Maps of the level of invasion of the Czech Republic by alien plants

Mapy invadovanosti České republiky nepůvodními rostlinami

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A series of maps showing the level of invasion of the Czech Republic by alien plants was developed based on a quantitative assessment of the level of invasion of 35 terrestrial habitat types at different altitudes. The levels of invasion were quantified for 18,798 vegetation plots, using two measures: proportion of the species that are aliens and total cover of alien species. Separate assessments were made for archaeophytes and neophytes. Within each habitat, the level of invasion was related to altitude using generalized linear models. The level of invasion, depending on the measure used, decreased with altitude in 16 out of 20 habitats for archaeophytes and 18 out of 23 for neophytes. In two habitats, one measure of the level of invasion increased with altitude for archaeophytes. The values of the level of invasion predicted by generalized linear models for particular combinations of habitats and altitudes were projected onto a land-cover map and digital elevation map of the country. Four maps showing the level of invasion were produced, based on the proportion of the species that are archaeophytes or neophytes, and cover of archaeophytes and neophytes. The maps show that both archaeophytes and neophytes are most common in lowland agricultural and urban areas, whereas they are sparsely represented in mountainous areas. At middle altitudes, agricultural areas are more invaded than forested areas. Outside agricultural and urban areas, high levels of invasion are found especially in lowland sandy areas and river corridors.

Keywords: altitude, archaeophyte, distribution, exotic species, habitat types, invasive species, land cover, neophyte, non-native species, plant community

Introduction

Knowledge of the distribution of alien plant species is important for planning their effective control and management. In the Czech Republic distributions of many alien species are mapped in grid atlases (Slavík 1986, 1990, 1998), in a monograph on selected weeds (Jehlík 1998) and in papers focusing on individual species (e.g., Pyšek 1991, Pyšek & Prach 1995, Mandák et al. 2004; see Pyšek et al. 2002b for further references). In addition, there is a long tradition of vegetation research and a large number of vegetation plot records (Chytrý & Rafajová 2003), which can be used for determining species distribution and classifying species habitat affinities based on their occurrence in vegetation plots (Chytrý & Tichý 2003, Sádlo et al. 2007). Despite this intensive research, areas that harbour most or least alien plant species have never been accurately identified at the scale of the country.

The importance of habitat types (hereafter habitats) in plant invasions has recently received considerable attention, which has revealed that alien plants differ in their habitat affinities at various scales (for regional scale see e.g., Sádlo et al. 2007, for continental Lambdon et al. 2008). Chytrý et al. (2005) demonstrate that the level of invasion (Richardson & Pyšek 2006, Chytrý et al. 2008a), measured as the proportion of species that are aliens or the total cover of alien species at a site, varies considerably among habitats in the Czech Republic. In a subsequent study (Chytrý et al. 2008a) it was shown that habitat is the strongest predictor of the local level of invasion, explaining 76.7% and 18.4% of the variation in the level of invasion by archaeophytes and neophytes, respectively. Altitude was identified as the second strongest predictor, with a decrease in the level of invasion with increasing altitude, explaining 2.3% and 5.9% of the variation for these two groups of aliens, respectively. These studies also confirm that the two groups of alien species in Central Europe, archaeophytes introduced from the beginning of Neolithic agriculture to AD 1500, and neophytes that arrived later (see Pyšek et al. 2002b, 2004a for definitions), need to be dealt with separately as they differ in their ecology, invasion dynamics and habitat affinities (Pyšek et al. 2004b, 2005).

The tight relationship between the level of invasion and habitats, as identified in these studies, makes it possible to produce large-scale maps of the level of invasion by combining quantitative data on the level of invasion of particular habitat with habitat distribution maps derived from remote sensing. Such an approach was recently used to produce an invasion map for the European Union (Chytrý et al. 2009). At the finer scale of the Czech Republic, however, the accuracy of an invasion map can be improved by incorporating information that could not be used at the European scale because of data constraints resulting from the coarser grain of that study. This concerns especially a finer classification of habitats and the relationship between the level of invasion and altitude.

In this study, we developed four invasion maps for the Czech Republic based on a quantitative assessment of the level of invasion of particular habitats at different altitudes. We produced the maps separately for archaeophytes and neophytes, and within each of these two groups of aliens we used two measures of the level of invasion: the proportion of species that are aliens and total cover of alien species.

Materials and methods

To quantify the local level of invasion of particular habitats at different altitudes we used the same data set as Chytrý et al. (2005, 2008a). It consisted of vegetation plot records (relevés) selected in a stratified random way from the Czech National Phytosociological Database (Chytrý & Rafajová 2003). Plots ranged in size from 1 to 500 m^2 (larger plots were from woodlands, smaller plots from low-growing herbaceous vegetation), contained lists of plant species with their cover-abundances recorded on the Braun-Blanquet or Domin scale (van der Maarel 1979) and were sampled between 1970 and 2004. We recognize that the level of invasion has changed to some extent during the past decades (e.g., Pyšek et al. 2005, Lambdon et al. 2008, Lososová & Simonová 2008), however, we prefer to use cumulative data collected over 35 years, because if we used a shorter period, some areas of the country or some habitats would be poorly represented.

In previous studies, these plots were classified into 32 habitats corresponding to the EUNIS habitat classification (Davies et al. 2004; http://eunis.eea.europa.eu/habitats.jsp), a standard classification of European habitats. Here, aquatic habitats (types C1 and C2) were not considered, because aquatic vegetation plots have mostly come from small water bodies or streams and data from these plots cannot be extrapolated to large water reservoirs, which are almost without macrophyte vegetation over most of their area but at the same time they are the only visible water bodies on a map at the country scale. Habitat type E5.6 Anthropogenic tall-forb stands was renamed E5.1 Anthropogenic herb stands according to the new version of the EUNIS classification and the type referred to as J6 Waste deposits in Chytrý et al. (2005) was re-coded to X Annual ruderal vegetation to reflect its contents more clearly. Habitat types G1 Broad-leaved woodland and G4 Mixed woodland were merged, because they include closely related vegetation types, such as pure beech forests and mixed spruce-fir-beech forests, respectively. Subsequently this merged habitat type was divided into seven finer forest habitat types, and habitat type G3 Coniferous woodland was divided into two finer types, each corresponding to the units of the national Map of Potential Natural Vegetation (Neuhäuslová et al. 1997). Thus, this study included 35 habitat types. We use shortened names for the habitat types throughout this paper. Their full names can be found in Davies et al. (2004) and their translation to phytosociological units in Chytrý et al. (2005). Due to the exclusion of aquatic habitats and some woodland plots that could not be unequivocally assigned to finer types, this study used only 18,798 vegetation plots, a subset of the 20,468 plots used by Chytrý et al. (2005, 2008a).

Only vascular plants were considered in this study. They were classified as archaeophytes (pre-AD 1500 aliens), neophytes (post-AD 1500 aliens), or native species according to Pyšek et al. (2002b), with the exception of *Arrhenatherum elatius*, which was treated as an archaeophyte in the current data set (Chytrý et al. 2005). Crop species on arable land were excluded from the data set, but planted trees (including alien trees) in forests were retained because it is unknown for most plots whether the trees were planted or regenerated spontaneously. Tree species native to the country but planted at the sites where they would be outcompeted by other tree species under natural conditions (especially *Picea abies* and *Pinus sylvestris*) were treated as native.

For each vegetation plot, the numbers of archaeophytes, neophytes and native species were counted and the total cover of the species within each category of aliens calculated. The total cover of vegetation in each plot was calculated from species cover values as recorded on the Braun-Blanquet or Domin scale, transformed into percentages according to van der Maarel (1979) and subsequently expressed as a proportion ranging from 0 to 1. The species cover values were summed for all the species of each species group (archaeophytes, neophytes, or native), assuming random overlap of areas covered by individual species. For example, the summed cover of two species x and y was calculated as $c_s = c_x + (1 - c_x) \times c_y$, where c_s was the summed cover, and c_x and c_y were covers of species x and y, respectively. The summed covers of several species calculated in this way were always between 0 and 1. This calculation, as well as editing of vegetation plot data and calculating the measures of the level of invasion were done using the JUICE 6.3 program (Tichý 2002).

In order to avoid the prediction of negative proportions or covers and respect their upper bounds, relationships between the level of invasion (proportion of species that are aliens or total cover of aliens) as a dependent variable and altitude as an independent variable, were established for particular habitats using generalized linear models (McCullagh & Nelder 1989). For the proportion of aliens a logit link function and binomial distribution of errors were used. The percentage cover of aliens was rounded to integers and fitted using a log link function and Poisson distribution of errors. ANOVA comparison of the residual deviance with the deviance of null model was based on the chi-square test for the proportion of aliens and F-test for the cover of aliens to compensate for over-dispersion, which occurred in most models. All statistical analyses were calculated using the R package (R Development Core Team 2009).

Distribution of habitats in the Czech Republic was mapped using the CORINE land-cover data with pixel resolution 250 × 250 m (Moss & Wyatt 1994, Bossard et al. 2000, version 8/2005 obtained from the European Environment Agency). To achieve this, EUNIS habitats were transformed to CORINE land-cover classes according to the crosswalk published by Chytrý et al. (2009: Table 1). Finer categories of deciduous woodlands were mapped where CORINE data indicated land-cover classes 311 Broad-leaved forest or 313 Mixed forest and at the same time the Map of Potential Natural Vegetation of the Czech Republic (Neuhäuslová et al. 1997; further PNV map) indicated the corresponding type of potential natural vegetation (G1.2 Riparian woods of EUNIS corresponded to units 1–6 and 25 of the PNV map, G1.61 Acidophilous beech woods to 24–25 and 27, G1.63–66 Mesic beech woods to 14–23, G1.7 Thermophilous oak woods to 28–35, G1.8 Acidophilous oak woods to 36–39, G1.A3 Oak-hornbeam woods to 7–12 and G1.A4 Ravine woods to 13). Habitat type G1.C Broad-leaved plantations was not included in the present study because it could not be discriminated from the natural broad-leaved woodlands on the land-cover maps. For areas occupied by the land-cover class 312 Coniferous forest on the CORINE map, EUNIS habitat type G3.42 Natural pine woods was mapped in places where the PNV map indicated units 40–42, G3.1D Natural spruce woods in places with units 43–45 and G3F Coniferous plantations in places where the PNV map indicated any type of broad-leaved woodland.

