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Fifty years of plant invasion dynamics in Slovakia along a 2,500 m altitudinal gradient

Jana Medvecká · Ivan Jarolímek · Dušan Senko · Marek Svitok

Abstract Knowledge on the main spatiotemporal trends in plant invasions of habitats is essential for a better understanding of the process of these invasions. The aim of this study was to determine the level of plant invasion, represented by relative richness and total cover of archaeophytes and neophytes, in 45 EUNIS habitat types along with spatiotemporal changes in invasion level with increasing altitude and time in Slovakia. In general, the most invaded habitats are those which are highly influenced by human activities. Generalized linear models and generalized linear mixed models were used to assess the associations between habitat-specific invasion level, altitude and time, respectively. There is a general decrease in the relative richness and total cover of archaeophytes and neophytes with increasing altitude in the invaded habitats. There is also an observable temporal trend in archaeophytes shifting from anthropogenic towards more natural habitats.

Importantly, the relative neophyte richness has recently been increasing, predominantly in semi-natural and natural habitats, which brings about major concerns for nature conservation. This may be the manifestation of a lag phase in the dispersal of neophytes. However, accompanied with a significant increase in the relative richness of archaeophytes in some natural habitats, it may indicate more complex changes in the invaded habitats and be an early warning sign for ecological degradation of these habitats.

Keywords Alien plants · Archaeophytes · EUNIS habitats · Neophytes · Spatiotemporal trends

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Introduction

Fact that some plant communities are more invaded than others has been focus of many scientific activities during the last decades (e.g. Tilman 1997; Stohlgren et al. 2006; Chytrý et al. 2008a, b; Vilà et al. 2007; Pinke et al. 2011). The actual level of invasion by alien plants is determined by the properties of the community (which may include invasibility, i.e. its vulnerability to invasion), the level of disturbance, propagule pressure of the alien species and characteristics of the alien species, especially their invasive potential (Lonsdale 1999). It can be expressed by various metrics, most frequently applied are alien species

richness, relative alien species richness, alien species cover and relative alien species cover (Catford et al. 2012).

To evaluate the differences in the level of invasion of various habitats several comparative studies of large datasets have been conducted on regional (e.g. Vilà et al. 2007), national (e.g. Chytrý et al. 2005; Maskell et al. 2006) or even continental levels (e.g. Chytrý et al. 2008b). According to the results, anthropogenic habitats are among the most invaded types of habitats.

Based on analyses of large datasets from various European regions, the most important proxies correlated with alien species richness are disturbance (Lonsdale 1999; Chytrý et al. 2008a), land use in the surrounding area (Pino et al. 2005; Celesti-Grapow et al. 2006; Chytrý et al. 2008a), the diversity of native species (Pyšek et al. 2002a; Chytrý et al. 2005; Vilà et al. 2007; Pino et al. 2005; Simonová and Lososová 2008), and altitude and associated climatic variables (Pino et al. 2005; Simonová and Lososová 2008). Several studies that have focused on the process of invasion along altitudinal gradients in mountain ecosystems (e.g. Pauchard and Alaback 2004; Arévalo et al. 2005; Becker et al. 2005; Fowler et al. 2008), have shown that alien species richness decreases with increasing altitude. Although mountain ecosystems are generally less invaded than surrounding areas, this could be related to a time-lag effect or less intensive human activities at higher elevations rather than an inherent resistance of mountain ecosystems to plant invasion (Pauchard et al. 2009; McDougall et al. 2011).

One of the very few studies, which focused on long-term changes in the levels of invasion (Aikio et al. 2012), used herbarium records to analyse the total number of alien species (alien species richness) per habitat in 11 terrestrial habitats in New Zealand and process of accumulation of alien plant species over the time in the analysed habitats. In general they found out that urban, roadside and sparse habitats had the highest number of records of alien species, which was increasing over time in all habitat types. In comparison to herbarium records, the phytosociological relevés, used in the study, contain list of all present species, both native and alien, in one plant community and thus bring more information. Their use enables to test, whether number of alien species per relevé (or in this case relative alien species richness) increases over time, and thus demonstrate that not only habitats contain alien species more frequently, but they also

harbour more alien species per relevé. Here, we present to the best of our knowledge the first analysis of dynamics of plant invasions level conducted on a large dataset of relevés involving a wide range of habitats over a long time period. We believe that this habitat-specific assessment of invasion levels across an altitudinal gradient and over time can facilitate a better understanding of invasion processes, and should be of value for biodiversity conservation. Knowledge of the dynamics of the level of invasion of various habitat types enables to identify, which habitats are at higher risk in the long-term, even if their level of invasion is currently low.

