and each plot was square-root transformed after adding 0.5 to each value. The data points were the square-root transformed values of individual plots (for the analyses within habitat types) or within-habitat averages of these transformed values (for the analyses between habitat types). Correlation and regression analyses were calculated using the STATISTICA 7 program (www.statsoft.com).

Taxonomy and nomenclature follows Kubát et al. (2002) for plants and Moravec et al. (1995) for phytosociological units.

Results

In total, the data set of vegetation plots contained 229 (11.7%) archaeophytes, 179 (9.1%) neophytes and 1556 (79.2%) native species. The average proportion (± standard deviation) of these three species groups in individual vegetation plots was in turn 9.0±17.5%, 2.3±5.9% and 88.7±19.9%.

Table 2. – Fifteen archaeophytes and neophytes with the broadest habitat range, i.e. occurring in the highest number of EUNIS habitat types ($n = 32$). Species are ranked in decreasing order according to the number of habitat types in which they were recorded.

Archaeophytes	No. of habitats	Neophytes	No. of habitats
Arrhenatherum elatius	23	*Impatiens parviflora*	22
Cirsium arvense	20	*Epilobium ciliatum*	21
Lapsana communis	19	*Agrostis gigantea*	17
Linaria vulgaris	19	*Bidens frondosa*	15
Silene latifolia	19	*Conyza canadensis*	15
Convolvulus arvensis	18	*Trifolium hybridum*	15
Echium vulgare	18	*Robinia pseudacacia*	14
Lamium album	18	*Medicago sativa*	12
Tanacetum vulgare	18	*Solidago canadensis*	12
Cirsium vulgare	17	*Erigeron annuus* s. lat.	11
Medicago lupulina	17	*Aster novi-belgii* s. lat.	10
Mentha arvensis	17	*Cytisus scoparius*	10
Fallopia convolvulus	16	*Juncus tenuis*	10
Lactuca serriola	16	*Lupinus polyphyllus*	10
Sonchus oleraceus	16	*Veronica persica*	10

Table 3. – Percentage of species with narrow and broad habitat ranges among native species, archaeophytes, and neophytes.

Species category	native	archaeophytes	neophytes
Specialists (in 1–5 habitats)	49.6	51.5	76.0
Intermediate (in 6–10 habitats)	21.7	27.5	18.4
Generalists (in > 10 habitats)	28.7	21.0	5.6

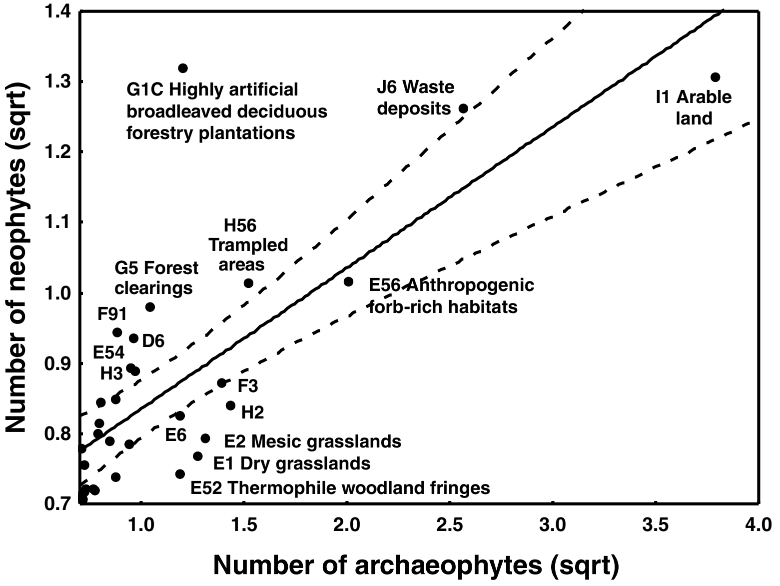

Fig. 1. – The relationship between the number of archaeophytes and neophytes, calculated from the mean values for habitats. The line was fitted with least-squares regression ($r = 0.780$, $P < 0.001$); 95% confidence interval is shown. The abbreviations refer to EUNIS habitats (see Table 1).