The two measures of the level of invasion (proportion of species that are aliens and total cover of aliens) were separately projected on the CORINE land-cover map of the Czech Republic, both for archaeophytes and neophytes. For each pixel of the CORINE map, mean altitude was taken from the global model SRTM version 2 (http://www2.jpl.nasa.gov/srtm), except for the areas of large open-cast mines in northern Bohemia where the original terrain was considered, taken from the ArcČR 500 data (ArcData Praha 1997–2000). Then the EUNIS habitats corresponding to the CORINE land-cover class occurring in the target pixel were considered, and for each of them the level of invasion predicted by the generalized linear models for the altitude of the target pixel used. Mean levels of invasion were used for the habitats for which the relationship between the level of invasion and altitude was non-significant. The weighted mean of these levels of invasion was used as the level of invasion mapped in the target pixel. Weights were proportional to the estimated contribution of the particular EUNIS habitats to the CORINE land-cover class occurring in that pixel, according to the crosswalk developed by Chytrý et al. (2009). Water bodies and rivers were left blank on the maps.

The range of the level of invasion varied considerably among different maps, therefore different categories with arbitrary boundaries were used for the best possible visualization in different maps. Due to large difference in the level of invasion between human-made and other (i.e. natural and semi-natural) habitats, the resulting maps mainly reflected the differences between arable land and settlement areas on the one hand and woodlands and grasslands on the other. Therefore, a second form of each map, showing only the level of invasion of the natural and semi-natural habitats after leaving the areas with human-made habitats blank, was produced. For this purpose, CORINE land-cover classes 111–243 (i.e., urban, industrial and agricultural) were considered as human-made, whereas the other classes as natural and semi-natural. Forest plantations were assigned to natural and semi-natural types. All GIS analyses and map visualizations were done using the ArcGIS 9.2 program (http://www.esri.com).

Results

The proportion of archaeophytes among all species significantly decreased with altitude in 20 habitats, increased in one (oak-hornbeam woods) and did not change in 14 (Table 1, Fig. 1). The cover of archaeophytes was significantly less at higher altitudes in 16 habitats, greater in one (dry grasslands) and did not change in 18 (Table 1, Fig. 2). In 14 habitats there was a decrease in both the proportion and cover of archaeophytes with altitude.

The proportion of neophytes significantly decreased with altitude in 23 habitats and did not change in 12 (Table 2, Fig. 3). Their cover decreased in 18 and did not change in 17 habitats (Table 2, Fig. 4). In 17 habitats there was a decrease in both the proportion and the cover of neophytes with altitude. In no habitat was there a significant increase in either the proportion or the cover of neophytes with altitude.

The invasion map based on the proportion of archaeophytes (Fig. 5) indicates that the highest levels of invasion occur in agricultural areas at low altitudes, followed by agricultural areas at middle altitudes and urban areas. When natural and semi-natural habitats are considered separately, moderate to high levels of invasion are indicated in (i) lowland and colline areas with coniferous (mainly pine) plantations on sandy soils, such as the Ralská pahorkatina Hills in northern Bohemia and sandy plains along the Labe river in central and eastern Bohemia, the lower Orlice river in eastern Bohemia and the Morava river in southern Moravia (mainly between the towns of Bzenec and Hodonín), (ii) military training areas where there are large areas of abandoned grasslands, particularly the Doupovské hory Mountains in north-western Bohemia and Oderské vrchy Hills in central Moravia, (iii) areas with open-cast coal mining near the towns of Most and Teplice in northern Bohemia, and (iv) alluvial landscapes along the Labe, Morava and lower Dyje rivers. Least invaded are predominantly forested landscapes at middle and high altitudes across the country. The cover of archaeophytes (Fig. 6) follows similar patterns as proportions.

The invasion map of the proportion of neophytes (Fig. 7) is similar to the corresponding map for archaeophytes (Fig. 5), showing the highest level of invasion in lowland agricultural areas, followed by mid-altitude agricultural areas and urban areas. However, the concentration of areas with high levels of invasion in the lowlands is more pronounced than for archaeophytes. The pattern of neophyte invasions of natural and semi-natural habitats (Fig. 7B) is also similar to that for archaeophytes (Fig. 5B), but higher levels of invasions are found along lowland rivers (especially the Labe, Morava and lower Dyje) and lower levels in colline to submontane areas with abandoned grasslands, such as the Doupovské hory Mountains. The pattern of neophyte cover (Fig. 8) is similar to that of the proportion of neophytes, but the difference between alluvial and other landscapes is even more pronounced when cover is considered.

Table 1. – Statistics of the general linear models for the relationship between two measures of the level of invasion by archaeophytes (dependent variables) and altitude (independent variable) for particular vegetation types: a, b – model parameters, P – significance of the model (models significant at P < 0.05 are in bold).

EUNIS habitat	n	Proportion of the species that are archaeophytes				Total percentage cover of archaeophytes			
		mean	a	b	P	mean	a	b	P
C3 Littoral zone	2891	0.025	–2.024	–0.003	**< 0.001**	1.1	1.177	–0.003	**< 0.001**
D1 Raised bogs	75	0.001	–3.751	–0.004	0.226	0	–1.329	–0.004	0.058
D2 Poor fens	375	0.005	–4.165	–0.001	0.107	0.3	–0.090	–0.002	**0.032**
D4 Base-rich fens	49	0.014	–2.890	–0.004	**0.035**	0.6	0.474	–0.003	0.073
D6 Brackish marshes	32	0.043	–3.525	0.003	0.173	1.5	0.496	0	0.905
E1 Dry grasslands	2508	0.060	–2.942	0	0.210	4.7	1.325	0.001	**0.030**
E2 Mesic grasslands	1698	0.053	–1.289	–0.004	**< 0.001**	11.5	4.455	–0.005	**< 0.001**
E3 Wet grasslands	2251	0.016	–2.534	–0.004	**< 0.001**	1.4	2.173	–0.004	**< 0.001**
E4 Alpine grasslands	94	0	–29.927	0.001	1.000	0	–27.303	0	1.000
E5.1 Anthropogenic herb stands	800	0.251	0.264	–0.004	**< 0.001**	24.3	3.934	–0.002	**< 0.001**
E5.2 Woodland fringes	369	0.041	–3.042	0	0.413	3.7	1.307	0	0.956
E5.4 Wet tall-forb stands	734	0.038	–0.612	–0.007	**< 0.001**	2.1	2.827	–0.006	**< 0.001**
E5.5 Subalpine tall-forb stands	218	0.001	–13.185	0.005	0.401	0	–13.924	0.008	0.191
E6 Saline grasslands	151	0.081	–1.674	–0.004	**< 0.001**	5.4	2.623	–0.004	0.091
F2 Alpine and subalpine scrub	24	0	–29.883	0.001	1.000	0	–25.303	0	1.000
F3 Temperate scrub	102	0.087	–0.913	–0.005	**< 0.001**	7.8	3.160	–0.003	0.086
F4 Heathlands	228	0.006	–3.741	–0.002	**0.007**	0.3	0.013	–0.002	**0.035**
F9.1 Riverine willow stands	20	0.016	–1.749	–0.007	0.053	0.6	2.164	–0.008	**0.022**
F9.2 Willow carrs	48	0.013	0.704	–0.016	**< 0.001**	0.3	3.279	–0.014	**< 0.001**
G1.2 Riparian woods	415	0.008	–2.600	–0.007	**< 0.001**	0.5	1.711	–0.007	**< 0.001**
G1.61 Acidophilous beech woods	207	0	–3.853	–0.007	0.117	0	–1.704	–0.004	0.289
G1.63-66 Mesic beech woods	438	0.002	–2.868	–0.007	**< 0.001**	0.1	0.628	–0.006	**< 0.001**
G1.7 Thermophilous oak woods	241	0.015	–4.119	0	0.838	1.3	0.322	0	0.962
G1.8 Acidophilous oak woods	167	0.011	–4.449	0	0.872	0.6	–1.002	0.001	0.616
G1.A3 Oak-hornbeam woods	410	0.004	–6.508	0.003	**0.040**	0.5	–1.549	0.002	0.455
G1.A4 Ravine woods	243	0.009	–3.849	–0.002	**0.021**	0.6	0.481	–0.002	**0.045**
G3.1D Natural spruce woods	299	0	–28.166	0	1.000	0	–27.303	0	1.000
G3.42 Natural pine woods	119	0.001	–5.923	0	0.987	0.1	–2.608	0	0.986
G3F Coniferous plantations	207	0.014	–2.512	–0.004	**< 0.001**	1.0	2.198	–0.005	**0.002**
G5 Forest clearings	491	0.042	–0.554	–0.006	**< 0.001**	3.1	4.194	–0.008	**< 0.001**
H2 Screes	50	0.107	–1.382	–0.002	**0.036**	6.8	2.350	–0.001	0.424
H3 Cliffs and walls	236	0.095	–0.768	–0.005	**< 0.001**	2.5	2.348	–0.004	**0.002**
H5.6 Trampled areas	777	0.218	–0.240	–0.003	**< 0.001**	18.1	3.942	–0.003	**< 0.001**
I1 Arable land	1441	0.555	1.165	–0.002	**< 0.001**	43.4	3.833	0	0.222
X Annual ruderal vegetation	390	0.473	0.644	–0.002	**< 0.001**	46.4	3.702	0	0.249