Slovakia is a Central European country located on the transition between a temperate oceanic and a continental climate. The majority of the country is mountainous and has a wide range of altitudes, ranging from a minimum of 94 m a.s.l. in Pannonia to a maximum of 2,655 m a.s.l. in the Western Carpathians (Šucha 2011), making the country an excellent model region for this type of analysis. Moreover, Slovakia has a long history of phytosociological research and a large database of phytosociological relevés (over 50,000). In the past few years, comprehensive surveys of almost all vegetation types of non-forest vegetation have been published (Valachovič 1995, 2001; Jarolímek et al. 1997; Kliment et al. 2007; Janišová et al. 2007), and an analysis of forest vegetation is currently being conducted.

We used a dataset of vegetation relevés from Slovakia to address three main objectives: (1) To assess the level of invasion, as represented by the relative richness and cover of archaeophytes and neophytes, within the 45 EUNIS habitat types occurring in Slovakia; (2) To analyse the association of altitude with the relative richness and total cover of archaeophytes and neophytes; (3) To determine long-term changes in the invasion level of habitats over the last five decades.

Methods

A dataset of relevés from the Central Database of Phytosociological Relevés for Slovakia (Hegedüšová and Šibík 2012, http://ibot.sav.sk/cdf/) was the main input. Each relevé contains basic geographical and ecological characteristics, date of collection and a list of all present plant species, with their abundance/

dominance values in the Braun-Blanquet semi-quantitative scale (Braun-Blanquet 1964).

From the original 51,523 relevés contained in the database, we omitted relevés that were located outside of Slovakia, were not assigned to any of the evaluated syntaxa or lacked geographical coordinates. To reduce the effect of different sample sizes within the same habitat, we eliminated relevés that either lacked information about the size of the plot or with area out of the intervals 1–50 m^2 for most of the non-forest vegetation (except for arable lands), 25–100 m^2 for arable lands, 10–100 m^2 for shrub vegetation and 50–400 m^2 for the forest vegetation.

Before the expansion of portable GPS devices geographical localization of relevés was less accurate. Therefore, we have decided to determine the missing data ex post by more exact methods using the GRASS GIS v6.4, GNU/GPL platform running on Debian GNU/Linux. This application helps us to identify the geographic coordinates of the historical relevés, stored in database, using Geographic information system (GIS) based on knowledge of certain known parameters (geomorphological unit, altitude, slope, slope aspect, type of biotope and description of the locality). In the self-tests of spatial accuracy we used records with known GPS coordinates. The diffusion of values was set as follows: aspect $\pm 7°$, altitude ± 5 m a.s.l. and slope aspect $\pm 5°$. The average value of differences between computed coordinates and control originals was 37.89 m. In points with one possibility the average of differences was 12.86 m. We also tested the accuracy of searching of coordinates by expert on standard paper topographic maps. In this step, an expert view of the scientist is important to solve problematic tasks (his/hers autonomy, responsibility and context evaluation). Accuracy of this method was 31.95 m. Due to the above-mentioned facts, we consider rounding altitude to integers as adequate.

If the relevés lacked information on altitude, the altitude was calculated using a Digital Elevation Model, generated from vectorised contour lines (at a scale of 1:10.000). The vertical accuracy is estimated at ± 5 m intervals. A model was developed using the Topo to Raster function (TopoGrid module) of ArcGIS ArcInfo™, which provides a smooth, hydrologically correct digital model of the surface. To focus on the last five decades, we retained only relevés that were made between 1960 and 2010. The relevés originated from numerous contributors across the decades and this fact

significantly reduces any subjective effect of authors choosing only "nice" and species-rich stands.

Each plot in the resulting dataset was assigned to one of the 45 habitat types based on the EUNIS habitat classification (Hill et al. 2004, revised in May 2007, available at http://eunis.eea.europa.eu/habitats.jsp), according to the corresponding vegetation types (see Table 1). The use of EUNIS, which is a standard classification of European habitats, enables much easier comparisons of the results to findings from other European and non-European countries than the use of a phytosociological system. EUNIS is a hierarchical system of habitat classification with levels from 1 to 6, where level 1 represents wide habitat complexes and higher levels represent more narrowly delimited habitats. In general, classification level 3 was used; level 2 was used for habitats that were either rare or not known to be highly invaded. Level 4 was used for habitats for which the subtypes are known to differ in the level of invasion. Habitat E5.1 (Anthropogenic herb stands) was divided into two subgroups, E5.1A and E5.1B, based on the prevalence of either perennials or annual species. Habitats C3.2 (Water-fringing reedbeds and tall helophytes other than canes) and D5 (Sedge and reedbeds, normally without free-standing water) were merged because it was not possible to separate these two habitats based on the phytosociological classification.