Table 4. Mean numbers and mean total covers of archaeophytes, neophytes and native species in vegetation plots assigned to particular habitat types. Absolute numbers of species among different habitats should not be directly compared because of the different plot sizes. EUNIS habitat names are abbreviated; for full names see Table 1. Arch – archaeophytes, Neo – neophytes, Nat – native species.

EUNIS habitat type	Mean number of species			Mean percentage number of species			Mean cover (%)		
	Arch	Neo	Nat	Arch	Neo	Nat	Arch	Neo	Nat
C1 Standing waters	0	0.1	3.5	0	3.9	96.1	0	5	67
C2 Running waters	< 0.1	0.1	9.8	0.2	1.0	98.8	< 1	1	61
C3 Littoral zone	0.4	0.3	9.3	2.5	2.9	94.6	1	4	73
D1 Raised bogs	< 0.1	0	9.7	0.1	0	99.9	< 1	0	48
D2 Poor fens and transition mires	0.1	< 0.1	18.2	0.5	0.1	99.4	< 1	< 1	65
D4 Base-rich fens	0.3	0.1	23.4	1.4	0.2	98.4	1	< 1	68
D6 Brackish marshes	0.6	0.5	10.8	4.3	3.9	91.9	1	2	74
E1 Dry grasslands	1.4	0.1	24.7	6.0	0.7	93.3	5	< 1	70
E2 Mesic grasslands	1.6	0.2	28.5	5.3	0.7	94.0	11	2	78
E3 Wet grasslands	0.5	0.2	30.3	1.6	0.5	97.8	1	< 1	86
E4 Alpine grasslands	0	< 0.1	13.7	0	0.1	99.9	0	< 1	77
E5.2 Woodland fringes	1.1	0.1	26.4	4.1	0.3	95.6	4	< 1	75
E5.4 Wet tall-forb stands	0.6	0.4	16.1	3.8	3.5	92.7	2	12	77
E5.5 Subalpine tall-forb stands	0.1	< 0.1	16.7	0.7	0.2	99.1	< 1	< 1	80
E5.6 Anthropogenic tall-forb stands	4.1	0.7	12	25.1	4.4	70.5	24	10	59
E6 Inland saline grasslands	1.2	0.2	16.3	8.1	1.1	90.9	5	1	75
F2 Alpine and subalpine scrub	0	0	23.8	0	0	100	0	0	90
F3 Temperate scrub	1.8	0.4	20.1	8.7	2.3	88.9	8	5	79
F4 Heathlands	0.1	< 0.1	13.6	0.6	0.2	99.3	< 1	< 1	72
F9.1 Riverine willow stands	0.4	0.6	17.3	1.6	2.9	95.4	1	3	88
F9.2 Willow carrs	0.2	0.2	12.7	1.3	1.6	97.1	< 1	< 1	88
G1 Broadleaved woodland	0.2	0.3	26.3	0.6	1.1	98.2	< 1	2	88
G1.C Broadleaved plantations	1.2	1.3	18.9	6.6	6.9	86.4	6	61	73
G3 Coniferous woodland	< 0.1	< 0.1	13.5	0.1	0.1	99.8	< 1	< 1	81
G3.F Coniferous plantations	0.3	0.2	18.8	1.4	0.9	97.7	1	2	85
G4 Mixed woodland	0.2	0.2	25.2	0.5	0.7	98.8	< 1	1	85
G5 Forest clearings	0.9	0.6	18.7	4.2	2.8	93.0	3	4	75
H2 Screes	1.9	0.3	14.4	10.7	1.4	87.9	7	1	45
H3 Cliffs and outcrops	0.6	0.4	7.0	9.5	7.0	83.6	3	3	28
H5.6 Trampled areas	2.2	0.6	9.2	21.8	6.0	72.2	18	3	54
I1 Arable land	14.6	1.4	10.2	55.5	5.6	38.9	43	10	32
J6 Waste deposits	6.6	1.3	5.8	47.3	9.6	43.2	46	11	34

Fifteen archaeophytes and fifteen neophytes with the broadest habitat range in terms of the number of habitats occupied are listed in Table 2. The proportion of species that are only found in a few habitats increases from native species through archaeophytes to neophytes while that of species found in several habitats decreases in the same direction (Table 3).