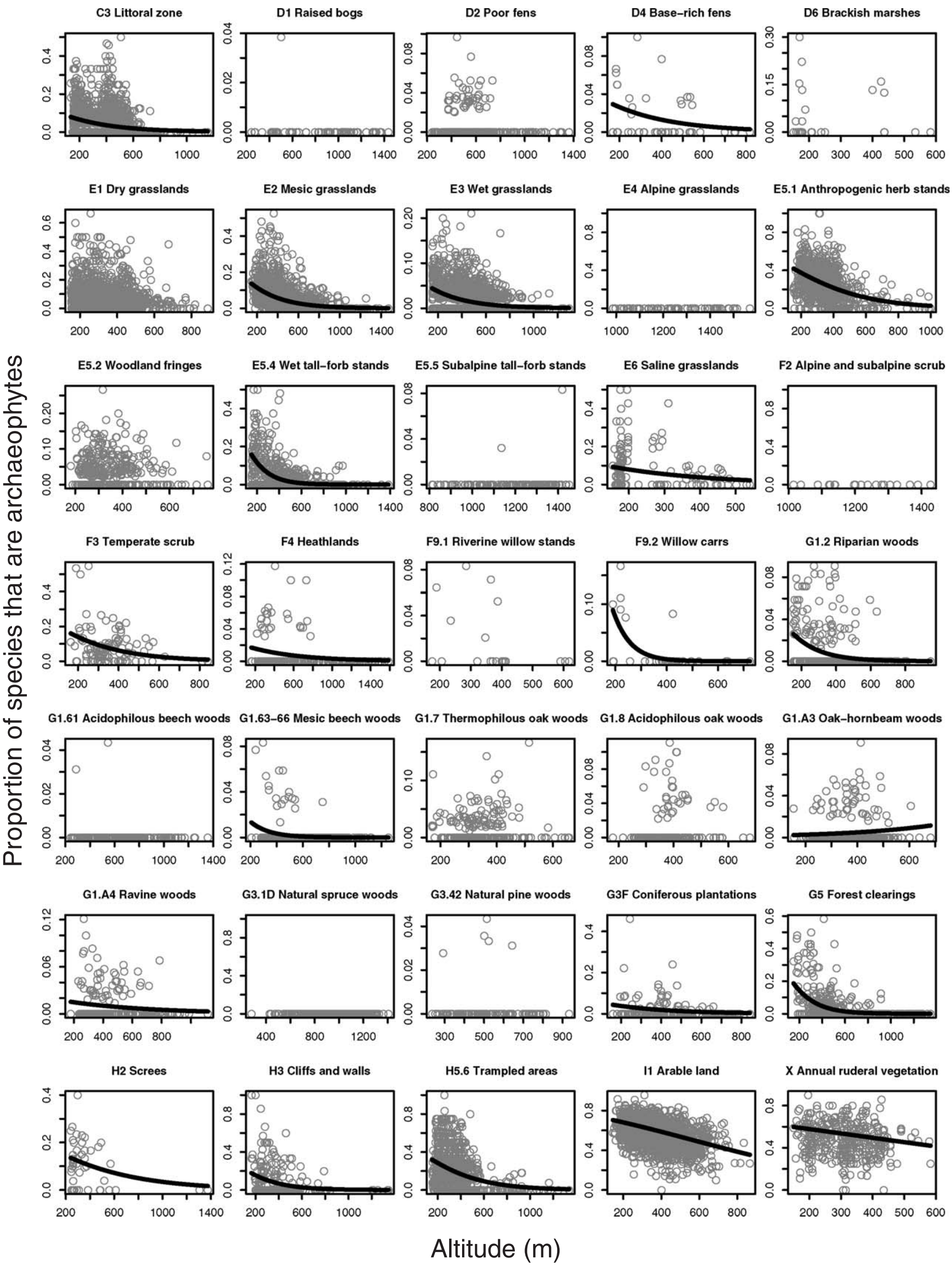

Fig. 1. – Relationships between the level of invasion by archaeophytes, measured as the proportion of the species that are archaeophytes, and altitude for particular habitats. Curves are fitted using generalized linear models (logit link function and binomial distribution of errors) for those habitats where the relationship was significant. See Table 1 for model statistics.

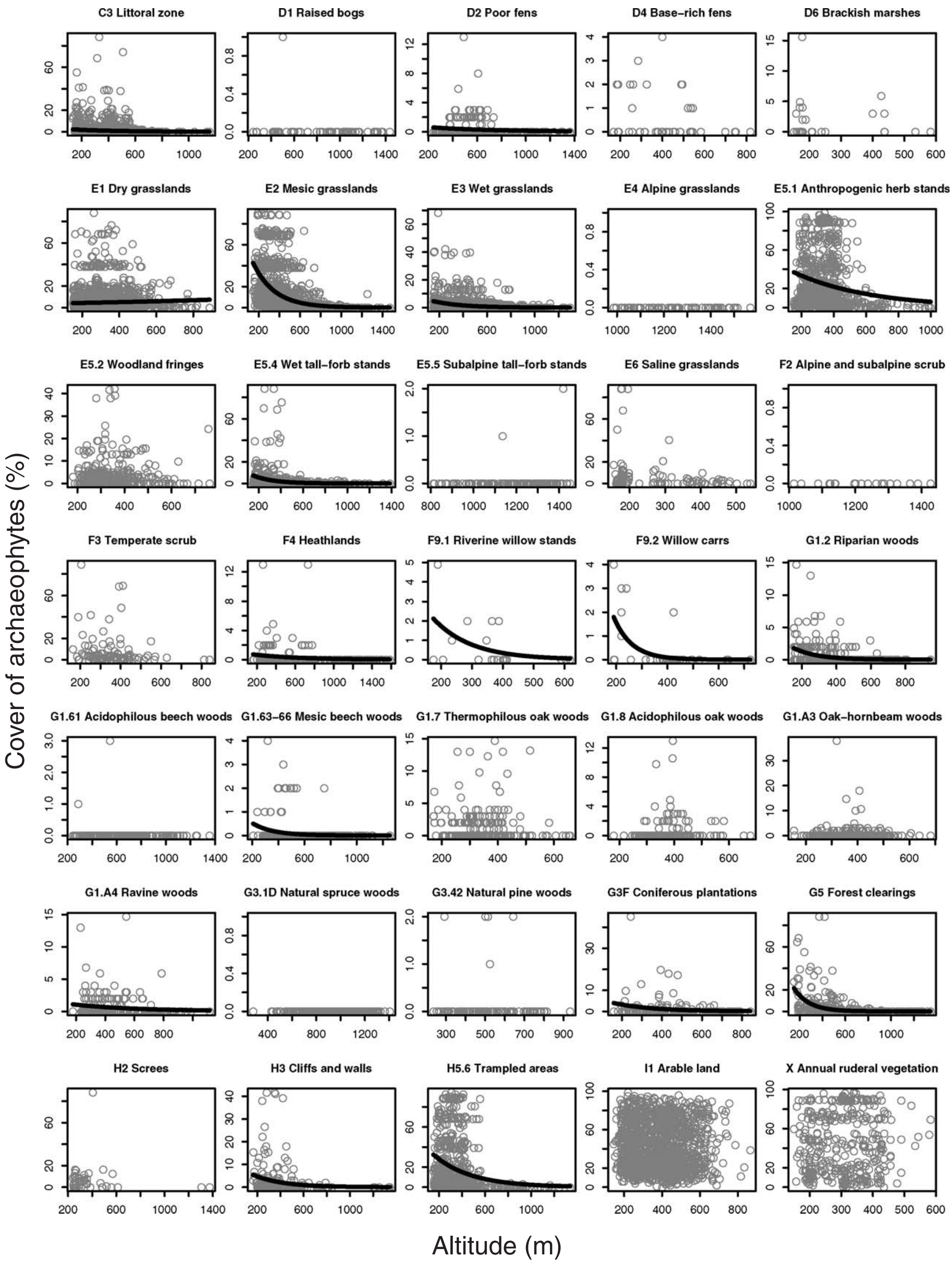

Fig. 2. – Relationships between the level of invasion by archaeophytes, measured as the total percentage cover of archaeophytes in vegetation plots, and altitude for particular habitats. Curves are fitted using generalized linear models (log link function and Poisson distribution of errors) for those habitats where the relationship was significant. See Table 1 for model statistics.

Table 2. – Statistics of the general linear models for the relationship between two measures of the level of invasion by neophytes (dependent variables) and altitude (independent variable) of particular vegetation types: a, b – model parameters, P – significance of the model (models significant at P < 0.05 are in bold).