All habitats were characterized as either natural, semi-natural or human-made. Built-up areas, parks, gardens, orchards, agricultural land, and all the types of ruderal vegetation and the other types of habitats that are seriously altered by human activity, e.g. recently felled areas were categorized as human-made. The semi-natural habitats included cultural landscapes that are moderately affected by man (excluding human-made habitats), such as pastures, regularly or irregularly mown grasslands and field balks. The forests and naturally treeless vegetation (alpine vegetation, wetlands, etc.) are natural habitats.

To increase the homogeneity of the dataset and prevent the oversampling of some regions, the dataset was geographically stratified using a geographical grid of 0.375 latitudinal × 0.625 longitudinal minute quadrangles, according to the above-mentioned habitat classification. One relevé per each habitat was retained in each stratum. The resulting dataset consisted of 16,184 relevés.

Nomenclature of taxa follows Marhold (1998), except for the aggregates defined in Supplementary material 1.

Table 1 List of EUNIS habitats used in the analyses and corresponding vegetation types, originally identifying the relevés

Code	Category	EUNIS habitat	Vegetation types
C1.2	N	Permanent mesotrophic lakes, ponds and pools	*Potametea* (except *Ranunculion fluitantis* and *Nymphaeion albae*), *Charetea fragilis*, *Hydrocharition morus-ranae*, *Utricularion vulgaris*
C1.3	S	Permanent eutrophic lakes, ponds and pools	*Nymphaeion albae, Lemnion minoris*
C1.4	N	Permanent dystrophic lakes, ponds and pools	*Sphagno-Utricularion minoris*
C2	N	Surface running waters	*Montio-Cardaminetea, Ranunculion fluitantis*
C3.2	N	Water-fringing reedbeds and tall helophytes other than canes, including D5	*Phalaridion arundinaceae, Sparganio-Glycerion, Phragmition australis, Cirsio brachycephali-Bolboschoenion compacti, Magnocaricion elatae*
C3.4	S	Species-poor beds of low-growing water-fringing or amphibious vegetation	*Isoeto-Litorelletea* (except *Sphagno-Utricularion minoris*), *Isoeto-Nanojuncetea*
C3.5	S	Periodically inundated shores with pioneer and ephemeral vegetation	*Bidentetea tripartitae, Oenanthion aquaticae*
D1	N	Raised and blanket bogs	*Oxycocco-Sphagnetea*
D2	N	Valley mires, poor fens and transition mires	*Scheuchzerio-Caricetea fuscae* (except *Caricion davallianae*)
D4	N	Base-rich fens and calcareous spring mires	*Caricion davallianae*
E1.1	N	Inland sand and rock with open vegetation	*Sedo-Scleranthetea, Festucetea vaginatae*
E1.2	N	Perennial calcareous grassland and basic steppes	*Festuco-Brometea*
E1.9	N	Open non-Mediterranean dry acid and neutral grassland, including inland dune grassland	*Koelerio-Corynephoretea*
E2.1	S	Permanent mesotrophic pastures and aftermath-grazed meadows	*Cynosurion cristati, Potentillion anserinae, Poion alpinae, Alchemillo-Poion supinae*
E2.2	S	Low and medium altitude hay meadows	*Arrhenatherion elatioris, Nardetea strictae* (except *Nardion*)
E2.3	S	Mountain hay meadows	*Polygono bistortae-Trisetion flavescentis,*
E2.8	H	Trampled mesophilous grasslands with annuals	*Saginion prucumbentis, Polygono-Poetea, Plantagini-Prunellion*
E3	S	Seasonally wet and wet grasslands	*Molinietalia* (except *Calthion palustris*), *Juncion effusi*
E4	N	Alpine and subalpine grasslands	*Nardion, Elyno-Seslerietea, Caricetea curvulae, Salicetea herbaceae, Carici rupestris-Kobresietea bellardii*
E5.1A	H	Anthropogenic herb stands of perennials	*Artemisietea vulgaris*
E5.1B	H	Anthropogenic herb stands of annuals	*Sisymbrietalia, Salsolion ruthenicae, Eragrostio-Polygonion arenastri*
E5.2	N	Thermophile woodland fringes—natural	*Trifolio-Geranietea sanguinei*
E5.41	S	Screens or veils of perennial tall herbs lining watercourses	*Senecionion fluviatilis*
E5.42	N	Tall-herb communities of humid meadows	*Calthion palustris*
E5.43	S	Shady woodland edge fringes	*Lamio albi-Chenopodietalia boni-henrici*
E5.5	N	Subalpine moist or wet tall-herb and fern stands	*Mulgedio-Aconitetea*
E6	N	Inland salt steppes	*Festuco-Puccinelietea, Thero-Salicornietea*
F2	N	Arctic, alpine and subalpine scrub	*Roso pendulinae-Pinetea mugo, Loiseleurio-Vaccinietea, Betulo carpaticae-Alnetea viridis*
F3	S	Temperate and mediterranean-montane scrub	*Rhamno-Prunetea, Franguletea*
F4	N	Temperate shrub heathland	*Calluno-Ulicetea*
F9.21	N	Grey willow carrs	*Salicion cinereae, Salicion incanae, Salicion triandrae*