Table 5. Pearson correlations between the numbers of archaeophytes, neophytes and native species, calculated within habitats. Square-root transformed species numbers were used for calculation. EUNIS habitat names are abbreviated; for full names see Table 1. *n* – number of plots, Arch – archaeophytes, Neo – neophytes, Nat – native species. Significance levels: *** P < 0.001, ** P < 0.01, * P < 0.05, n.s. – non-significant.

EUNIS habitat type	*n*	Arch vs. Nat	Neo vs. Nat	Arch vs. Neo
C1 Standing waters	1028	n.s.	0.080 **	n.s.
C2 Running waters	254	0.152 *	0.163 **	n.s.
C3 Littoral zone	2891	0.371 ***	0.295 ***	0.481 ***
D1 Raised bogs	75	0.369 **	n.s.	n.s.
D2 Poor fens and transition mires	375	0.371 ***	n.s.	0.137 **
D4 Base-rich fens	49	n.s.	n.s.	n.s.
D6 Brackish marshes	32	n.s.	n.s.	n.s.
E1 Dry grasslands	2508	0.080 ***	–0.105 ***	0.156 ***
E2 Mesic grasslands	1698	0.106 ***	–0.109 ***	0.331 ***
E3 Wet grasslands	2251	0.119 ***	n.s.	0.089 ***
E4 Alpine grasslands	94	n.s.	n.s.	n.s.
E5.2 Woodland fringes	369	0.107 *	n.s.	n.s.
E5.4 Wet tall-forb stands	734	–0.121 ***	–0.230 ***	0.476 ***
E5.5 Subalpine tall-forb stands	218	–0.149 *	n.s.	n.s.
E5.6 Anthropogenic tall-forb stands	800	n.s.	n.s.	0.273 ***
E6 Inland saline grasslands	151	n.s.	0.211 **	0.343 ***
F2 Alpine and subalpine scrub	24	n.s.	n.s.	n.s.
F3 Temperate scrub	102	n.s.	n.s.	0.308 **
F4 Heathlands	228	0.365 ***	0.135 *	n.s.
F9.1 Riverine willow stands	20	n.s.	n.s.	0.642 **
F9.2 Willow carrs	48	n.s.	n.s.	n.s.
G1 Broadleaved woodland	1660	0.226 ***	0.098 ***	0.209 ***
G1.C Broadleaved plantations	27	n.s.	n.s.	n.s.
G3 Coniferous woodland	385	0.334 ***	0.173 ***	n.s.
G3.F Coniferous plantations	207	0.267 ***	0.170 *	0.277 ***
G4 Mixed woodland	855	0.233 ***	0.213 ***	0.373 ***
G5 Forest clearings	491	0.129 **	0.270 ***	0.449 ***
H2 Screes	50	0.445 *	n.s.	0.521 ***
H3 Cliffs and outcrops	236	–0.216 ***	–0.221 ***	0.356 ***
H5.6 Trampled areas	777	–0.154 ***	n.s.	0.314 ***
I1 Arable land	1441	0.265 ***	0.080 **	0.151 ***
J6 Waste deposits	390	0.406 ***	0.136 **	0.275 ***
No. of positive significant correlations		17	12	19
No. of negative significant correlations		4	4	0
No. of non-significant correlations		11	16	13

The highest numbers of aliens, both archaeophytes and neophytes, are found on arable land (Table 4). This habitat is followed by waste deposits, anthropogenic tall-forb stands and trampled habitats. High numbers of neophytes are also found in broadleaved forestry plantations. It is important to note, however, that the absolute numbers of species cannot be directly compared between habitats because the plots used in the analysis varied in size. When the habitat comparison is based on the proportional covers of alien species instead of numbers, these five habitats remain among the most invaded, however, the dominance of neophytes becomes striking in the broadleaved plantations of non-native trees such as *Populus ×canadensis* or *Robinia pseudacacia*. A comparatively high cover of neophytes is also found in wet tall-forb stands, despite the few neophytes in this habitat. Raised bogs, alpine grasslands, alpine and subalpine scrub and natural coniferous woodlands are entirely or nearly free of alien species (Table 4).

