SEPARATING HABITAT INVASIBILITY BY ALIEN PLANTS FROM THE ACTUAL LEVEL OF INVASION

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Abstract. Habitats vary considerably in the level of invasion (number or proportion of alien plant species they contain), which depends on local habitat properties, propagule pressure, and climate. To determine the invasibility (susceptibility to invasions) of different habitats, it is necessary to factor out the effects of any confounding variables such as propagule pressure and climate on the level of invasion. We used 20 468 vegetation plots from 32 habitats in the Czech Republic to compare the invasibility of different habitats. Using regression trees, the proportion of alien plants, including archaeophytes (prehistoric to medieval invaders) and neophytes (recent invaders), was related to variables representing habitat properties, propagule pressure, and climate. The propagule pressure was expressed as the proportion of surrounding urban and industrial or agricultural land, human population density, distance from a river, and history of human colonization in the region. Urban and industrial land use had a positive effect on the proportion of both archaeophytes and neophytes. Agricultural land use, higher population density, and longer history of human impact positively affected the proportion of archaeophytes.

Disturbed human-made habitats with herbaceous vegetation were most invaded by both groups of aliens. Neophytes were also relatively common in disturbed woody vegetation, such as broad-leaved plantations, forest clearings, and riverine scrub. These habitats also had the highest proportion of aliens after removing the effect of propagule pressure and climate, indicating that they are not only the most invaded, but also most invasible. These habitats experience recurrent disturbances and are rich, at least temporarily, in available nutrients, which supports the hypothesis that fluctuating resources are the major cause of habitat invasibility. The least invaded habitats were mires and alpine-subalpine grasslands and scrub. After removing the effect of propagule pressure and climate, some habitats actually invaded at an intermediate level had very low proportions of aliens. This indicates that these habitats (e.g., dry, wet, and saline grasslands, base-rich fens, and broad-leaved deciduous woodlands) are resistant to invasion.

Key words: archaeophyte; biological invasions; Central Europe; Czech Republic; disturbance; exotic species; invasion resistance; neophyte; plant community; propagule pressure.

Introduction

Human-mediated introductions of alien plant species outside their natural range have significantly changed the diversity of various ecosystems worldwide (Williamson 1996, Mack et al. 2000, Rejmánek et al. 2004, Daehler 2006, Palmer 2006, Richardson 2006). Several comparative studies demonstrate that ecosystems or habitats differ considerably in the numbers and/or proportions of alien species (Crawley 1987, Rejmánek 1989, Kowarik 1995, Pyšek et al. 1998, 2002a, Lonsdale 1999, Chytrý et al. 2005, Rejmánek et al. 2005). These differences can result from habitat properties such as availability of resources unexploited by resident species,

competitive ability of native species, allelopathic interactions, effects of natural enemies, or the disturbance regime (Williamson 1996, Shea and Chesson 2002, Rejmánek et al. 2004, Hierro et al. 2005, Richardson and Pyšek 2006). The theory of fluctuating resource availability (Davis et al. 2000) posits that habitat invasibility is enhanced by pulses in resource availability due to an increased input from external sources or decreased consumption of available resources; the major driver is disturbance which delivers resources to the system and/or decreases their consumption by removing resident vegetation. Alpert et al. (2000) and Shea and Chesson (2002) proposed very similar explanations for habitat invasibility.

However, a large fraction of the variance in alien species richness among sites can be attributed to propagule pressure, i.e., the rate of influx of alien propagules into the target site (Williamson 1996,

Lonsdale 1999, Rouget and Richardson 2003, Lockwood et al. 2005, Colautti et al. 2006, Moore and Elmendorf 2006). To answer the question why some habitats are more invaded than others, one must separate the effects of habitat properties from those of propagule pressure and from other potentially confounding factors, such as climate. In order to achieve this we need to distinguish between the "level of invasion" and "habitat invasibility" (Chytrý et al. 2005, Hierro et al. 2005, Richardson and Pyšek 2006). The former refers to the actual number or proportion of aliens in a habitat whereas the latter denotes the relative number or proportion of aliens when the effects of propagule pressure and confounding variables other than local habitat properties are held constant. Technically, between-habitat comparisons of invasibility can be done in statistical models in which habitat is the predictor variable and residuals from the regression of alien richness on the confounding variables (including measures of propagule pressure) the response variable (Williamson 1996, Lonsdale 1999).

So far, very little is known about the relative importance of habitat properties vs. propagule pressure and other factors as determinants of the actual level of invasion of different habitats (Rouget and Richardson 2003, Colautti et al. 2006). Seed addition experiments (e.g., Tilman 1997) suggest that increased propagule pressure may strongly contribute to the level of invasion. However, such experiments are usually confined to a single habitat or single site, and do not explain between-habitat differences. Observational studies have not provided significant insights either, as they are mostly restricted to a few habitats, single or a few species, use limited numbers of replicates, or fail to separate the effect of habitat properties from that of propagule pressure. Only recent compilations of large databases of vegetation survey plots, which include thousands of records of species composition from all the major habitats of a country or large region (Hennekens and Schaminée 2001), can be used to rigorously compare the levels of invasion between habitats. However, recently published studies (Kowarik 1995, Chytrý et al. 2005, Maskell et al. 2006, Vilà et al. 2007) have not taken into account the variance in propagule pressure between sites and habitats.

The effect of propagule pressure on a broad geographic scale, for a variety of habitats and a large species pool of potential invaders, can be quantified through proxy variables closely related to propagule pressure. Since invasions are human-mediated processes, suitable proxy variables are those that quantify the degree of human activity in the landscape, such as human population density or proportion of the area that is residential, industrial, or agricultural. Accidental or deliberate introductions of alien plants take place mostly in such areas and their naturalized populations produce propagules that spread into the surroundings. Some natural features, such as rivers, can also aid the dispersal of alien plants (Pyšek and Prach 1993); therefore the distance of a site from a river can be another suitable proxy variable for propagule pressure. Joint analysis of such proxy variables, records of species composition of vegetation plots, and information on habitat properties can provide new insights into the relative contribution of habitat properties on the observed level of invasion.

The alien flora of temperate Europe, which is the focus of this paper, comprises two groups of species with different invasion histories: archaeophytes, which arrived before AD 1500, and neophytes, which arrived after that date (Pyšek et al. 2002b). The distinction between these two groups is important, because they differ, to some extent, in their habitat affinities (Kowarik 1995, Pyšek et al. 2002a, 2004, 2005, Kühn et al. 2003, Chytrý et al. 2005). The former are more often associated with dry habitats, grasslands, and agricultural landscape, while the latter are common especially in warm areas, where they invade different habitats on both dry and wet sites. In the context of the present study, the distinction between archaeophytes and neophytes is of particular interest, because due to their shorter residence time in invaded areas (Pyšek and Jarošík 2005), many neophytes have probably not yet occupied all the suitable habitats. Therefore we hypothesize that the distribution of neophytes is relatively less dependent on habitat type and more dependent on propagule pressure than the distribution of archaeophytes.