Table 1 continued

Code	Category	EUNIS habitat	Vegetation types
G1.1	N	Riparian and gallery woodland, with dominant alder, poplar or willow	*Alnion glutinosae*, *Alnion incanae*, *Salicion albae*
G1.5	N	Broadleaved swamp woodland on acid peat	*Molinio-Betuletea pubescentis*
G1.6	N	Beech woodland	*Luzulo-Fagion*, *Fagion*
G1.7	N	Thermophilous deciduous woodland	*Quercetalia pubescenti-petraeae*
G1.8	N	Acidophilous oak-dominated woodland	*Quercetea robori-petreae*
G1.A	N	Meso- and eutrophic oak, hornbeam, ash, sycamore, lime, elm and related woodland	*Tilio-Acerion*, *Carpinion betuli*
G1.C	H	Highly artificial broadleaved deciduous forestry plantations	*Robinietea*, stands dominated by *Ailanthus altissima*
G3.1	N	Fir and spruce woodland	*Vaccinio-Picetea* (except *Dicrano-Pinion*)
G3.4	N	Scots pine woodland south of the taiga	*Erico-Pinetea*, *Pulsatillo-Pinetea*, *Dicrano-Pinion*
G3.D	N	Boreal bog conifer woodland	*Vaccinio uliginosi-Pinetea sylvestris*
G5.8	H	Recently felled areas	*Epilobietea angustifolii*
H2	N	Screes	*Thlaspietea rotundifolii*
H3	N	Inland cliffs, rock pavements and outcrops	*Asplenietea trichomanis*
I1	H	Arable land and market gardens	*Centaureetalia cyani*, *Atriplici-Chenopodietalia albi*, *Eragrostion*

Category of naturalness: human-made (H), semi-natural (S) and natural (N) is provided. Syntaxonomical delimitation and nomenclature of syntaxa follows Jarolímek and Šibík (2008)

In the analyses of species composition of individual relevés, we considered only vascular plants. Cultivated crops were excluded from the dataset. Potentially cultivated alien trees were retained, because even though it was not possible to unequivocally state whether they were deliberately planted, the structure of the data indicates that the majority were reproducing naturally.

All plants were classified as archaeophytes (alien species introduced before AD 1500), neophytes (alien species introduced after AD 1500) or native species according to Medvecká et al. (2012). Various studies have shown that it is important to distinguish between archaeophytes and neophytes, as the two groups have different habitat affinities in Central Europe (Chytrý et al. 2005; Pyšek et al. 2005).

For each relevé, we calculated the relative richness and total cover of archaeophytes, neophytes and alien species together using the software JUICE 7.0 (Tichý 2002), and the method described by Chytrý et al. (2005) was used to calculate the total cover. Relative alien species richness (alien species richness as a percentage of community richness) was used as a measure of invasion level. As total alien species richness, the percentage of alien species also accounts

for the species richness of the invading community. Relative richness is used to lessen the influence of plot size, making the metric more comparable among sites (Catford et al. 2012). Alien species cover was employed as a second measure of invasion level. As it is expressed as the percentage of the total area occupied by alien species, it is not affected by the sample size. However, use of the semi-quantitative Braun-Blanquet 7 or 9 degree scale (Braun-Blanquet 1964; Westhoff and Van Den Maarel 1978) to express cover with intervals of 25 % for the last three cover classes must be taken into consideration when interpreting the results. For the purpose of analyses all values were expressed as proportions ranging from 0 to 1.