EUNIS habitat	n	Proportion of the species that are neophytes				Total percentage cover of neophytes			
		mean	a	b	P	mean	a	b	P
C3 Littoral zone	2891	0.029	–2.741	–0.002	**< 0.001**	3.5	2.060	–0.002	**< 0.001**
D1 Raised bogs	75	0	–28.078	0	1.000	0	–26.303	0	1.000
D2 Poor fens	375	0.001	–3.491	–0.006	**0.017**	0.2	–2.084	0.001	0.770
D4 Base-rich fens	49	0.002	–6.309	0.001	0.814	0.1	–2.692	0.002	0.578
D6 Brackish marshes	32	0.039	–3.104	0	0.950	2.1	1.570	–0.004	0.266
E1 Dry grasslands	2508	0.007	–3.392	–0.007	**< 0.001**	0.4	0.218	–0.004	**0.002**
E2 Mesic grasslands	1698	0.007	–3.575	–0.004	**< 0.001**	1.7	3.611	–0.008	**< 0.001**
E3 Wet grasslands	2251	0.005	–4.204	–0.002	**< 0.001**	0.5	0.206	–0.002	**0.001**
E4 Alpine grasslands	94	0.001	–7.021	0	0.993	0.1	–0.229	–0.001	0.839
E5.1 Anthropogenic herb stands	800	0.044	–0.936	–0.006	**< 0.001**	10.3	4.058	–0.005	**< 0.001**
E5.2 Woodland fringes	369	0.003	–6.527	0.002	0.396	0.1	–2.497	0.002	0.432
E5.4 Wet tall-forb stands	734	0.035	–0.263	–0.009	**< 0.001**	11.8	5.382	–0.008	**< 0.001**
E5.5 Subalpine tall-forb stands	218	0.001	4.870	–0.012	**0.022**	0.5	12.981	–0.013	**< 0.001**
E6 Saline grasslands	151	0.011	–3.205	–0.004	**0.014**	1.3	1.212	–0.004	0.246
F2 Alpine and subalpine scrub	24	0	–29.883	0.001	1.000	0	–25.303	0	1.000
F3 Temperate scrub	102	0.023	–2.188	–0.006	**0.003**	5.3	2.572	–0.003	0.395
F4 Heathlands	228	0.002	–5.669	–0.001	0.438	0	–2.064	–0.002	0.226
F9.1 Riverine willow stands	20	0.029	–2.259	–0.003	0.172	3.3	4.076	–0.009	**0.041**
F9.2 Willow carrs	48	0.016	–1.684	–0.007	**0.021**	0.4	1.328	–0.006	**0.035**
G1.2 Riparian woods	415	0.016	–2.515	–0.005	**< 0.001**	3.8	3.028	–0.005	**< 0.001**
G1.61 Acidophilous beech woods	207	0.004	–2.005	–0.007	**< 0.001**	0.3	2.546	–0.007	**< 0.001**
G1.63-66 Mesic beech woods	438	0.006	–1.851	–0.007	**< 0.001**	0.9	4.822	–0.011	**< 0.001**
G1.7 Thermophilous oak woods	241	0.007	–3.703	–0.004	**0.018**	2.5	1.655	–0.002	0.439
G1.8 Acidophilous oak woods	167	0.013	–3.250	–0.003	0.148	0.6	–1.070	0.001	0.532
G1.A3 Oak-hornbeam woods	410	0.011	–2.758	–0.006	**< 0.001**	1.8	2.491	–0.006	**0.016**
G1.A4 Ravine woods	243	0.012	–2.418	–0.005	**< 0.001**	3.0	3.359	–0.005	**< 0.001**
G3.1D Natural spruce woods	299	0	–28.166	0	1.000	0	–27.303	0	1.000
G3.42 Natural pine woods	119	0.004	–4.380	–0.003	0.317	0.1	–1.527	–0.002	0.555
G3F Coniferous plantations	207	0.009	–1.700	–0.008	**< 0.001**	2.0	4.882	–0.012	**< 0.001**
G5 Forest clearings	491	0.028	–1.972	–0.003	**< 0.001**	4.0	3.321	–0.004	**< 0.001**
H2 Screes	50	0.014	–3.145	–0.002	0.322	0.8	0.723	–0.003	0.405
H3 Cliffs and walls	236	0.070	–0.179	–0.008	**< 0.001**	2.9	3.969	–0.009	**< 0.001**
H5.6 Trampled areas	777	0.060	–2.225	–0.001	**< 0.001**	3.3	1.104	0	0.605
I1 Arable land	1441	0.056	–1.057	–0.002	**< 0.001**	9.6	2.370	0	0.483
X Annual ruderal vegetation	390	0.096	–0.464	–0.003	**< 0.001**	10.7	3.830	–0.005	**< 0.001**

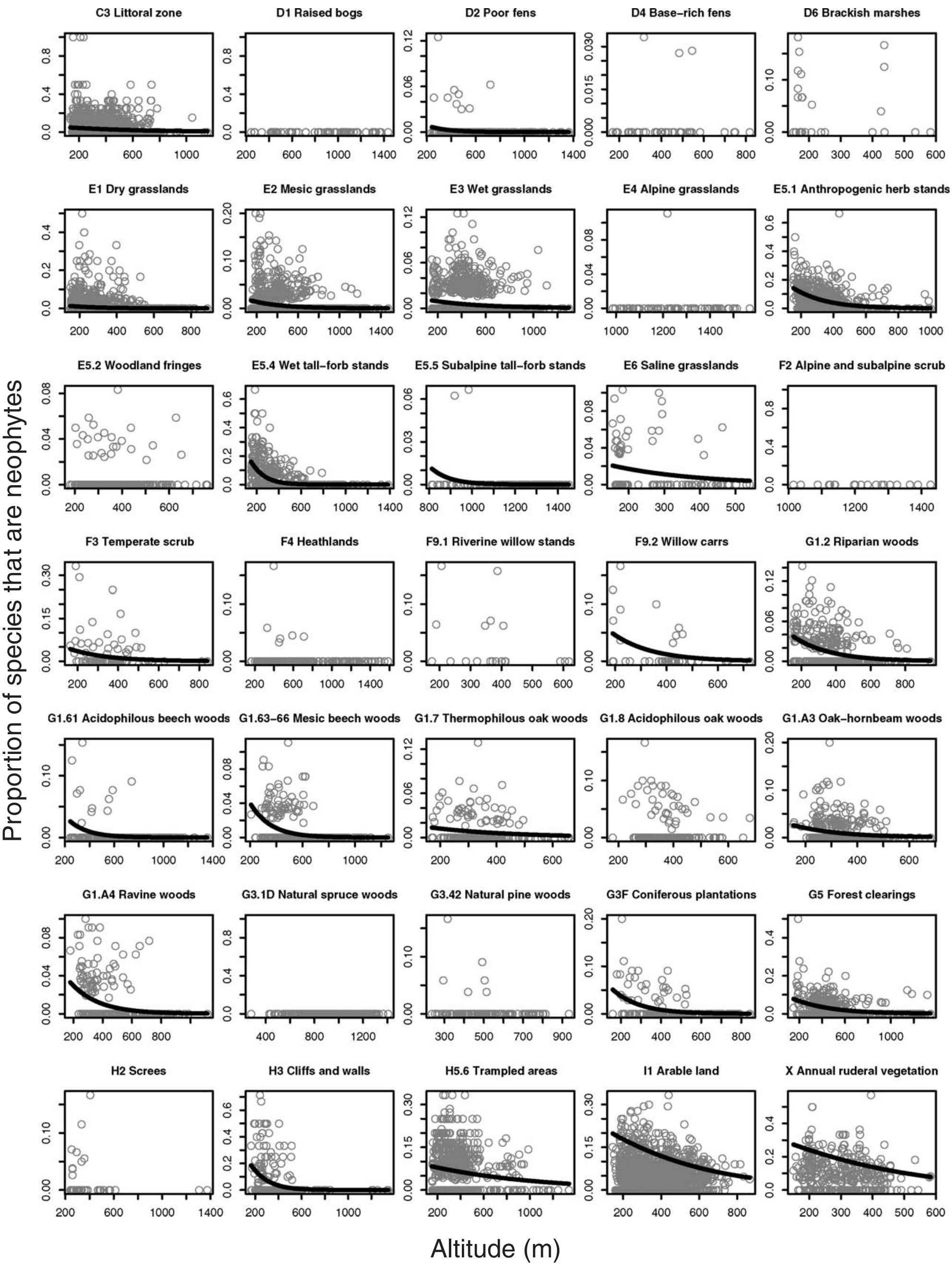

Fig. 3. – Relationships between the level of invasion by neophytes, measured as the proportion of the species that are neophytes, and altitude for particular habitats. Curves are fitted using generalized linear models (logit link function and binomial distribution of errors) for those habitats where the relationship was significant. See Table 2 for model statistics.