In this paper, we approach the problem of habitat vs. propagule limitation of alien species invasions by analyzing 20 468 vegetation plots from 32 habitats in the Czech Republic, a country which includes nearly all the habitats of temperate Europe except coastal ones (Chytrý et al. 2001) and has a well-studied native and alien flora (Pyšek et al. 2002b). To our knowledge, this is the largest data set ever used to assess the pattern of plant invasions across different habitats. Our main questions are: (1) What are the relative effects of local habitat properties, propagule pressure, and climate on the level of invasion by archaeophytes and neophytes? (2) Does the actual level of invasion reflect habitat invasibility? (3) Which habitats are easily invaded and which are resistant to invasion?

MATERIALS AND METHODS

Vegetation data

The data source for this study is the database of vegetation plot records (relevés) for the Czech Republic (Chytrý and Rafajová 2003). For each plot there is a list of vascular plants with their cover-abundances recorded on the Braun-Blanquet or Domin scale (van der Maarel 1979) and basic information on geographic location, habitat, and vegetation structure. Of the 63 730 plots in the database in July 2004, we omitted those that (1) could not be unequivocally assigned to one of the habitat types (Table 1); (2) lacked an accurate geographic location; (3) were of extreme size with respect to

TABLE 1. Overview of the European Nature Information System (EUNIS) habitat types used in this study.

EUNIS code	Habitat name	No. plots
C1	surface standing waters	1028
C2	surface running waters	254
C3	littoral zone of inland surface waterbodies (combined with D5 [sedge and reedbeds, normally without free-standing water])	2891
D1	raised and blanket bogs	75
D2	valley mires, poor fens, and transition mires	375
D4	base-rich fens	49
D6	inland saline and brackish marshes and reedbeds	32
E1	dry grasslands	2508
E2	mesic grasslands	1698
E3	seasonally wet and wet grasslands	2251
E4	alpine and subalpine grasslands	94
E5.2	thermophile woodland fringes	369
E5.4	moist or wet tall-herb and fern fringes and meadows	734
E5.5	subalpine moist or wet tall-herb and fern habitats	218
E5.6	anthropogenic forb-rich habitats	800
E6	inland saline grass and herb-dominated habitats	151
F2	arctic, alpine, and subalpine scrub habitats	24
F3	temperate and mediterraneo-montane scrub habitats	102
F4	temperate shrub heathland	228
F9.1	riverine and lakeshore (*Salix*) scrub	20
F9.2	*Salix* carr and fen scrub	48
G1	broad-leaved deciduous woodland	1660
G1.C	highly artificial broad-leaved deciduous forestry plantations	27
G3	coniferous woodland	385
G3.F	highly artificial coniferous plantations	207
G4	mixed deciduous and coniferous woodland	855
G5	lines of trees, small anthropogenic woodlands, recently felled woodland, early-stage woodland, and coppice	491
H2	screes	50
H3	inland cliffs, rock pavements, and outcrops (including walls)	236
H5.6	trampled areas	777
I1	arable land and market gardens	1441
X	annual ruderal vegetation	390

Note: EUNIS is the standard international classification of European habitats (Davies and Moss 2003).

plot sizes commonly used in Europe for sampling particular vegetation types (i.e., <50 m^2 or >500 m^2 for woodlands; <10 m^2 or >100 m^2 for scrub; <4 m^2 or >100 m^2 for grasslands, wetlands, and aquatic habitats; and <1 m^2 or >50 m^2 for low-growing vegetation in stressed or disturbed habitats [Chytrý and Otýpková 2003]); or (4) were recorded before 1970 (in order to focus the analysis on the relatively recent patterns of habitat invasion). Although the vegetation plots in the database provided a representative sample of all the major habitats and all regions within the country, their distribution was influenced by the various sources of the data and purposes of the sampling. Therefore, we selected a stratified subsample of the database (see Chytrý et al. 2005 and Knollová et al. 2005 for details) in order to reduce local oversampling of some areas or some habitats. This resulted in a data set with 20 468 plots, which was used in the analysis.

Response and predictor variables

Response variables were (1) proportional number of archaeophyte species and (2) proportional number of neophyte species. For each plot, the total number of vascular plant species (excluding planted crops), number of archaeophytes (pre-AD 1500 aliens), and neophytes (post-AD 1500 aliens) were counted. Classification of species into archaeophytes and neophytes followed Pyšek et al. (2002b) except for *Arrhenatherum elatius*, which was treated as an archaeophyte (see Chytrý et al. 2005 for reasons). We used proportions of archaeophytes and neophytes relative to all species occurring in the plot. We refrained from using absolute species numbers because they may be affected by the size of the plots (Chytrý 2001). There were on average 9.2% ± 17.5% (mean ± SD) archaeophytes and 2.3% ± 5.9% neophytes per plot. In total in all plots, there were 219 archaeophytes, 171 neophytes, and 1451 native species. In the preliminary analyses, we also used total covers of archaeophytes, neophytes, and native species as response variables. Hovewer, the results were generally similar to those obtained for proportional numbers of species; therefore we do not present them in this paper.

Predictor variables were divided into three groups that represented (1) habitat properties, (2) proxy variables of propagule pressure, and (3) climate.

Habitat properties.—

1. *EUNIS habitat type* (hereafter termed "habitat," 32 categories, Table 1).—Each plot was assigned to one

of the habitats in the EUNIS classification (European Nature Information System; Davies and Moss 2003), which is the standard international classification of European habitats. This assignment was based on the expert-based classification of the plots to the phytosociological classification system used in the Czech Republic, which was converted to the EUNIS habitats, following the cross-classification of Chytrý et al. (2001). We used EUNIS habitats on hierarchical level 2 and in a few heterogeneous habitats also on level 3 (Table 1). We distinguished two types of human-made ruderal vegetation (perennial and annual), which are known to differ strongly in the level of invasion (Chytrý et al. 2005) but cannot be assigned to a definite EUNIS habitat. Therefore, we interpreted perennial ruderal vegetation as habitat E5.6 (anthropogenic tall-forb stands), and introduced an ad hoc category X (annual ruderal vegetation). In a previous paper, which contains the descriptive statistics of this data set (Chytrý et al. 2005), the latter category is labeled as J6 (waste deposits).

2. *Total percentage vegetation cover.*—This was calculated from species cover values recorded on the Braun-Blanquet or Domin scale and transformed into percentages as recommended by van der Maarel (1979). Total vegetation cover was calculated from covers of individual species using a model based on the assumption of random species overlap (see Chytrý et al. 2005 for details).

Propagule pressure.—Proxy variables included the following.