The level of invasion was assessed using generalized linear models (GLM), with binomial error distribution and the logit link function employed in order to test the effect of altitude and time on the relative alien species richness and alien species cover, respectively. In the case of higher variance than expected for binomial models (overdispersion), quasi-likelihood models were used. Only habitats with a higher frequency of occurrence of alien species (>5 % of relevés) were included in the analyses. Initially, full

models were fitted to the data, including both predictors. The full models were simplified following backward stepwise deletion associated with likelihood-ratio tests. Separate models were built for each habitat type. Spatial correlograms were used to check for autocorrelation in the residuals of the final models. To deal with the difficulties caused by significant spatial autocorrelation, some data sets were re-fitted using generalized mixed effect models (GLMM) (Dormann et al. 2007). GLMMs with spatially structured random effects were fitted using penalised quasi-likelihood. However, for some habitats, relevés were highly clustered in space and the GLMMs with spatially structured random effects showed significant positive autocorrelation at short lag distances. In order to accommodate the spatial autocorrelation among those relevés, hierarchically structured GLMMs were fitted. In these cases, the data were hierarchically structured in the sense that relevés in close proximity were nested within spatial clusters (groups) and those groups were introduced as random-effects in the GLMMs. The same models were used to assess temporal change in the number of native species. The final dataset used in the GLMs and GLMMs consisted of 11,231 relevés. For comparative purposes and to facilitate interpretation of the results, fully standardised regression coefficients (b_M^*) (Menard 2004) were extracted from full models for each habitat. GLMs were also used to compare the level of invasion across habitats. If an overall test was significant, a multiple comparison procedure was performed using Tukey contrasts. Mean values and 95 % confidence intervals were displayed in order to provide information on the magnitude of the differences and to facilitate interpretation of the results. Confidence intervals were estimated using 10,000 non-parametric bootstrap replications and applying the bias-corrected and accelerated percentile method (Efron 1987). All the analyses were performed in the R language environment (R Development Core Team 2012).

Results

In total, the stratified dataset contained 181 archaeophytes, 127 neophytes and 2,075 native species. The average relative richness of the archaeophytes and neophytes in individual relevés was 4.2 and 1.3 %,

respectively. The average relative richness of aliens together in individual relevés was 5.5 %, varying from 0 to 100 %. The altitude of the relevés used in the analyses ranged from 94 to 2,632 m, with an average of 627 m. In total, 33.6 % of the relevés contained at least one alien species, and 26.5 and 17.3 % contained at least one archaeophyte and neophyte, respectively.

The ratio of archaeophytes to neophytes was usually higher than 5:1 for open and more xerothermophilous vegetation, such as E1.1 (inland sands and rocks with open vegetation), E1.2 (perennial calcareous grasslands and basic steppes), E5.1A (anthropogenic herb stands of perennials), E5.2 (thermophile woodland fringes—natural), E5.43 (shady woodland edge fringes), E6 (inland salt steppes), G3.4 (Scots pine woodlands), H2 (screes) and I1 (arable land). In contrast, the average relative neophytes richness is higher than the relative archaeophyte richness in more mesophilous and hygrophilous habitats, such as C2 (surface running waters), C3.2 (water-fringing reedbeds and tall helophytes other than canes), D2 (valley mires, poor fens and transition mires), E3 (seasonally wet and wet grasslands), E5.41 (screens or veils of perennial tall herbs lining watercourses), E5.42 (tall-herb communities of humid meadows) and G1.1 (riparian and gallery woodlands with dominant alder, poplar or willow). Several aquatic habitats contained only neophytes.