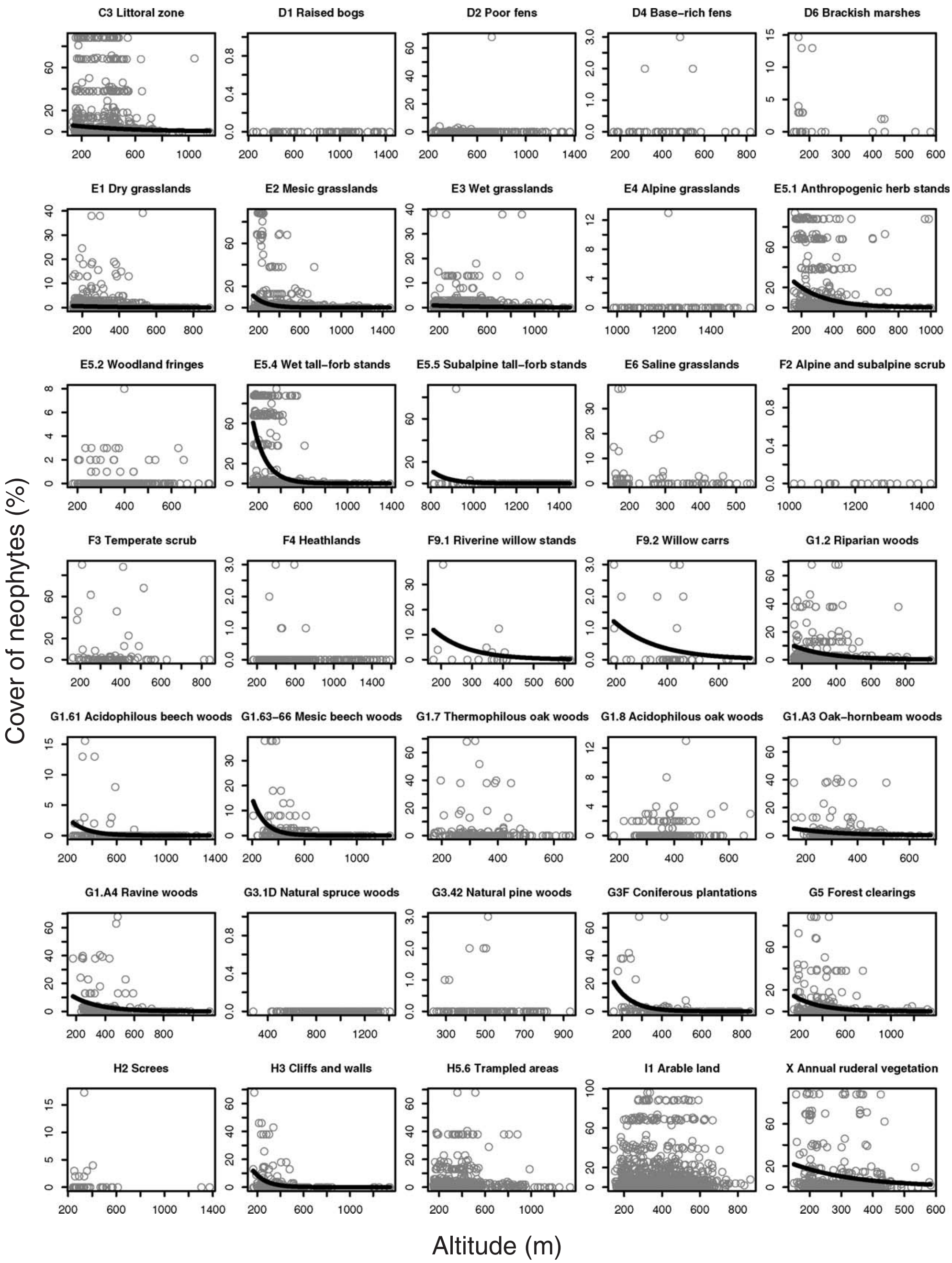

Fig. 4. – Relationships between the level of invasion by neophytes, measured as the total percentage covers of neophytes in vegetation plots, and altitude for particular habitats. Curves are fitted using generalized linear models (log link function and Poisson distribution of errors) for those habitats where the relationship was significant. See Table 2 for model statistics.

Discussion

Habitats and altitude as predictors of the level of invasion

Plant invasion maps developed in this study are based on the quantification of the relationships between the level of invasion (Richardson & Pyšek 2006, Chytrý et al. 2008a), habitats and altitude. Habitats are identified as strong predictors of the level of invasion in recent studies in the Czech Republic (Chytrý et al. 2005, 2008a, Simonová & Lososová 2008, Lososová & Grulich 2009), Europe (Kowarik 1995, Maskell et al. 2006, Vilà et al. 2007, Chytrý et al. 2008b, Thiele et al. 2009) and the United States (Stohlgren et al. 2006). A general decrease in the level of invasion with altitude is also reported for the Czech Republic (Mihulka 1998, Pyšek et al. 2002a, Lososová et al. 2004, Pyšek et al. 2005, Chytrý et al. 2008a, Simonová & Lososová 2008), other regions of Central Europe (Becker et al. 2005) and mountainous areas on other continents (Pauchard & Alaback 2004, McDougall et al. 2005, Kalwij et al. 2008). This decrease with altitude seems to be nearly ubiquitous, although its causes are still insufficiently explained and debatable (see Becker et al. 2005 for an overview of some relevant hypotheses). One might suspect that the negative relationship between the level of invasion and altitude occurs because less invasible habitats are more common at high altitudes. However, our analysis shows that the level of invasion decreases with altitude for most of the habitats, if they are considered separately. This suggests that there are probably other causes than the general tendency for there to be more invasion-prone habitats at high altitudes (Becker et al. 2005). One such cause may be the intensity of propagule pressure, assumed to be lower in areas with lower density of human population, i.e. mainly in the mountainous areas.

This study identified that in two habitats the level of invasion increased with altitude: the proportion of archaeophytes in oak-hornbeam woods and the cover of archaeophytes in dry grasslands (Table 1). We think that in both cases the interpretation of this result should not be overemphasized, because the P values of the statistical tests, though indicating significant results, were rather high (0.040 and 0.030, respectively) and as there were 140 statistical tests (Tables 1 and 2) some significant positive results are expected as a matter of chance for habitats where there are actually no relationships. In dry grasslands, however, the increase in archaeophyte cover with increase in altitude can be real, in spite of the fact that the proportion of archaeophytes in this habitat was independent of altitude (Table 1), and despite Essl & Dirnböck's (2008) report of a decrease in archaeophyte diversity with increasing altitude in dry grasslands at the edge of the Northern Limestone Alps in Austria. At low altitudes these grasslands mostly occur at very dry sites, where they are quite stable for long periods of time even without disturbances, whereas at high altitudes they always depend on management such as grazing, which can, to some extent, support invasions. Morever, the cover of the mesophilous grass *Arrhenatherum elatius* (considered as an archaeophyte in this study) increases in many subtypes of dry grassland in climatically wetter areas at middle altitudes, until dry grassland ultimately changes into *Arrhenatherum*-dominated mesic grassland.

By combining information on habitats with altitude, we have considerably improved the previous quantitative assessment of the level of invasion of habitats in the Czech Republic (Chytrý et al. 2005). For the first time, we also provide data on the level of invasion of different types of broad-leaved and coniferous woodland in the Czech Republic (Moravec 1998–2003, Knollová & Chytrý 2004, Boublík et al. 2007, Roleček 2007,

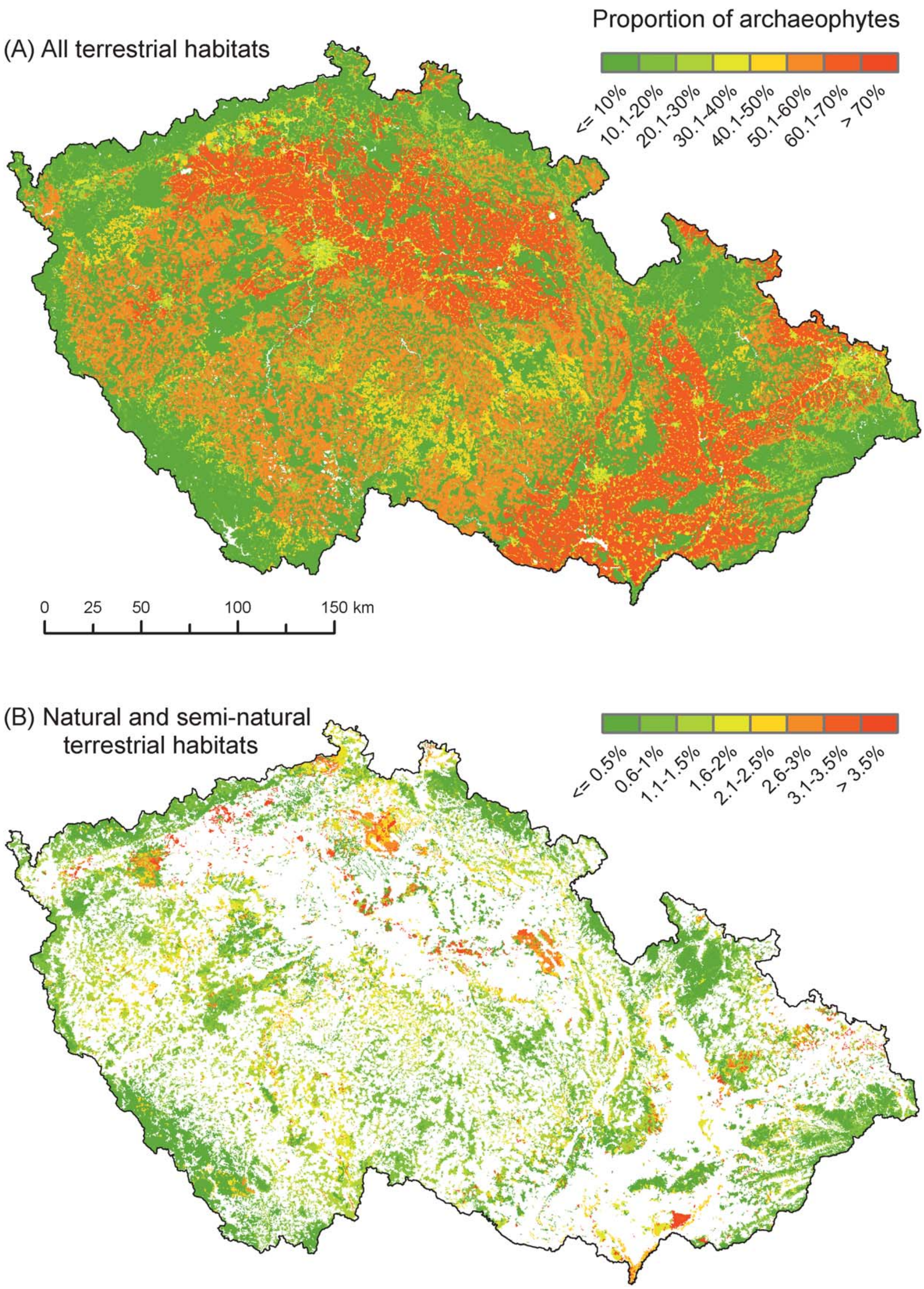

Fig. 5. – Level of invasion by archaeophytes, measured as the proportion of the species that are archaeophytes. Note the scales of the two maps differ.