1. *Proportional area of urban and industrial land in the surrounding landscape.*—This was measured in circles of a 0.5 km radius around each plot using the CORINE land-cover map in the ArcGIS 8.3 software (ESRI, Redlands, California, USA). CORINE land cover is a standard land-cover data set for Europe based on remote sensing data (*available online*).[6] The category "urban and industrial land" was created by merging several narrowly defined categories of the original land-cover map. The selection of 0.5 km radius is based on the propagule pressure being strongest within a few hundred meters of the source and declining rapidly with increasing distance (Rouget and Richardson 2003, Novák and Konvička 2006).

2. *Proportional area of agricultural land in the surrounding landscape.*—This is measured in the same way as the previous variable.

3. *Human population density.*—This was measured in the administrative district where the plot was located. The country is divided into 206 districts with population density ranging from 32 to 2339 (median 98) inhabitants/km^2, and area from 48 to 1243 (median 319) km^2.

4. *Distance from a river* (two categories: 1 if the plot was situated <100 m from a river or a permanent creek;

0 if >100 m).—This variable was derived from a digital hydrologic map in the ArcGIS 8.3 program.

5. *Altitudinal floristic region.*—This was divided into three categories (Thermophyticum, Mesophyticum, and Oreophyticum) according to the phytogeographic division of the Czech Republic (Skalický 1988). These three regions roughly correspond to areas with different histories of human impact: Thermophyticum to the lowlands, which were settled in the Neolithic; Mesophyticum to the uplands, which were mainly colonized and deforested in the Middle Ages; and Oreophyticum to the mountains, which were colonized during the past five centuries. As the history of human impact may be correlated with the propagule pressure of alien species in these entire regions, we used these regions as an additional surrogate of propagule pressure, hypothetically operating on a coarse scale.

Climate variables.—These are from Vesecký et al. (1958) and included the following.

1. *Altitude* (range 135–1585 m above sea level).—In the Czech Republic, altitude is negatively correlated with mean annual temperature and positively with mean annual precipitation. However, there are local anomalies in the rain-shadow areas in the lee of some mountain ranges. Altitude is correlated with altitudinal floristic region, however the former is more related to climate while the latter better reflects landscape history.

2. *Mean annual temperature* (range 1.0–9.5°C; 50-yr average).

3. *Mean annual precipitation* (range 425–1700 mm; 50-yr average).

Statistical analysis

To model the proportions of archaeophytes and neophytes in vegetation plots, regression trees (Breiman et al. 1984) were constructed using binary recursive partitioning in CART v. 5.0 program (Breiman et al. 1984, Steinberg and Colla 1995). The values of response variables (percentages of archaeophytes and neophytes, respectively) were weighted by the total number of species in each plot. To find the optimal tree, a sequence of nested trees of decreasing size, each the best of all trees of its size, was constructed, and their resubstitution relative errors, corresponding to residual sums of squares, were estimated. A random subset of the data (a test subset), comprising approximately 20% of all vegetation plots, was used to obtain estimates of the cross-validated relative errors of these trees. These estimates were then plotted against tree size, and the tree with the smallest number of terminal nodes was selected as the optimal tree with the provision that estimated cross-validated relative error rate be within one standard error of the minimum (1-SE rule; Breiman et al. 1984). Following De'ath and Fabricius (2000), a series of 50 cross-validations were run, and the modal (most likely) single tree was chosen. The total variance explained by the best single tree was calculated as $R^2 = 1$ − (resubstitution relative error). To compare the results

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[6] ⟨http://reports.eea.europa.eu/COR0-landcover/en⟩
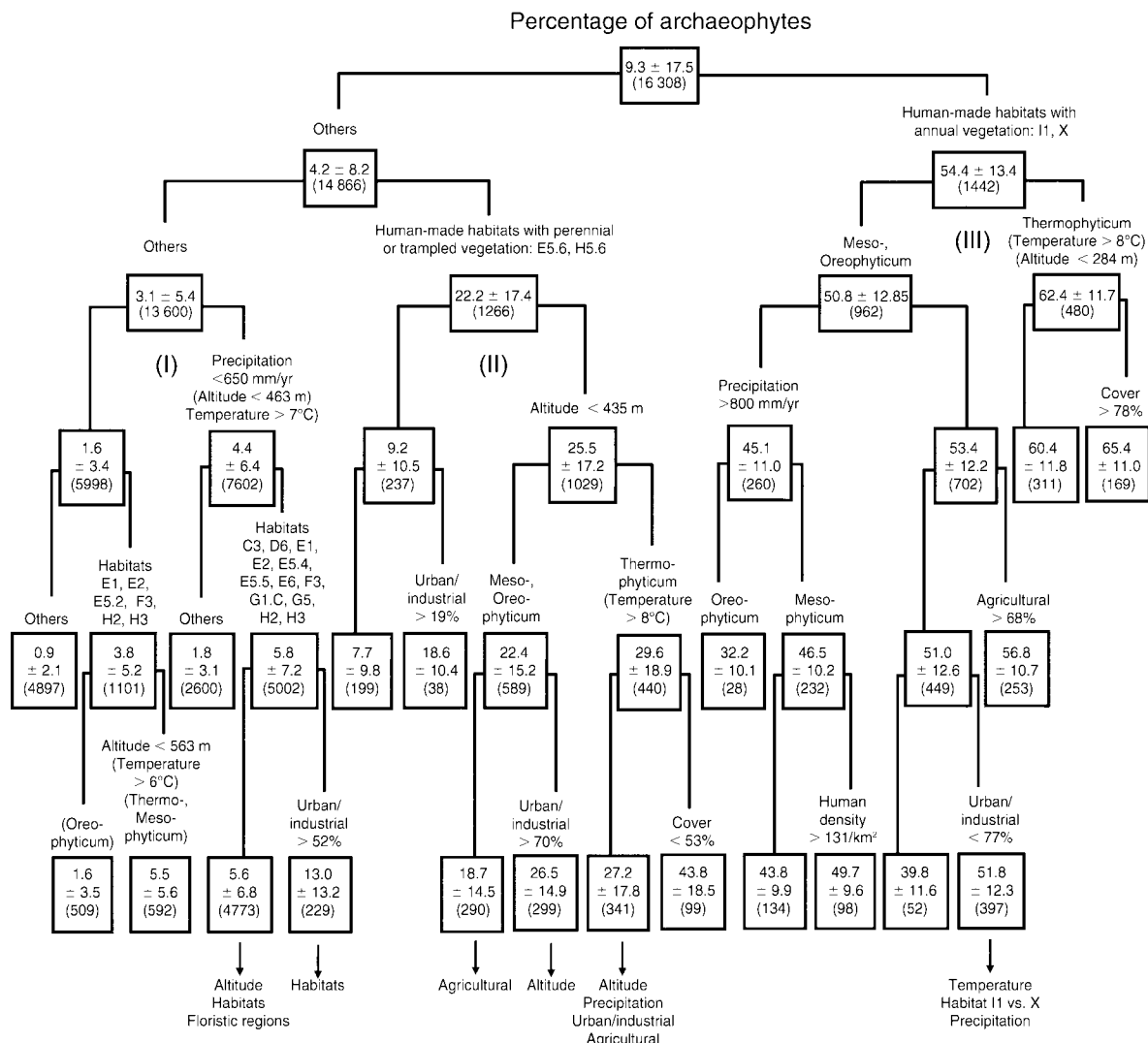
Percentage of archaeophytes