There were significant differences in the level of invasion among habitats, irrespective of whether defined by the relative richness of neophytes (F = 109.21, $p < 0.001$), relative richness of archaeophytes (F = 447.65, $p < 0.001$), cover of neophytes (F = 118.56, $p < 0.001$) or cover of archaeophytes (F = 410.44, $p < 0.001$). In general, the most invaded habitats were anthropogenic habitats, such as E5.1A and E5.1B (anthropogenic herb stands of annuals and perennials), I1 (arable land), E2.8 (trampled habitats) and G1.C (highly artificial broadleaved deciduous forestry plantations) (Fig. 1). The more or less seminatural habitats, such as E5.43 (woodland fringes), E5.41 (communities of perennial tall herbs lining watercourses) and C3.4 (species-poor beds of low-growing water-fringing or amphibious vegetation), tended to contain relatively high relative richness of alien species. Conversely, the least invaded were extreme habitats, such as bogs and mires and subalpine and alpine habitats. In total, 5 habitats contained no aliens at all, namely C1.4 (permanent dystrophic lakes,
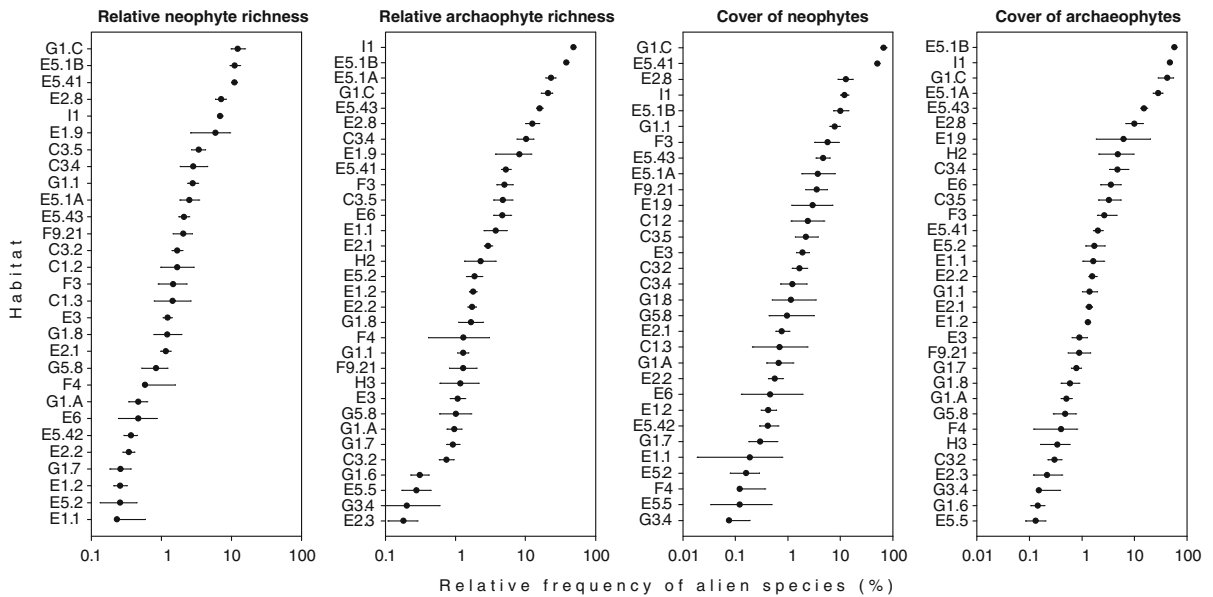
Fig. 1 Relative proportion and cover of alien species in studied EUNIS habitats. Mean values (*circles*) and 95 % bootstrap confidence intervals (*error bars*) are displayed

ponds and pools), D1 (raised and blanket bogs), F2 (alpine and subalpine scrub), G1.5 (broadleaved swamp woodland on acid peat) and G3.D (boreal bog conifer woodland). For details on pair-wise comparisons among habitats see Supplementary material 2.

In total, 32 and 29 of the 45 habitats analysed contained more than 5 % of the relevés invaded by archaeophytes and neophytes, respectively. The invasion level decreased with altitude in most of the studied habitats (Fig. 2). A significant decline in neophyte and archaeophyte relative species richness was recorded in 18 (62.1 %) and 19 (59.4 %) habitats, respectively. The analysis of alien species cover gave similar results. A significant decline in the cover of neophytes and archaeophytes was observed in 15 (51.7 %) and 18 (56.3 %) habitats, respectively. Both natural and anthropogenic habitats showed a similar altitudinal pattern of invasion level.

Considering temporal trends in invasion level, the relative neophyte richness significantly increased over the last 50 years in 11 (37.9 %) predominantly semi-natural and natural habitats, and decreased in 1 (3.4 %) habitat, namely G1.C (Highly artificial broadleaved deciduous forestry plantations) (Fig. 3). The relative archaeophyte richness significantly increased over time in 8 habitats (25 %), predominantly semi-natural and natural, and decreased in 7 (21.9 %) habitats. The pattern for the total cover was a bit

different, the total cover of archaeophytes showed a significant positive trend in 10 habitats (31.3 %), negative trend in 2 (6.3 %), and neophytes showed an increasing temporal trend in 12 habitats (41.4 %), without clear distinction between natural, semi-natural and human-made habitats. Details on minimal adequate models explaining the level of habitat invasions are given in Supplementary material 3.