No relationship between the number of archaeophytes and native species was found in the analysis across different habitats ($r = –0.116$, $P = 0.527$). Analyses performed within habitats revealed positive relationship in 17 habitats, negative in 4 and non-significant in 11 (Table 5). There was also no dependence of the number of neophytes on the number of native species in the between-habitat analysis ($r = –0.258$, $P = 0.123$). The within-habitat analyses revealed 12 positive, 4 negative and 16 non-significant relationships (Table 5). By contrast, there were strong positive relationships between the number of archaeophytes and neophytes, both in the between-habitat ($r = 0.780$, $P < 0.001$; Fig. 1) and within-habitat analyses (19 positive, none negative, 13 non-significant; Table 5). Archaeophytes tend to be over-represented in semi-natural dry and mesic grasslands and neophytes in disturbed habitats with woody vegetation on fertile soils, such as broadleaved forestry plantations, forest clearings and riverine willow scrub (Fig. 1).

Discussion

Level of invasion and habitat invasibility

It needs to be pointed out that the data analysed in this paper do not allow to evaluate invasibility of the individual habitat types, understood as their intrinsic susceptibility to invasion. Instead, the level of invasion (Hierro et al. 2005), expressed as the number of alien species and their proportional contribution to the total species richness, or the proportion of the total community cover they make up, was evaluated. It is suggested that variations in the level of invasion among recipient communities could be simply due to differences in the number of aliens arriving in the communities (Williamson 1996, Lonsdale 1999). Whether a region, plant community or habitat is more invasible than another is not simply whether it has more alien species, but whether it is intrinsically more susceptible to invasion (Lonsdale 1999). The number of alien species in a community/habitat is the product of both the number of alien species introduced and their survival rate in the new environment (Lonsdale 1999). Real differences in invasibility can only be assessed by analysing residuals from the relationship between invasion success and propagule pressure (Williamson 1996). Indeed, models incorporating propagule pressure are markedly superior to those invoking only environmental parameters for explaining distribution patterns and abundance of invaders at a regional scale (Rouget & Richardson 2003). Unfortunately, propagule pressure is difficult to measure, particularly on a large spatial scale. Therefore large-scale studies usually use quantitative surrogates for propagule pressure, e.g. human population size or density (Pyšek et al. 2002b, 2003a, McKinney 2004, Taylor & Irwin 2004). The aim of the present study was to quantify the level of invasion of different habitats in the Czech Republic, so no attempt was made to separate the effects of habitat invasibility and propagule pressure; such analyses are for future studies, for which this paper provides the basic descriptive statistical figures.

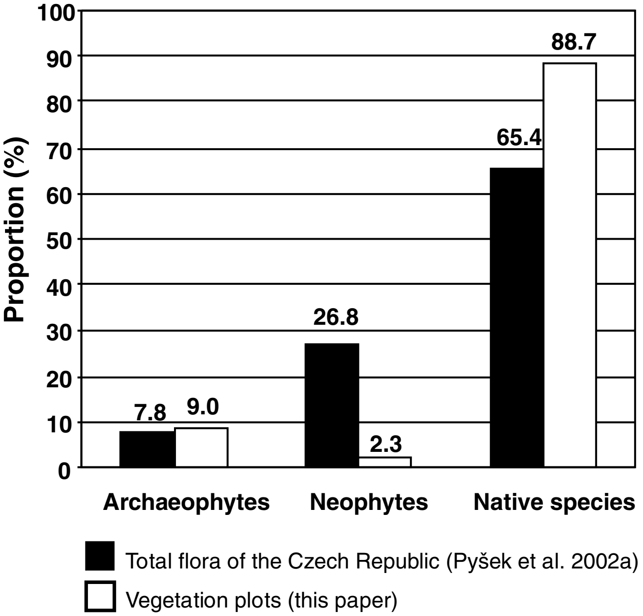

Fig. 2. – Percentage proportions of alien and native species in the total flora of the Czech Republic and in the vegetation plots analysed in the present study.