Fig. 1. Regression tree explaining the percentage of archaeophytes (level of invasion) in vegetation plots. Each node of the tree is described by the splitting variable and its split value, mean and standard deviation of percentage of archaeophytes, and number of plots at that node (in parentheses). The lower part of the tree is not shown: nonterminal nodes at the bottom of the figure are labeled with the names of splitting variables at their daughter nodes. Main branches of the tree are labeled I, II, and III. See Table 1 for habitat codes.

of regression trees with traditional parametric models, procedures based on generalized linear models (GLMs) were employed (e.g., Crawley 2002). Their findings were very similar to those of regression trees and are not presented.

The level of invasion, i.e., actual mean proportions of archaeophytes and neophytes, and invasibility, i.e., mean proportions of archaeophytes or neophytes after removing the effects of all variables except habitat properties, were compared among habitats by a posteriori multiple comparisons among means for unequal sample sizes, using the Tukey method with 95% simultaneous confidence intervals (Sokal and Rohlf 1995). Levels of invasion, based on angular (arcsine square-root) transformed proportions to normalize the data and weighted by the total number of species in each

plot to avoid undue influence of species-poor plots, were compared. Invasibility was determined by factoring out the effects of variables of groups 2 (propagule pressure) and 3 (climate). These variables were fitted using GLMs with binomial errors and logit link function (Crawley 2002:513), and by calculating Pearson's standardized residuals of these models (Hastie and Pregibon 1993:205). Residuals from these models were then examined as the response variables (Lonsdale 1999, Pyšek et al. 2005).

RESULTS

Regression tree models for the proportion of alien species

The optimal regression tree for the percentage of archaeophytes (Fig. 1) explained 86.4% of the total

TABLE 2. Variance in proportional representation of archaeophytes and neophytes explained by individual predictors, expressed in terms of the improvement values of the optimal regression trees.

Predictor	Archaeophytes (%)	Neophytes (%)
Habitat properties		
Habitat type	76.7	18.4
Vegetation cover	0.6	0.9
Propagule pressure		
Surrounding urban and industrial land	1.0	3.1
Surrounding agricultural land	0.6	†
Human density	0.1	†
Distance from a river	†	†
Altitudinal floristic region	2.9	†
Climate		
Altitude	2.3	5.9
Temperature	0.1	†
Precipitation	2.1	†
Total	86.4	28.3

Note: Values are percentages of the total variance explained by the model and are obtained by adding all values of each predictor for the model.

† These variables were not selected by the regression tree model.

variance. Most variance was explained by habitat type (76.7%), while the other variables each explained less than 3% (Table 2). The first divisions of the optimal tree (Fig. 1) separated three habitat groups: I, natural and seminatural habitats, with a low percentage of archaeophytes (3.1% ± 5.4%; mean ± SD); II, anthropogenic tall-forb stands (E5.6), and trampled habitats (H5.6), with an intermediate percentage of archaeophytes (22.2% ± 17.4%); and III, annual vegetation in human-made habitats, both on arable land (I1) and at ruderal sites (X), with a high percentage of archaeophytes (54.4% ± 13.4%). In the next division, each of these three groups was divided according to climate variables. Consistently in each group, a higher percentage of archaeophytes was found in warm and dry lowlands or low-altitude hilly landscapes. The lowest percentage of archaeophytes (0.9% ± 2.1%) was found in natural and seminatural vegetation in areas with precipitation >650 mm/yr, except for some types of grasslands (E1, E2, E5.2), temperate scrub (F3), screes (H2), and cliffs/walls (H3). In contrast, the highest percentage of archaeophytes (65.4% ± 11.0%) was found in relatively dense (cover > 78%) annual vegetation in human-made habitats (I1, X) of warm areas at low altitudes.

The optimal regression tree for the percentage of neophytes (Fig. 2) explained 28.3% of the total variance. Habitat was the most important predictor (18.4%), followed by altitude (5.9%), surrounding urban and industrial land (3.1%), and vegetation cover (0.9%; Table 2). This tree first separated two habitat groups (Fig. 2): I, most of the natural and seminatural habitats, with low percentages of neophytes (0.7% ± 2.1%; mean ± SD); and II, human-made habitats (E5.6, H5.6, I1 and

X), disturbed woody vegetation (F9.1, riverine willow stands; G1.C, broad-leaved plantations; G5, forest clearings), standing waters and their littoral zones (C1, C3), and cliffs/walls (H3; 4.6% ± 6.0%), with high percentages of neophytes (4.6% ± 6.0%). The lowest percentage of neophytes (0.3% ± 1.1%) was found in natural and seminatural habitats (except disturbed woody vegetation, standing waters and their littoral zones, and cliffs/walls) at altitudes above 465 m. The highest percentage of neophytes (26.7% ± 20.3%) occurred in human-made habitats, disturbed woody vegetation, standing waters and their littoral zones, and cliffs/walls at altitudes below 365 m that were surrounded by urban and industrial land and had open vegetation cover (>23%).

Net effects of habitats on the proportion of alien species

Fig. 3 compares actual proportions of aliens in habitats and their relative proportions, expressed as residuals of the proportions of aliens from the model that included all the explanatory variables except habitat. The former is the level of invasion while the latter is habitat invasibility, i.e., the expected proportion of aliens if propagule pressure and climate were constant across habitats.

Habitats with the largest proportion of archaeophytes (Fig. 3A) are arable land (I1), annual ruderal vegetation (X), anthropogenic tall-forb stands (E5.6), and trampled areas (H5.6). If actual proportions are compared (Fig. 3A), most of the habitats included in the analysis significantly differ from one another (Tukey test, $P <$ 0.05, not shown). In contrast, the first three of the above mentioned habitats are significantly different from all the others in their invasibility (Fig. 3B), while most of the other habitats do not differ significantly in invasibility from each other. This indicates that these human-made habitats would be the most invaded even if they experienced the same propagule pressure and climate as the other habitats. Thus, they are not only highly invaded but also highly invasible.

The results for neophytes are similar. The most invaded habitats are the same as for archaeophytes, but broad-leaved forestry plantations (G1.C) and cliffs/walls (H3) also exhibit high levels of invasion (Fig. 3C).