Observed changes in the relative alien species richness may reflect an actual increase in the number of alien species or a decrease in the number of native species. However, in most of the habitats the number of native species significantly increased (15 habitats) or did not change (12 habitats) over the last five decades. Therefore, we assume that the observed positive temporal trends in the relative richness of alien species are not artefacts of a decline in native species, but a true increase of invasion level.

Discussion

Current level of invasion

Even though Slovak alien flora contains more neophytes than archaeophytes—634 neophytes and 284 archaeophytes, representing 15.3 and 6.8 %, respectively, of the total number of taxa (Medvecká et al.
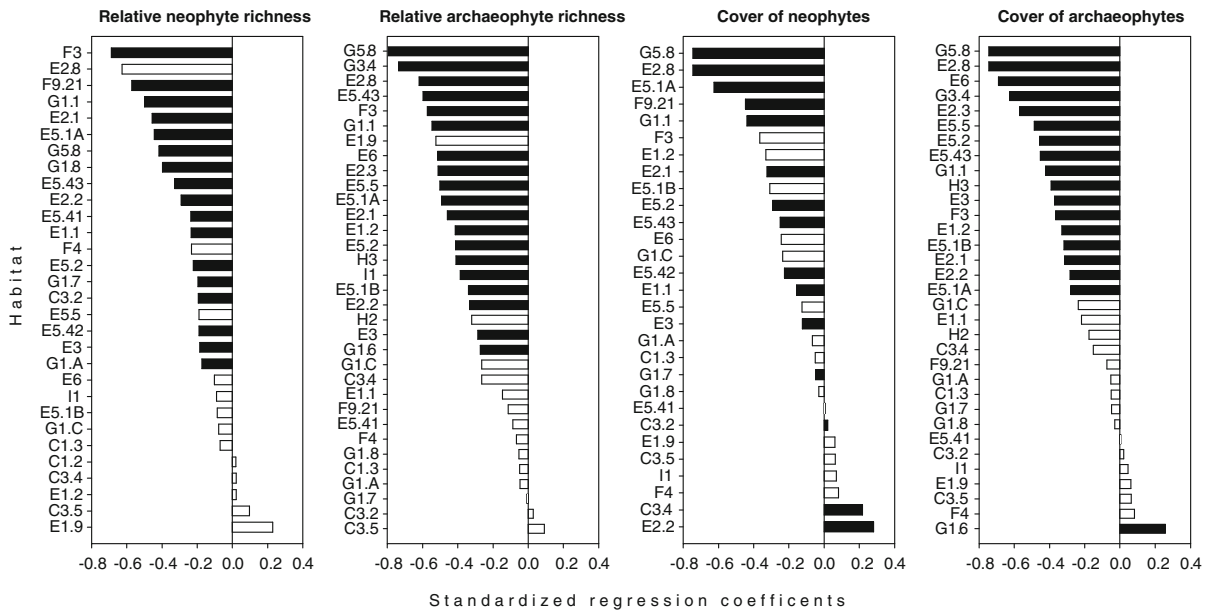
Fig. 2 Standardized regression coefficients for the variable altitude of logit GLMs that relate relative frequency of alien species to altitude and year in EUNIS habitats. Coefficients significant at α = 5 % are highlighted by filled black columns
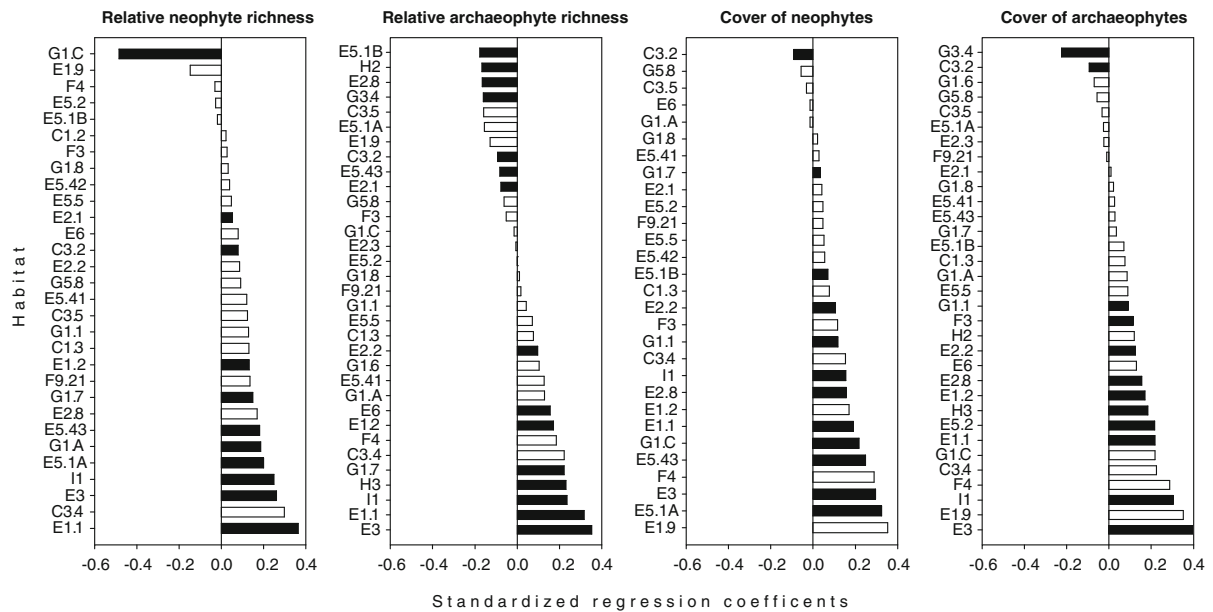
Fig. 3 Standardized regression coefficients for the variable year of logit GLMs that relate relative frequency of alien species to altitude and year in EUNIS habitats. Coefficients significant at α = 5 % are highlighted by filled black columns