Effects of scale on the level of invasion

Unlike other studies, which assessed the proportional representation of alien species in larger areas, such as countries (Essl & Rabitsch 2002, Pyšek et al. 2002a), cities (Pyšek 1998), or grid squares of floristic mapping (Kühn et al. 2003, Deutschewitz et al. 2004, Pino et al. 2005), plots ranging in size from units to hundreds of m^2 were used in this study. This shift to a finer scale strongly affected the representation of neophytes. This group of aliens makes up 26.8% of the flora of the Czech Republic (Pyšek et al. 2002a) and 25.2% of the flora of an average Central European city (Pyšek 1998), but only 2.3% of the species found in an average vegetation plot (Fig. 2). Even annual ruderal vegetation (waste deposits), the habitat with the highest proportion of neophytes, contained only 10.5% neophytes. This might be partly caused by a bias in the phytosociological database towards less invaded plots. Especially in natural and semi-natural vegetation, phytosociologists may tend to place their plots in sites less affected by invasions. However, due to the strong tradition of carrying out vegetation research in man-affected habitats in the Czech Republic, also stands with many alien species can be considered reasonably well represented in our data set. In spite of the possible bias in the data, we may conclude that the number of neophyte species is low in most habitats. This contrasts with a quite high number of neophyte species in the total flora of the country, but it is mainly due to rare casual species (Pyšek et al. 2002a). A similar pattern was found by Kowarik (1995) in the city of Berlin, where neophytes were over-represented among rare and very rare species. In our data set, there are also many species of neophytes that are restricted to a few habitats, as well as few species that are found in more than 10 habitats (Tables 2 & 3). To a large extent, this is a consequence of the rarity of most neophytes, but it is unclear whether there is also a high proportion of true habitat specialists among neophytes. Interestingly, the proportion of archaeophytes is similar in the total flora of the country (7.8%) and vegetation plots (9.0%) (Fig. 2). The proportion of archaeophytes restricted to 1–5 habitats is close to the corresponding figure for native species and that of archaeophytes found in more than 10 habitats is only slightly lower than that of native species (Table 3). This reflects that during the long time since their arrival, many archaeophytes have spread over the territory and succeeded to colonize different habitats (Pyšek et al. 2005).

Level of invasion of different habitats

The current study demonstrated a considerable variation in the level of invasion of different habitats (Table 4). As already documented in studies from other parts of Central Europe (Kowarik 1995, Walter et al. 2005) the most invaded habitats are those most affected by man, such as arable land, waste deposits, anthropogenic tall-forb stands or trampled areas. By contrast, the least invaded are nutrient-poor habitats in the mountains, such as alpine grasslands or scrub, bogs or natural coniferous woodlands.

The decreasing number and proportion of alien species with increasing altitude is reported by many studies, performed either within single habitats or across different habitats (Mihulka 1998, Pyšek et al. 2002b, 2005, Lososová et al. 2004). There seems to be no single unequivocal explanation of this pattern. It is possible that most of the alien species that spread into the temperate zone originated from warm areas (Pyšek et al. 2003b) and the cold mountainous climate is beyond their ecological tolerance. Interestingly, invasions of montane species from one mountain range to another are uncommon, probably due to the strong migration barrier posed by lowlands. Another possible explanation is that the stressful mountainous habitats are inherently less invasible than the more favourable habitats at low altitudes. However, the higher level of invasion of low-altitudinal habitats can simply result from the higher immigration of propagules of alien species with the transport of people and goods, which is much more intensive in densely populated lowlands and mid altitudes than in the mountains (Lonsdale 1999). Similarly, it is difficult to determine whether the high proportion of alien species in anthropogenic habitats is due to an increased input of the propagules of alien species in densely populated areas or intrinsic habitat properties, such as frequent disturbances, canopy openness, fine-scale heterogeneity or high nutrient supply.