Some habitats are characterized by an intermediate level of invasion by both archaeophytes and neophytes (central position in the ranking of habitats in Fig. 3A, C) but this is, to a certain extent, due to their location in warm low-altitude areas with a high propagule pressure (e.g., dry grasslands [E1], wet grasslands [E3], woodland fringes [E5.2], inland saline grasslands [E6], base-rich fens [D4], and broad-leaved woodlands [G1]; for archaeophytes also saline marshes [D6]; for neophytes also mesic grasslands [E2] and mixed woodlands [G4]). The shift of these habitats to the right in Fig. 3B, D indicates that if they were found in areas with the same propagule pressure and climate as the other habitats, they would be less invaded than most other habitats.
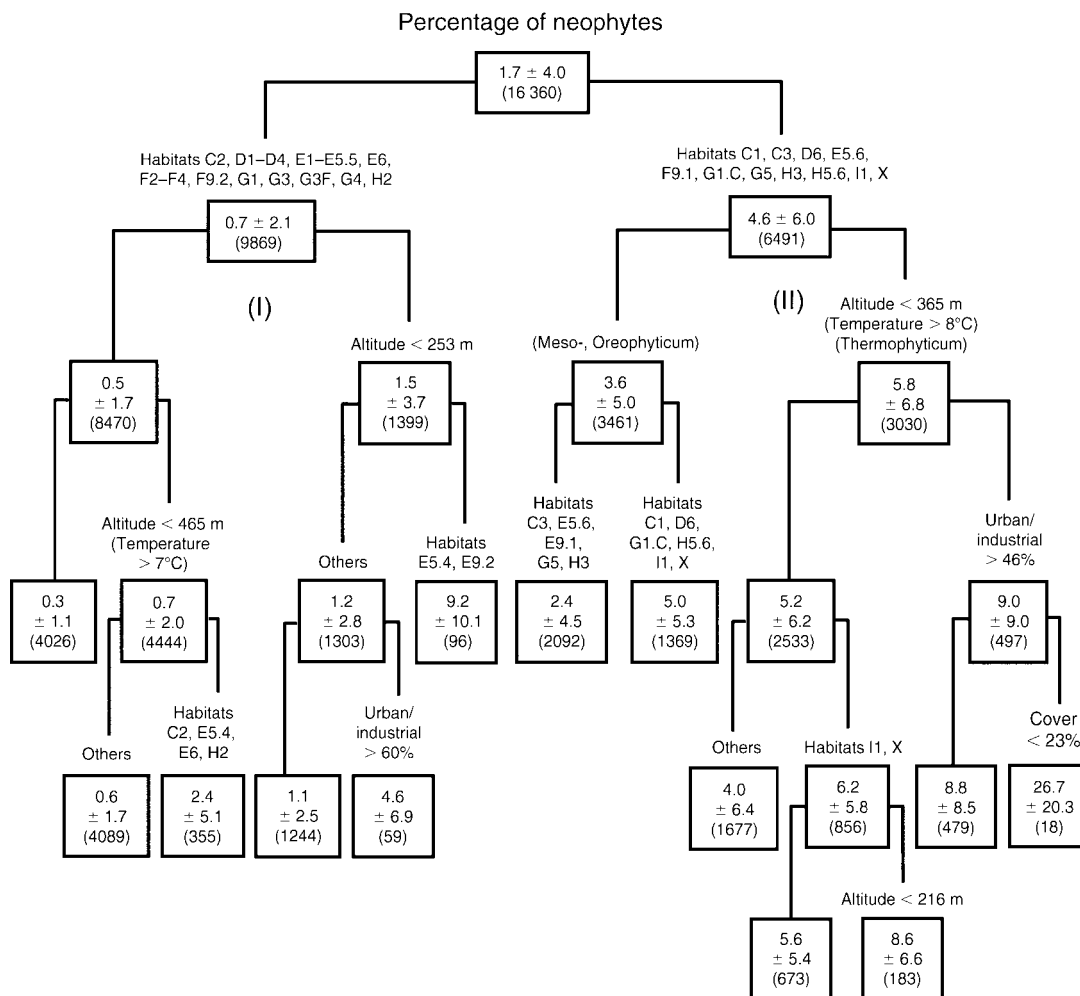
Percentage of neophytes

1.7 ± 4.0
(16 360)

Habitats C2, D1–D4, E1–E5.5, E6,
F2–F4, F9.2, G1, G3, G3F, G4, H2

Habitats C1, C3, D6, E5.6,
F9.1, G1.C, G5, H3, H5.6, I1, X

0.7 ± 2.1
(9869)

4.6 ± 6.0
(6491)

(I)

(II)

Altitude < 365 m
(Temperature > 8°C)
(Thermophyticum)

Altitude < 253 m

(Meso-, Oreophyticum)

0.5 ± 1.7
(8470)

1.5 ± 3.7
(1399)

3.6 ± 5.0
(3461)

5.8 ± 6.8
(3030)

Altitude < 465 m
(Temperature > 7°C)

Others

Habitats
E5.4, E9.2

Habitats
C3, E5.6,
E9.1,
G5, H3

Habitats
C1, D6,
G1.C, H5.6,
I1, X

Urban/
industrial
> 46%

0.3 ± 1.1
(4026)

0.7 ± 2.0
(4444)

1.2 ± 2.8
(1303)

9.2 ± 10.1
(96)

2.4 ± 4.5
(2092)

5.0 ± 5.3
(1369)

5.2 ± 6.2
(2533)

9.0 ± 9.0
(497)

Habitats
C2, E5.4,
E6, H2

Urban/
industrial
> 60%

Others

Habitats I1, X

Cover
< 23%

Others

0.6 ± 1.7
(4089)

2.4 ± 5.1
(355)

1.1 ± 2.5
(1244)

4.6 ± 6.9
(59)

4.0 ± 6.4
(1677)

6.2 ± 5.8
(856)

8.8 ± 8.5
(479)

26.7 ± 20.3
(18)

Altitude < 216 m

5.6 ± 5.4
(673)

8.6 ± 6.6
(183)

FIG. 2. Regression tree explaining the percentage of neophytes (level of invasion) in vegetation plots. Each node of the tree is described by the splitting variable and its split value, mean and standard deviation of percentage of neophytes, and number of plots at that node (in parentheses). Main branches of the tree are labeled I and II. See Table 1 for habitat codes.

Thus they seem to possess some mechanism of resistance to invasion.

DISCUSSION

Habitat vs. propagule limitation

In this study, habitats were identified as much more important determinants of the level of invasion than either propagule pressure or climate (Table 2). It could be argued that proxy variables only give a very rough estimate of real propagule pressure, and therefore a more accurate measure of propagule pressure would explain more of the variance in the level of invasion between sites or habitats. Still, this analysis shows that some of these proxies are closely associated with the level of invasion, at least in some habitats and certain macroclimatic regions. The inclusion of the proxies of propagule pressure in the analysis clearly demonstrated which habitats are susceptible or resistant to alien plant invasions.