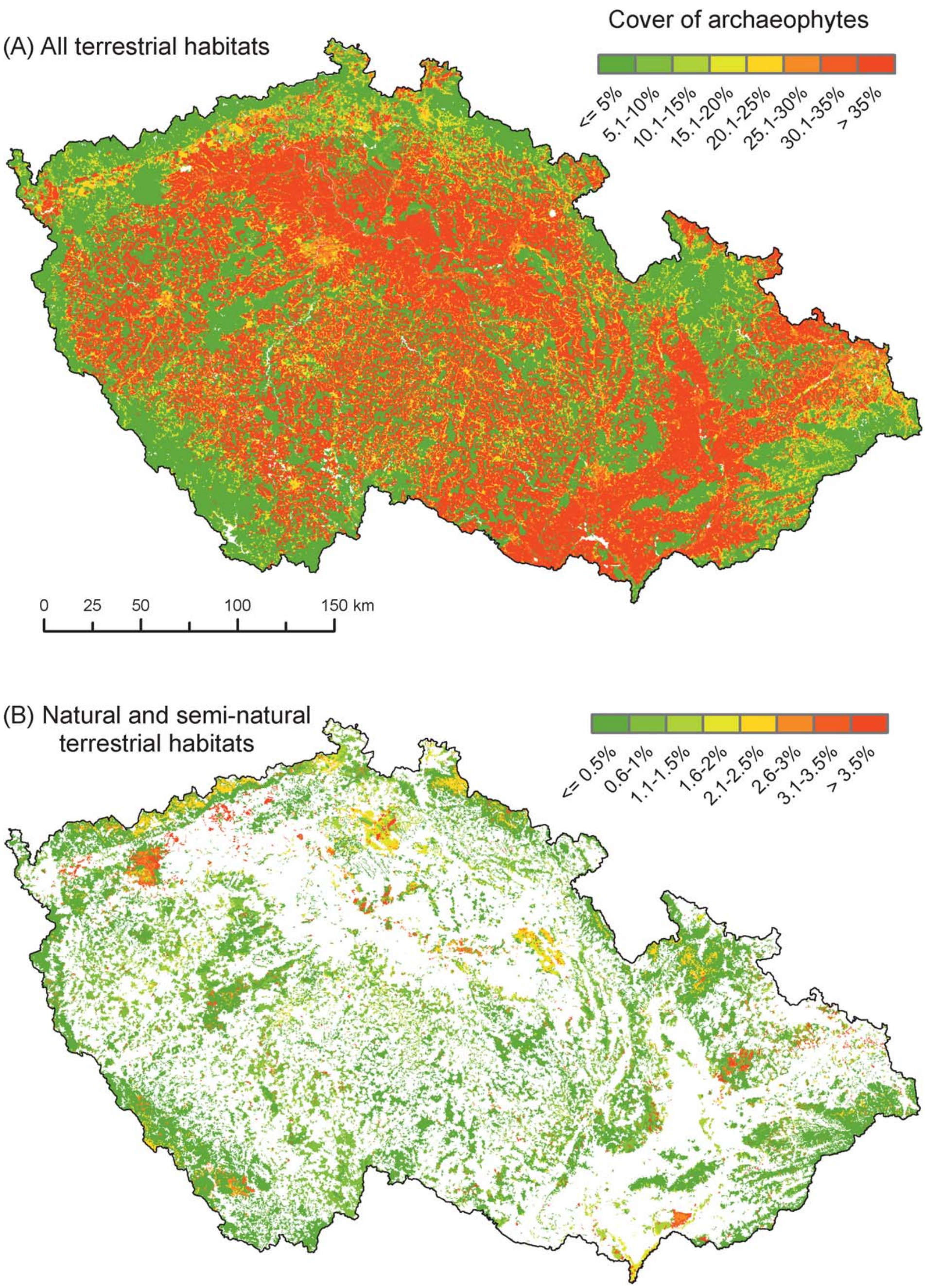

Fig. 6. – Level of invasion by archaeophytes, measured as the total cover of archaeophytes in vegetation plots. Note the scales of the two maps differ.

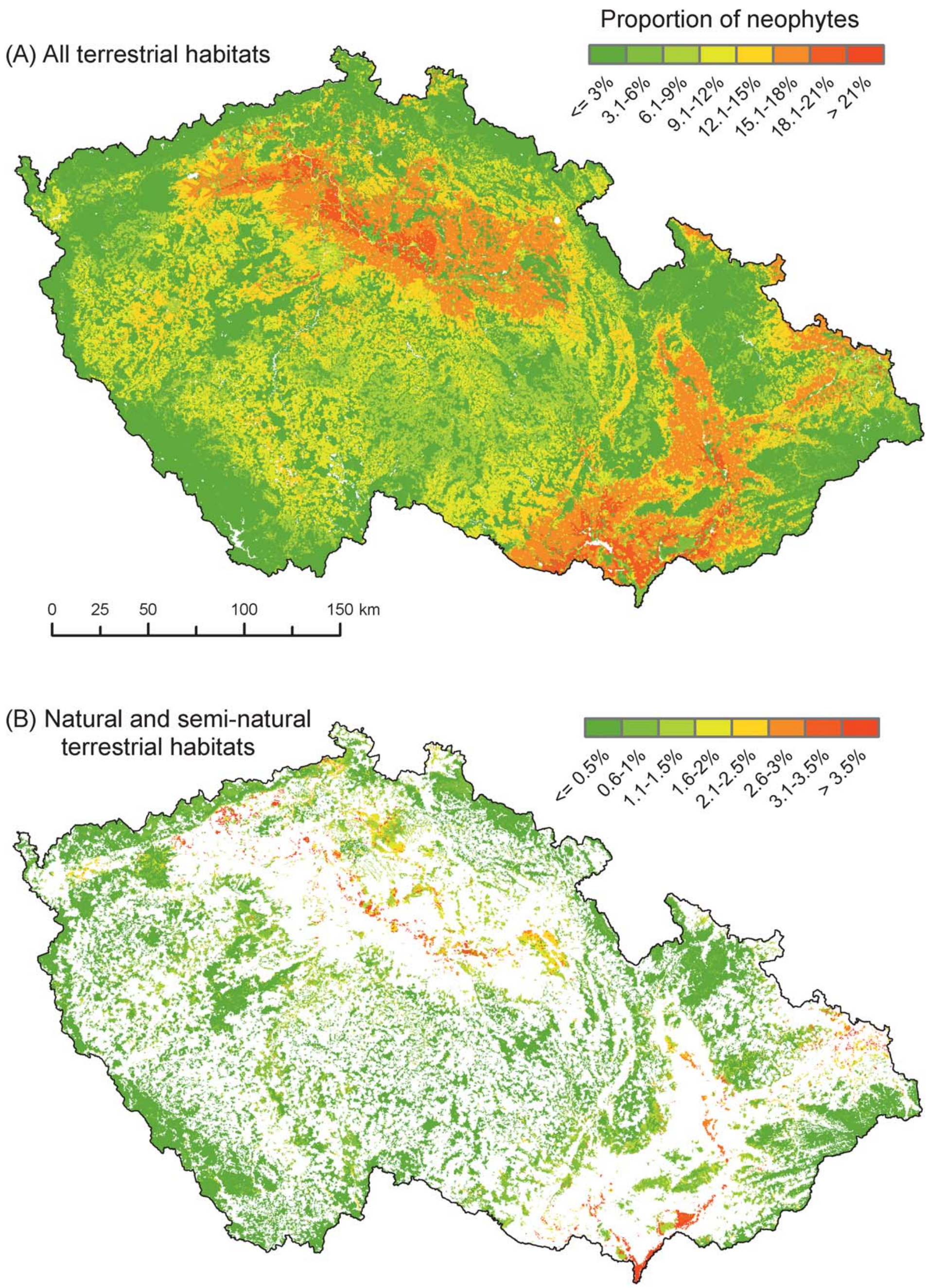

Fig. 7. – Level of invasion by neophytes, measured as the proportion of the species that are neophytes. Note the scales of the two maps differ.

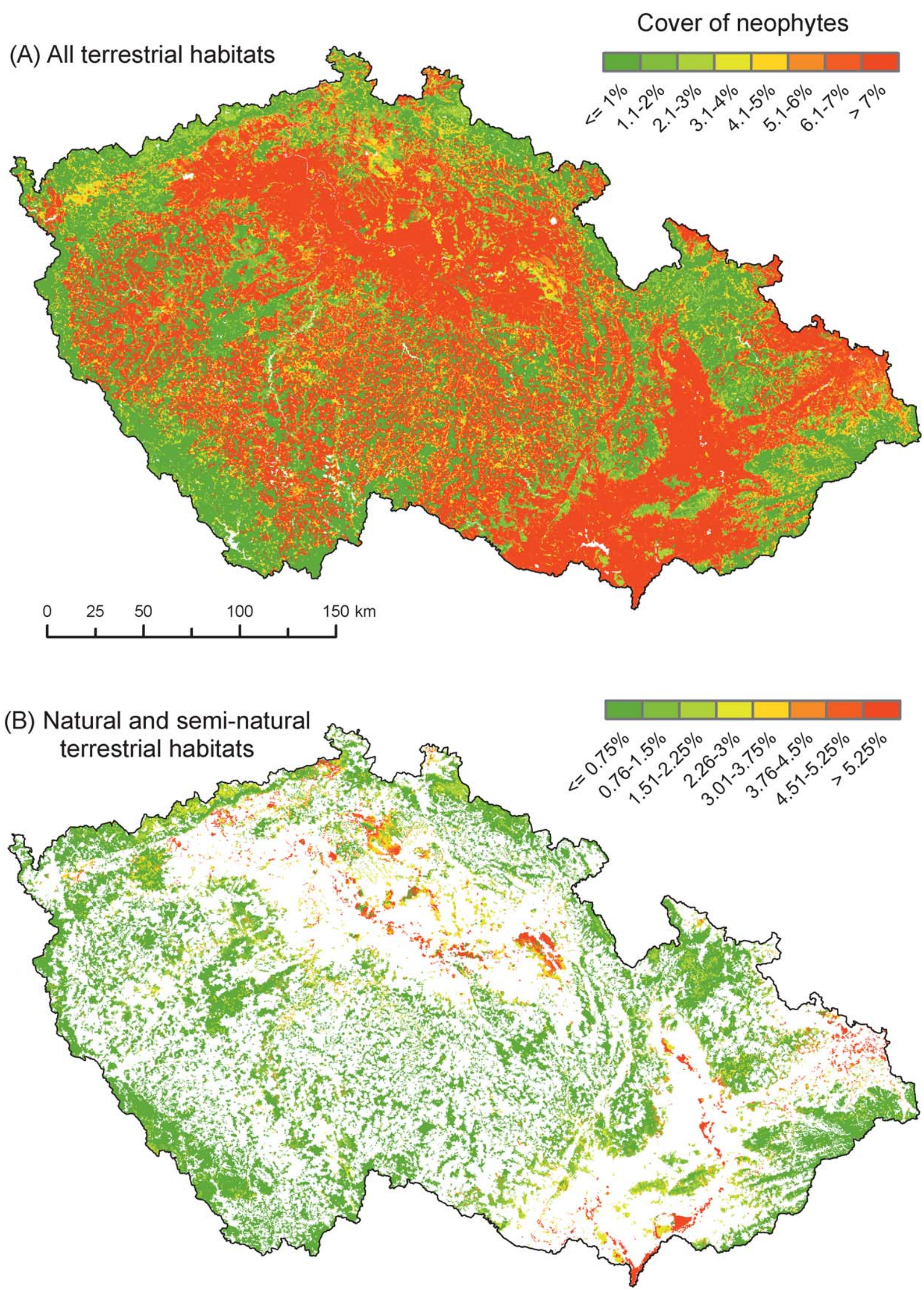

Fig. 8. – Level of invasion by neophytes, measured as the total cover of neophytes in vegetation plots. Note the scales of the two maps differ.