Another tendency, which can be seen in our data, is that habitat types with dense vegetation have comparatively low numbers of alien species, while habitat types with open vegetation vary considerably in the number of aliens they harbour. Nutrient-rich habitats, such as arable land and waste deposits, where the vegetation is sparse mainly due to disturbances, contain many aliens. By contrast, nutrient-poor habitats, such as cliffs, screes or bogs, where the canopy is open mainly due to nutrient limitation, are usually invaded to a lesser degree. It seems from this comparison that the extent of the canopy is not a reliable predictor of the level of invasion in between-habitat comparisons. Open habitats are mainly invaded if fertile, i.e. open mainly due to disturbance, whereas those that are open due to environmental stress are less prone to invasions. However, it is probably impossible to test this hypothesis using observational data, because invading aliens either increase the total vegetation cover or decrease the cover of native species, making it difficult to separate cause and effect.

Relationships between alien and native plants

One of the frequently debated issues in invasion ecology is the relationship between richness of alien and native species. Elton (1958) suggested that communities richer in native species tend to be more resistant against invasions by alien species. Several recent studies do not confirm this hypothesis and, more importantly, demonstrate that the relationship depends on the spatial scale of the study, namely the size of the sampling units (Levine 2000, Levine et al. 2002, Fridley et al. 2004, Herben et al. 2004). In larger sampling units, species richness of aliens usually increases with that of native species, because both species groups positively respond to increasing landscape heterogeneity and availability of different habitats (Shea & Chesson 2002, Davies et al. 2005). Positive relationships between the number of alien and native species were found for natural or administrative regions, islands, nature reserves or grid cells of plant distribution atlases (Planty-Tabacchi et al. 1996, Lonsdale 1999, Pyšek et al. 2002b, Deutschewitz et al. 2003, Kühn et al. 2003, Espinosa-García et al. 2004, Pino et al. 2005; see Herben et al. 2004 for further references). On the scale of vegetation plots, where neigbourhood interactions between plants can be important, both positive and negative relationships were found (Stohlgren et al. 1999, Sax 2002, Brown & Peet 2003, Gilbert & Lechowicz 2005). In the present study, based on vegetation plots, both positive and negative relationships were also found within different habitats, but positive and non-significant relationships prevailed (Table 5). Alien versus native species richness relationships calculated between habitats were not confirmed for either archaeophytes or neophytes. These results suggest that at the scale of the vegetation plots (up to hundreds m^2), the relationship between alien and native species richness depends on the habitat, but the prevalence of positive relationships indicates that this scale is probably still too large to allow neigbourhood interactions to become the main determinant of community structure.

The relationship between species richness of archaeophytes and neophytes was generally positive, as revealed both in the analysis across different habitats (Fig. 1) and in separate analyses for most of the habitats. Still there are some remarkable differences in habitat affinities between these two groups of aliens. Within the most invaded habitats, i.e. arable land and waste deposits, archaeophytes tend to be over-represented in the former and neophytes in the latter (Fig. 1). A similar result is reported by Kühn et al. (2003) in a study based on an analysis of the grid distribution atlas of vascular plants in Germany. This pattern reflects the history of invasion. While most archaeophytes initially spread into landscapes dominated by agricultural land use, because their invasion was facilitated or directly caused by agricultural activities, many neophytes spread in urbanized landscapes with developed transport facilities and industrial infrastructure. Archaeophytes also tend to be over-represented in dry and mesic grasslands, which probably reflects their ecology in the native range. Most archaeophytes came to Central Europe from the Near East or southern Europe (Pyšek et al. 2002a, 2005), where they were components of dry, open grasslands or therophytic habitats, and have retained their affinity for grasslands in their secondary range. By contrast, neophytes tend to be over-represented in disturbed, nutrient-rich habitats associated with woodland or scrub, such as broadleaved deciduous forestry plantations, forest clearings or riverine willow scrub. This probably reflects the fact that many neophytes in Central Europe originated from the temperate forest biome of eastern North America or eastern Asia (Pyšek et al. 2002a).