To evaluate the relative role of habitat properties, propagule pressure, and other factors, it is important to consider the context of the study. For example, Rouget and Richardson (2003) report a higher importance of propagule pressure than of environmental variables in the distribution of three invasive tree species in South Africa. However, they studied the recent spread of individual invasive populations, in which offspring usually tend to establish near their parents, and propagule pressure is crucial. Our study differs from such studies in focusing on many different habitats and multispecies assemblages, which experienced tens to thousands of years of invasion history. In this context, the importance of habitat clearly increases.

Invasible and invasion-resistant habitats

The level of invasion of different habitats in the Czech Republic follows similar patterns to those reported from other parts of Europe (Crawley 1987, Kowarik 1995,
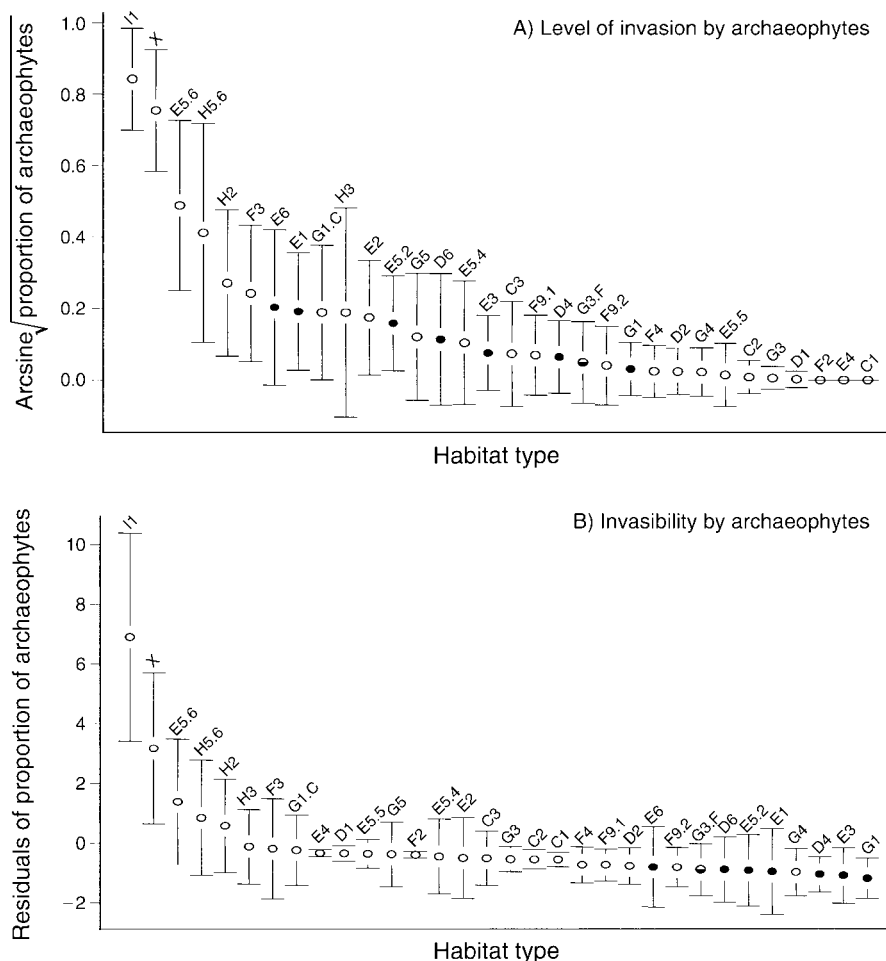
FIG. 3. Proportion of archaeophytes and neophytes in particular habitats (mean ± SD). (A, C) Level of invasion, i.e., actual (arcsine square-root transformed) proportion of archaeophytes or neophytes in vegetation plots. (B, D) Invasibility, i.e., proportion of archaeophytes or neophytes after removing the effects of propagule pressure and climate, using residuals from the regression of archaeophyte or neophyte proportion on these confounding variables. Habitats are ranked by the decreasing level of invasion or invasibility, respectively. Full and semi-open circles indicate the habitats that shifted by ≥10 and ≥5 positions, respectively, after removing the effects of propagule pressure and climate. See Table 1 for habitat codes and sample sizes.

Walter et al. 2005, Vilà et al. 2007), i.e., disturbed human-made habitats are most invaded while nutrient-poor montane habitats are least invaded or not invaded. However, previous studies did not attempt to identify whether this pattern reflects differences in the local properties of these habitats, macroclimate of wider regions, or propagule pressure by aliens, which is indeed much stronger in human-made habitats than in sparsely populated mountain areas. Our study shows that propagule pressure, as well as location in a warm low-altitude area, increases the level of habitat invasion, but habitat properties are crucial.

Human-made habitats in Central Europe, especially those dominated by annual plants, appear to be not only the most invaded, but also the most invasible by both archaeophytes and neophytes (Table 3). For neophytes, the most invaded habitats also include frequently or previously disturbed woody vegetation such as broad-leaved deciduous plantations, forest clearings and riverine willow stands. This difference between archaeophytes and neophytes possibly reflects ecological compatibility between each of the two groups of aliens and the recipient habitats. Most archaeophytes in Central Europe are natives of the Middle East and the Mediterranean Basin (di Castri 1989), where they mostly grow in dry grasslands. In contrast, most neophytes originated from the deciduous forest biome of eastern North America or eastern Asia (Pyšek et al. 2002b), which explains their affinity for mesic or wet habitats dominated by woody plants.