Douda 2008). Using this finer detailed information, we developed much more accurate invasion maps of the Czech Republic than we could for Europe (Chytrý et al. 2009). At the European scale, it was not possible to include either altitudinal information, due to the large variation in altitudinal vegetation belts across Europe, or a finer classification of habitats, due to poor compatibility of the vegetation classification systems used in different countries. However, as already suggested by the regression tree models presented by Chytrý et al. (2008a), both habitats and altitude were good predictors at the scale of the Czech Republic.

Geographical patterns of invasion by archaeophytes and neophytes

For both archaeophytes and neophytes, the maps reflect and give more precision to the basic pattern shown for neophytes at the European scale (Chytrý et al. 2009), i.e. agricultural and urban areas are most invaded, especially in the lowlands, while mountainous areas are least invaded. For proportions of archaeophytes and neophytes, areas with intensive agriculture are more invaded than large cities such as Prague or Brno (Figs 5A and 7A) due to the larger proportion of aliens in arable fields than in ruderal vegetation and grasslands typical of cities (Chytrý et al. 2005, Lososová & Grulich 2009).

By separating natural/semi-natural (parts B of Figs 5–8) from man-made habitats, we revealed that part of the variation in the level of invasion that would have otherwise remained hidden by the overriding contrast between natural/semi-natural and man-made habitats. Within natural and semi-natural habitat types, high levels of invasion were mainly found in various lowland habitats, e.g. in pine plantations and along streams, especially on the floodplains of large lowland rivers, which are consistently shown to support invasions in previous studies (Pyšek & Prach 1993, Planty-Tabacchi et al. 1996, Naiman & Décamps 1997, Tickner et al. 2001, Richardson et al. 2007). Very similar spatial patterns of invasions by archaeophytes and neophytes as in the Czech Republic are recorded at a landscape scale in central Germany (Deutschewitz et al. 2003).

General similarity of the invasion maps for archaeophytes and neophytes reflects the high correlation between the occurrence of these two groups of aliens (Chytrý et al. 2005, 2008b). However, there are some fine-scale differences between them, contrary to the similarity revealed at a coarse scale (Pyšek et al. 2005, Chytrý 2008b). For example, neophytes more strongly respond to altitude, being more concentrated in the lowlands than archaeophytes. Also, neophytes more heavily invade river corridors than archaeophytes.

Methodological considerations and remarks on the interpretation of the maps

This study is the first that provides rather detailed maps of plant invasions at a country scale. These maps involve a finer spatial resolution (250 × 250 m) than the maps based on the grid atlases of floras (e.g., Pino et al. 2005, Gassó et al. 2009), which usually use cells larger than 5 × 5 km, often equal or larger than 10 × 10 km. Further, our maps show a fine-scale level of invasion, based on vegetation plots smaller than 500 m^2, while the maps based on grid cells report proportions of alien species in the flora of a landscape segment and do not quantify local cover of alien species. Maps that use a larger grain also report higher proportions of aliens, because many aliens are rare and therefore are recorded only in larger areas (Chytrý et al. 2005, Hulme 2008).

It must be emphasized that the maps presented here are predictive, based on an interpolation of existing vegetation-plot data, and contain some degree of uncertainty. Sources of uncertainty include the quality of the interpretation of satellite images, the accuracy of the crosswalk between habitats and land-cover classes and representativeness of the underlying vegetation database, which, although resampled in a stratified way, includes plots sampled at preferentially selected sites (Roleček et al. 2007). In particular, actual mean covers of aliens on arable land can be lower than reported here, because the relevés used for this study were often sampled in field margins, which were less affected by herbicide application, and therefore had on average a higher cover of weeds than the interior parts of the fields. Moreover, the levels of invasion of habitats were treated as country-wide averages, disregarding the potential variation among regions within the country. For this reason, the levels of invasion in some areas can be over- or underestimated in the maps. For example, the relatively high levels of invasion of the areas planted with pine forests in the Ralská pahorkatina Hills in northern Bohemia and along the lower Orlice river in eastern Bohemia, or in abandoned areas with successional vegetation in the Doupovské hory Mountains in northern Bohemia (Vojta 2007, Kopecký & Vojta 2009) can be slightly overestimated.

The maps clearly need to be validated by field studies and improved in the future when more accurate data become available. Despite possible inaccuracies, however, these maps represent the best available approximation of the spatial pattern of plant invasions across the country, because a detailed fine-scale survey of the whole alien flora is not available for the Czech Republic and most other countries. Thus these maps may serve as a tool for risk assessment of alien plant invasions, as well as for planning their management and control.

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Souhrn

Série map invadovanosti území České republiky nepůvodními druhy rostlin byla vytvořena na základě kvantitativního vyhodnocení invadovanosti pro 35 terestrických biotopů v různých nadmořských výškách. Invadovanost byla stanovena pro 18 798 fytocenologických snímků pomocí dvou měr: podílu nepůvodních druhů ze všech druhů ve snímku a celkové pokryvnosti nepůvodních druhů. Poprvé byla invadovanost kvantifikována pro různé typy českých listnatých a jehličnatých lesů. Invadovanost byla hodnocena samostatně pro archeofyty a neofyty a v rámci každého biotopu byla vztažena k nadmořské výšce pomocí zobecněných lineárních modelů. V závislosti na použité míře invadovanost klesala s nadmořskou výškou v 16–20 biotopech pro archeofyty a v 18–23 biotopech pro neofyty. Jen ve dvou biotopech jedna z měr invadovanosti rostla s nadmořskou výškou, a to pro archeofyty. Hodnoty invadovanosti předpovězené zobecněnými lineárními modely pro jednotlivé kombinace biotopů a nadmořských výšek byly promítnuty na kombinovanou mapu krajinného pokryvu a výškopisu České republiky. Byly vytvořeny čtyři mapy invadovanosti vyjadřující jednak podíl, jednak pokryvnost nepůvodních druhů, a to zvlášť pro archeofyty a neofyty. Mapy ukazují, že obě tyto skupiny nepůvodních druhů jsou nejhojnější v nížinných zemědělských oblastech a městech, zatímco v horách jsou vzácné. Ve středních nadmořských výškách jsou zemědělské oblasti invadovány více než lesnatá území. Mimo zemědělskou krajinu a lidská sídla jsou hodně invadovány zejména nížinné oblasti s písčinami a nivy řek.

References

Becker T., Dietz H., Billeter R., Buschmann H. & Edwards P. J. (2005): Altitudinal distribution of alien plant species in the Swiss Alps. – Persp. Pl. Ecol. Evol. Syst. 7: 173–183.

Bossard M., Feranec J. & Otahel J. (2000): CORINE land cover technical guide: addendum 2000. – European Environment Agency, Copenhagen.

Boublík K., Petřík P., Sádlo J., Hédl R., Willner W., Černý T. & Kolbek J. (2007): Calcicolous beech forests and related vegetation in the Czech Republic: a comparison of formalized classifications. – Preslia 79: 141–161.

Chytrý M., Jarošík V., Pyšek P., Hájek O., Knollová I., Tichý L. & Danihelka J. (2008a): Separating habitat invasibility by alien plants from the actual level of invasion. – Ecology 89: 1541–1553.

Chytrý M., Maskell L. C., Pino J., Pyšek P., Vilà M., Font X. & Smart S. M. (2008b): Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. – J. Appl. Ecol. 45: 448–458.

Chytrý M., Pyšek P., Tichý L., Knollová I. & Danihelka J. (2005): Invasions by alien plants in the Czech Republic: a quantitative assessment across habitats. – Preslia 77: 339–354.

Chytrý M., Pyšek P., Wild J., Pino J., Maskell L. C. & Vilà M. (2009): European map of alien plant invasions based on the quantitative assessment across habitats. – Diversity Distrib. 15: 98–107.

Chytrý M. & Rafajová M. (2003): Czech National Phytosociological Database: basic statistics of the available vegetation-plot data. – Preslia 75: 1–15.

Chytrý M. & Tichý L. (2003): Diagnostic, constant and dominant species of vegetation classes and alliances of the Czech Republic: a statistical revision. – Folia Fac. Sci. Nat. Univ. Masarykianae Brunensis, Biol. 108: 1–231.

Davies C. E., Moss D. & Hill M. O. (2004): EUNIS Habitat Classification Revised 2004. – European Environment Agency, Copenhagen & European Topic Centre on Nature Protection and Biodiversity, Paris.

Deutschewitz K., Lausch A., Kühn I. & Klotz S. (2003): Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. – Glob. Ecol. Biogeogr. 12: 299–311.

Douda J. (2008): Formalized classification of the vegetation of alder carr and floodplain forests in the Czech Republic. – Preslia 80: 199–224.