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Souhrn

Kvantitativní zastoupení invazních druhů rostlin v různých biotopech České republiky bylo stanoveno na základě propojení České národní fytocenologické databáze, Katalogu nepůvodních druhů České republiky a evropské klasifikace biotopů EUNIS (tab. 1). Bylo použito 20 468 fytocenologických snímků klasifikovaných do 32 biotopů. Fytocenologické snímky obsahovaly v průměru 9,0 % archeofytů a 2,3 % neofytů. Zatímco podíl archeofytů ve snímcích je podobný jejich podílu na celkovém počtu druhů květeny ČR, podíl neofytů ve snímcích je výrazně menší (obr. 2) kvůli vzácnosti většiny druhů této skupiny. Nepůvodní druhy zastoupené v největším počtu biotopů jsou vyjmenovány v tab. 2. Mezi neofyty silně převažují druhy s výskytem v několika málo biotopech a jen 5,6 % z nich bylo zaznamenáno ve více než deseti biotopech. Ve skupině archeofytů a zejména původních druhů je podíl druhů zaznamenaných ve více biotopech větší (tab. 3).

Nejvíce nepůvodních druhů bylo zaznamenáno na orné půdě, v jednoleté ruderální vegetaci, v antropogenních vysokobylinných porostech a na sešlapávaných stanovištích, kde průměrný podíl archeofytů dosahuje 18–56 % a neofytů 4,2–9,5 % (tab. 4). Hodně neofytů se také vyskytuje v lesních kulturách s nepůvodními listnatými stromy. V uvedených biotopech jsou nepůvodní rostliny zastoupeny nejen největšími počty druhů, ale dosahují také největší pokryvnosti. Velká pokryvnost neofytů je charakteristická také pro vysokobylinnou vegetaci vlhkých půd, kde však jsou zastoupeny poměrně malým počtem druhů. Ve fytocenologických snímcích vrchovišť, alpínských trávníků, alpínské a subalpínské keřové vegetace a v přirozených jehličnatých lesích nepůvodní druhy zcela nebo téměř chybějí.

Klasická, avšak kontroverzní hypotéza, podle které nepůvodní druhy rostlin více pronikají do společenstev druhově chudých, byla diskutována na základě výpočtu korelací mezi zastoupením archeofytů, neofytů a původních druhů. Při srovnání různých biotopů nebyl prokázán vztah mezi počtem druhů archeofytů nebo neofytů a původních druhů, byl však zjištěn pozitivní vztah mezi počtem druhů archeofytů a neofytů (obr. 1). Přestože je výskyt obou těchto skupin nepůvodních druhů ve fytocenologických snímcích silně korelován, jsou archeofyty poměrně hojně zastoupeny v polopřirozených suchých trávnících a loukách, kde jsou neofyty spíše vzácnější; naopak neofyty se častěji vyskytují v narušovaných biotopech s dřevinnou vegetací na produktivních půdách, jako jsou lesní kultury s nepůvodními listnatými stromy, lesní paseky nebo vrbové křoviny podél vodních toků. Rovněž dvojice nejvíce invadovaných biotopů, plevelová vegetace na orné půdě a jednoletá ruderální vegetace, se liší poměrem archeofytů k neofytům, který je u první vyšší a u druhé nižší (obr. 1). Při srovnání snímků v rámci jednotlivých biotopů byly vztahy mezi počty archeofytů, neofytů a původních druhů většinou pozitivní nebo nesignifikantní, jen u mála biotopů negativní (tab. 5). Toto zjištění nepodporuje klasickou představu, že by druhově bohatší společenstva byla odolnější vůči pronikání nepůvodních druhů, alespoň ne u většiny biotopů a na plochách o velikosti fytocenologických snímků. Tím se předložená studie shoduje s většinou analýz publikovaných v poslední době, které však pracovaly s řádově menšími počty opakování a často srovnávaly počty druhů na plochách větších než jsou plochy fytocenologických snímků.

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