The main difference between the most invasible and other habitats is the disturbance regime. All of the most invasible habitats experience strong disturbances (Table 3). The most invasible habitat, arable land, experiences a complete removal of aboveground biomass at least once a year. Ruderal vegetation is also strongly and
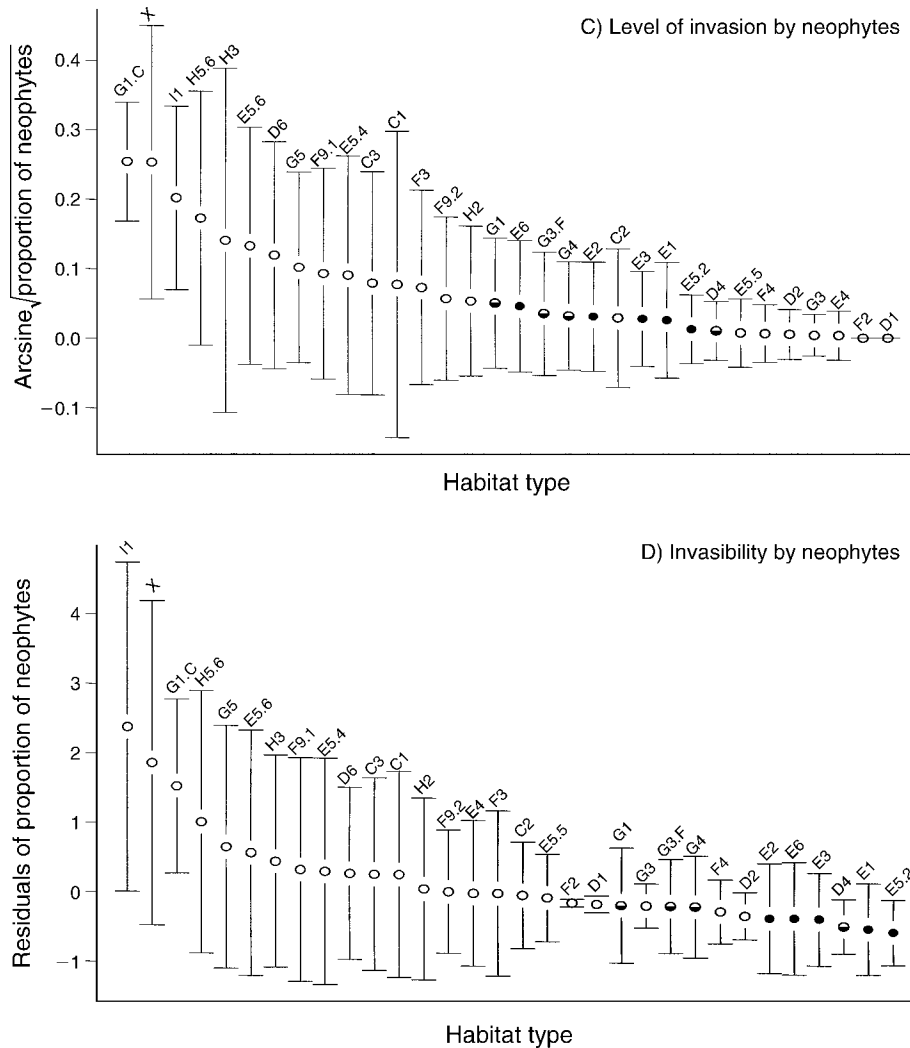
FIG. 3. Continued.

frequently disturbed, and the more it is disturbed, the more it is invaded (see the increasing level of invasion from anthropogenic tall-forb stands to annual ruderal vegetation, Fig. 3). Other habitats ranked as highly invasible are also associated with disturbance or alteration of the typical disturbance regime (Alpert et al. 2000): forest clearings created by felling, broad-leaved plantations by afforestation of previously defor-ested land, and riverine willow stands recurrently disturbed by floods. Disturbance in some of these habitats is coupled with temporary increases in resource availability, e.g., fertilization of arable land, nutrient input into ruderal vegetation in human settlements, sedimentation of nutrient-rich mud after floods, or increased light availability after opening the woodland canopy. The occurrence of these processes in the most invaded habitats is consistent with the theory of fluctuating resource availability (Davis et al. 2000) and the concept of resource opportunity in fluctuating environment (Shea and Chesson 2002).

There are, however, some habitats which occur in areas with intermediate to high propagule pressure but contain lower proportions of aliens than expected from the intensity of propagule pressure (Fig. 3). This suggests they are more resistant to invasions than their actual level of invasion would suggest. Such habitats include dry, wet, and saline grasslands, woodland fringes, base-rich fens, and, to a lesser extent, also broad-leaved deciduous woodlands and coniferous plantations. Most of these habitats are perennial grasslands, which are also frequently disturbed by grazing or mowing (Chytrý 2007). However, such disturbances do not result in significant temporary increase in nutrient availability, because vegetation is never disturbed completely and resident plants respond to damage by rapid uptake of free nutrients to support their fast regrowth. Several studies from other regions of the temperate zone also conclude that grazing does not favor aliens more than native species (e.g., Stohlgren et al. 1999), especially in areas where grasslands were

TABLE 3. Position of major temperate habitats along the level of invasion–invasibility continuum.

Habitat	Level of invasion	Invasibility	Propagule pressure	Disturbance	Nutrient availability
Alpine and subalpine grasslands, bogs, coniferous woodlands	low	probably low	low	rare	low, stable
Mown and grazed grasslands from the lowlands to the montane belt, broad-leaved woodlands	intermediate	low	high	rare or of intermediate frequency and moderate intensity	low to high, stable or moderately fluctuating
Human-made habitats, including ruderal vegetation and arable weed vegetation	high	high	high	frequent and strong, in some cases irregular and unpredictable	usually high, strongly fluctuating

Notes: The level of invasion is defined as the actual proportion of alien species relative to all species present in the habitat. Invasibility relates to relative proportion of alien species if propagule pressure and climate were constant across the habitats. Note that habitat invasibility cannot be assessed for habitats with constantly low levels of invasion (see Fig. 3 for details).

historically intensively grazed by large mammals, such as Eurasia or the Great Plains of North America (Mack 1989). In contrast, grasslands of the American West, South America, or Australia that evolved under weak herbivore impact, are prone to invasion (Mack 1989, McIntyre and Lavorel 1994). These observations are consistent with the hypothesis that alterations of typical disturbance regimes are more important for invasions than disturbances per se (Alpert et al. 2000).

In this study, the effect of disturbance is indicated by the positive relationships between the proportion of aliens and vegetation cover (see also Stohlgren et al. 2006). For both archaeophytes and neophytes, this was the case for habitats on fertile soils at low altitudes, where low cover indicates disturbance (e.g., anthropogenic tall-herb stands and trampled areas). However, it was not the case for habitats on infertile soils where low vegetation cover may result from environmental stress rather than disturbance (Figs. 1 and 2). It is interesting that this relationship was positive for archaeophytes in annual vegetation in human-made habitats, reflecting the fact that annual archaeophytes are most numerous on arable land, where vegetation cover is often high, in spite of frequent disturbances (see Plate 1).

Unfortunately, our data set is not suitable for assessing the invasibility of the least invaded habitats, such as high-mountain grasslands and scrub, bogs, poor fens, and transition mires. These habitats usually occur in areas with very low propagule pressure of aliens (Table 3), thus it is impossible to test whether they experience low levels of invasion because of habitat resistance or just because of their remoteness from the sources of alien propagules. However, the vegetation structure in some of these habitats is similar to that of invasion-resistant lowland habitats, which may indicate that these habitats may also be rather resistant to invasion.

Archaeophytes and neophytes: both are aliens, but not alike

The two groups of aliens with different residence times in Central Europe, archaeophytes and neophytes, show some similarities and some differences in environ-

mental affinities. The strongest pattern, common to both the archaeophytes and neophytes in Central Europe (Pyšek et al. 2002a, 2005, Kühn et al. 2003) and elsewhere (Stohlgren et al. 2002, Keeley et al. 2003, Dark 2004), is the decrease in the proportion of these species with increasing altitude at the benefit of native species. Furthermore, archaeophytes were found, both in this and previous studies (Kühn et al. 2003, Pyšek et al. 2005) to be associated with low rainfall and well-drained soils.