Essl F. & Dirnböck T. (2008): Diversity of native and alien vascular plant species of dry grasslands in central Europe. – Appl. Veg. Sci. 11: 441–451.

Gassó N., Sol D., Pino J., Dana E. D., Lloret F., Sanz-Elorza M., Sobrino E. & Vilà M. (2009): Exploring species attributes and site characteristics to assess plant invasions in Spain. – Diversity Distrib. 15: 50–58.

Hulme P. E. (2008): Contrasting alien and native plant species-area relationships: the importance of spatial grain and extent. – Glob. Ecol. Biogeogr. 17: 641–647.

Jehlík V. (ed.) (1998): Cizí expanzivní plevele České republiky a Slovenské republiky [Alien expansive weeds of the Czech Republic and Slovak Republic]. – Academia, Praha.

Kalwij J. M., Robertson M. P. & van Rensburg B. J. (2008): Human activity facilitates altitudinal expansion of exotic plants along a road in montane grassland, South Africa. – Appl. Veg. Sci. 11: 491–498

Knollová I. & Chytrý M. (2004): Oak-hornbeam forests of the Czech Republic: geographical and ecological approaches to vegetation classification. – Preslia 76: 291–311.

Kopecký M. & Vojta J. (2009): Land use legacies in post-agricultural forests in the Doupovské Mountains, Czech Republic. – Appl. Veg. Sci. 12: 251–260.

Kowarik I. (1995): On the role of alien species in urban flora and vegetation. – In: Pyšek P., Prach K., Rejmánek M. & Wade P. M. (eds), Plant invasions: general aspects and special problems, p. 85–103, SPB Academic Publ., Amsterdam.

Lambdon P. W., Pyšek P., Basnou C., Hejda M., Arianoutsou M., Essl F., Jarošík V., Pergl J., Winter M., Anastasiu P., Andriopoulos P., Bazos I., Brundu G., Celesti-Grapow L., Chassot P., Delipetrou P., Josefsson M., Kark S., Klotz S., Kokkoris Y., Kühn I., Marchante H., Perglová I., Pino J., Vilà M., Zikos A., Roy D. & Hulme P. E. (2008): Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. – Preslia 80: 101–149.

Lososová Z., Chytrý M., Cimalová Š., Kropáč Z., Otýpková Z., Pyšek P. & Tichý L. (2004): Weed vegetation of arable land in Central Europe: gradients of diversity and species composition. – J. Veg. Sci. 15: 415–422.

Lososová Z. & Grulich V. (2009): Chorological spectra of arable weed vegetation types in the Czech Republic. – Phytocoenologia 39: 235–252.

Lososová Z. & Simonová D. (2008): Changes during the last century in species composition of synanthropic vegetation in Moravia (Czech Republic). – Preslia 80: 291–305.

Mandák B., Pyšek P. & Bímová K. (2004): History of the invasion and distribution of *Reynoutria* taxa in the Czech Republic: a hybrid spreading faster than its parents. – Preslia 76: 15–64.
Maskell L. C., Firbank L. G., Thompson K., Bullock J. M. & Smart S. M. (2006): Interactions between non-native plant species and the floristic composition of common habitats. – J. Ecol. 94: 1052–1060.
McCullagh P. & Nelder J. A. (1989): Generalized linear models. – Chapman & Hall, London.
McDougall K. L., Morgan J. W., Walsh N. G. & Williams R. J. (2005): Plant invasions in treeless vegetation of the Australian Alps. – Persp. Pl. Ecol. Evol. Syst. 7: 159–171.
Mihulka S. (1998): The effect of altitude on the pattern of plant invasions: a field test. – In: Starfinger U., Edwards K., Kowarik I. & Williamson M. (eds), Plant invasions: ecological mechanisms and human responses, p. 313–320, Backhuys Publ., Leiden.
Moravec J. (ed.) (1998–2003): Přehled vegetace České republiky. Svazek 1–4 [Vegetation survey of the Czech Republic. Vol. 1–4]. – Academia, Praha.
Moss D. & Wyatt B. K. (1994): The CORINE Biotopes Project: a database for conservation of nature and wildlife in the European Community. – J. Appl. Geogr. 14: 327–349.
Naiman R. J. & Décamps H. (1997): The ecology of interfaces: riparian zones. – Ann. Rev. Ecol. Syst. 28: 621–658.
Neuhäuslová Z., Moravec J., Chytrý M., Sádlo J., Rybníček K., Kolbek J. & Jirásek J. (1997): Mapa potenciální přirozené vegetace České republiky 1 : 500 000 [Map of the potential natural vegetation of the Czech Republic 1 : 500,000]. – Botanický ústav AV ČR, Průhonice.
Pauchard A. & Alaback P. B. (2004): Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of South-Central Chile. – Conserv. Biol. 18: 238–248.
Pino J., Font X., Carbó J., Jové M. & Pallares L. (2005): Large-scale correlates of alien plant invasion in Catalonia (NE of Spain). – Biol. Conserv. 122: 339–350.
Planty-Tabacchi A.-M., Tabacchi E., Naiman R. J., Deferrari C. & Décamps H. (1996): Invasibility of species-rich communities in riparian zones. – Conserv. Biol. 10: 598–607.
Pyšek P. (1991): *Heracleum mantegazzianum* in the Czech Republic: the dynamics of spreading from the historical perspective. – Folia Geobot. Phytotax. 26: 439–454.
Pyšek P., Jarošík V., Chytrý M., Kropáč Z., Tichý L. & Wild J. (2005): Alien plants in temperate weed communities: prehistoric and recent invaders occupy different habitats. – Ecology 86: 772–785.
Pyšek P., Jarošík V. & Kučera T. (2002a): Patterns of invasion in temperate nature reserves. – Biol. Conserv. 104: 13–24.
Pyšek P. & Prach K. (1993): Plant invasions and the role of riparian habitats: a comparison of four species alien to Central Europe. – J. Biogeogr. 20: 413–420.
Pyšek P. & Prach K. (1995): Invasion dynamics of *Impatiens glandulifera*: a century of spreading reconstructed. – Biol. Conserv. 74: 41–48.
Pyšek P., Richardson D. M., Rejmánek M., Webster G., Williamson M. & Kirschner J. (2004a): Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. – Taxon 53: 131–143.
Pyšek P., Richardson D. M. & Williamson M. (2004b): Predicting and explaining plant invasions through analysis of source area floras: some critical considerations. – Diversity Distrib. 10: 179–187.
Pyšek P., Sádlo J. & Mandák B. (2002b): Catalogue of alien plants of the Czech Republic. – Preslia 74: 97–186.
R Development Core Team (2009): R: a language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, URL: [http://www.R-project.org].
Richardson D. M., Holmes P. M., Esler K. J., Galatowitsch S. M., Stromberg J. C., Kirkman S. P., Pyšek P. & Hobbs R. J. (2007): Riparian vegetation: degradation, alien plant invasions, and restoration prospects. – Diversity Distrib. 13: 126–139.
Richardson D. M. & Pyšek P. (2006): Plant invasions: merging the concepts of species invasiveness and community invasibility. – Progr. Phys. Geogr. 30: 409–431.
Roleček J. (2007): Formalized classification of thermophilous oak forests in the Czech Republic: what brings the Cocktail method? – Preslia 79: 1–21.
Roleček J., Chytrý M., Hájek M., Lvončík S. & Tichý L. (2007): Sampling design in large-scale vegetation studies: do not sacrifice ecological thinking to statistical purism! – Folia Geobot. 42: 199–208.
Sádlo J., Chytrý M. & Pyšek P. (2007): Regional species pools of vascular plants in habitats of the Czech Republic. – Preslia 79: 303–321.
Settele J., Hammen V., Hulme P., Karlson U., Klotz S., Kotarac M., Kunin W., Marion G., O'Connor M., Petanidou T., Peterson K., Potts S., Pritchard H., Pyšek P., Rounsevell M., Spangenberg J., Steffan-Dewenter

I., Sykes M., Vighi M., Zobel M. & Kühn I. (2005): ALARM: Assessing LArge-scale environmental Risks for biodiversity with tested Methods. – GAIA – Ecol. Persp. Sci. Soc. 14: 69–72.
Simonová D. & Lososová Z. (2008): Which factors determine plant invasions in man-made habitats in the Czech Republic? – Persp. Pl. Ecol. Evol. Syst. 10: 89–100.
Slavík B. (1986): Fytokartografické syntézy ČSR 1 [Phytocatographical syntheses of the Czech Socialistic Republic 1]. – Botanický ústav ČSAV, Průhonice.
Slavík B. (1990): Fytokartografické syntézy ČR 2 [Phytocartographical syntheses of the Czech Republic 2]. – Botanický ústav ČSAV, Průhonice.
Slavík B. (1998): Phytocartographical syntheses of the Czech Republic 3. – Academia, Praha.
Stohlgren T. J., Jarnevich C., Chong G. W. & Evangelista P. H. (2006): Scale and plant invasions: a theory of biotic acceptance. – Preslia 78: 405–426.
Thiele J., Kollmann J. & Andersen U. R. (2009): Ecological and socioeconomic correlates of plant invasions in Denmark: the utility of environmental assessment data – Ambio 38: 89–94.
Tichý L. (2002): JUICE, software for vegetation classification. – J. Veg. Sci. 13: 451–453.
Tickner D. P., Angold P. G., Gurnell A. M. & Mountford J. O. (2001): Riparian plant invasions: hydrogeomorphological control and ecological impacts. – Progr. Phys. Geogr. 25: 22–52.
van der Maarel E. (1979): Transformation of cover-abundance values in phytosociology and its effects on community similarity. – Vegetatio 38: 97–114.
Vilà M., Pino J. & Font X. (2007): Regional assessment of plant invasions across different habitat types. – J. Veg. Sci. 18: 35–42.
Vojta J. (2007): Relative importance of historical and natural factors influencing vegetation of secondary forests in abandoned villages. – Preslia 79: 229–244.

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