In addition to certain differences in habitat affinites, this study also revealed a different role of propagule pressure in determining the representation of archaeophytes and neophytes. Both groups tend to increase in vegetation surrounded by urban and industrial land (Figs. 1 and 2), which suggests a positive effect of human-mediated propagule pressure. Archaeophytes also positively respond to the increasing proportion of agricultural land in their surroundings (Fig. 1). This is not surprising, given that archaeophytes arrived in Central Europe with the spread of agriculture (Pyšek and Jarošík 2005) and for millenia any new arrival colonized predominantly rural areas. Agricultural activities result in a high archaeophyte propagule pressure, even now.

The historical inertia in the distribution of archaeophytes is also demonstrated by the fact that the difference among altitudinal floristic regions, particularly between Thermophyticum, i.e., the low-altitude area inhabited since the Neolithic, and the other two regions, both colonized later, explained more of the variance for this group of aliens than altitude did. Conversely, neophytes respond more to climate than to altitudinal floristic region (Table 2). This pattern suggests that in the area that experienced several millenia of human impact and agricultural cultivation, early plant invaders had enough time to spread and occupy most sites with suitable habitats. In the other floristic regions, which were more intensively settled as late as in the Middle Ages, there has not been enough time for archaeophytes to become widespread. This supports the concept of a positive relationship between alien species distribution and residence time, i.e., the time since introduction into
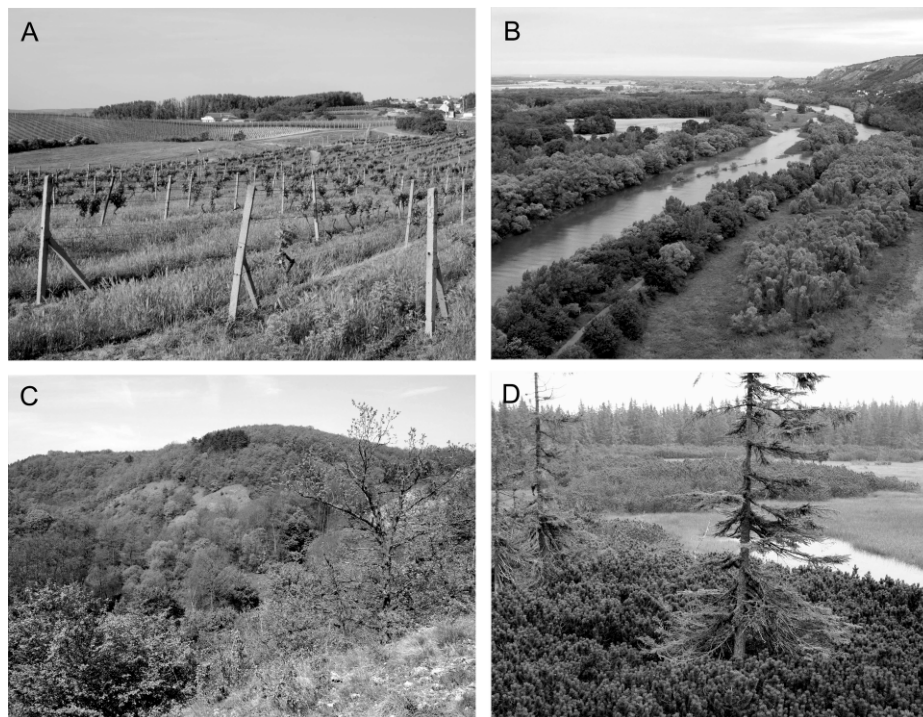
PLATE 1. (A) Agricultural land experiences the highest level of invasion by archaeophytes and one of the highest levels of invasion by neophytes; for both of these groups of alien plants, it is the most invasive habitat of Central Europe. (B) Riverine scrub and related vegetation types disturbed by floods are moderately invaded and moderately invasible by neophytes, but less so by archaeophytes. (C) Broad-leaved deciduous woodlands and dry grasslands are moderately invaded due to their frequent occurrence in the areas with high propagule presssure, but they are poorly invasible. (D) Montane coniferous woodlands and bogs are among the least invaded habitats of Central Europe; probably they are also poorly invasible. Photo credits: M. Chytrý.

a new region (Rejmánek et al. 2004, Pyšek and Jarošík 2005).

The relationship between residence time and the distribution pattern of alien plants is also demonstrated by the fact that the relative roles of habitats vs. propagule pressure differ between archaeophytes and neophytes. Habitat type has a much larger effect than propagule pressure on the distribution of archaeophytes, but this difference is not as large for neophytes (Table 2). Also in other Central European studies, neophytes occur most frequently in areas with a high propagule pressure, i.e., more urban land or denser human population (Pyšek et al. 2002a, 2005, Deutschewitz et al. 2003, Kühn et al. 2003). This suggests that alien plants with longer residence times are more closely associated with the range of habitats that meet their ecological requirements. In contrast, relatively recently introduced alien plants in Central Europe are absent from many sites with suitable habitats.

Open questions

This study is the first to describe the pattern of plant invasion across all the major habitats in a large and heterogeneous area, using the fine-scale resolution of small vegetation plots and taking measures of propagule pressure and climate into account. We ascertained that the level of habitat invasion is affected by variations in

propagule pressure and climate across landscapes, but local habitat properties are much more important determinants of the proportion of alien species in vegetation. Since the between-habitat patterns in the level of invasion revealed in the Czech Republic correspond to those reported from elsewhere, we hypothesize that the relative importance of habitat vs. propagule limitation is similar in other regions of the temperate zone, particularly in the Old World, where ecosystems may differ in invasibility from those in the New World (di Castri 1989, Mack 1989). Tests of this hypothesis are dependent on the compilation of vegetation-plot databases for other parts of the world outside Europe (Mucina et al. 2000, Wiser et al. 2001; see also VegBank [*available online*]).[7]

However, in addition to habitat properties and propagule pressure there is another, so far little studied factor that affects the proportion of alien species in different habitats. It is habitat-specific species pools (Sádlo et al. 2007). It may be that some habitats have lower levels of invasion simply due to smaller pools of ecologically matching alien species. Separation and quantification of the relative importance of habitat properties and differences in the habitat-specific species

[7] ⟨www.vegbank.org⟩

pools would require comparisons of the level of invasion across habitats in the target area with the size of habitat-specific species pools in the source areas (Prinzing et al. 2002, Pyšek et al. 2004, Hierro et al. 2005). Also the fact that some habitats in the source areas are more remote from the centers of human activity may be important, because species of such habitats probably have a lower probability of being transported to new regions. We envisage such comparative studies of species–habitat relationships between biogeographic provinces as a promising avenue of future research, which may contribute to a more comprehensive understanding of the macroecological patterns of habitat invasibility.

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