2012)—there were more archaeophytes than neo-phytes present in the analysed dataset. Most of the neophytes are casuals with one or a few localities; therefore, the chance that they will be recorded using the standard methods used in vegetation surveys is much lower than for the archaeophytes, which are predominantly naturalised and widely distributed.

The average relative richness of archaeophytes and neophytes in the relevés within the entire stratified dataset (4.1 and 1.3 %, respectively) was low, similar to other

European countries (Maskell et al. 2006; Vilà et al. 2007). A slightly higher relative alien richness was found in the neighbouring Czech Republic, where the relevés contained an average of 9 % archaeophytes and 2.3 % neophytes (Chytrý et al. 2005). One of the possible causes of this discrepancy is the fact that many taxa that are alien in the Czech Republic are considered to be native or possibly native in parts of Slovakia, e.g. *Atriplex patula*, *Cirsium arvense*, *C. vulgare*, *Medicago lupulina*, *Plantago major* and *Rumex alpinus* (see Medvecká et al. 2012; Pyšek et al. 2002b). Other possible causes are the higher population density in the Czech Republic, which supports higher propagule pressure, generally higher altitudes in Slovakia in comparison with Czech Republic or the difference in relief of the two countries. Mountain ranges are located along the borders of the Czech Republic and do not prevent dispersion over the country, while the dissected relief of Slovakia with numerous basins separated by mountain chains may act as a barrier to the dispersion of alien species.

The higher relative alien species richness in anthropogenic habitats is in accordance with observations from other countries (Chytrý et al. 2005, 2008b; Maskell et al. 2006; Vilà et al. 2007). Similarly, there are habitats that are poorly invaded or even contain no alien species at all, such as bogs and mires and alpine and subalpine vegetation. These results indicate that disturbance and an excess of nutrients may contribute to a higher level of invasion, whereas environmental stress and a lack of nutrients limit the distribution of alien species (Chytrý et al. 2008a). Therefore, our results indirectly support the theory that two of the main factors affecting the invasibility of plant communities are disturbance (Hobbs and Huenneke 1992; Norton et al. 1995; Catford et al. 2011) and an excess of nutrients (Huenneke et al. 1990; Seabloom et al. 2003).

Our findings reflect the fact that archaeophytes and neophytes differ in their ecology and habitat preferences (Pyšek et al. 2005; Sádlo et al. 2007). Archaeophytes, which are often of Mediterranean and Sub-Mediterranean origin, were more frequent in xerothermophilous habitats, while neophytes, which originate mostly from Europe, Asia and North America, were more represented in mesophilous and hygrophilous habitats.

Altitudinal distribution of alien species

There is a general decrease in the relative alien species richness with increasing altitude, and, above a certain altitude (1,300 m a.s.l.), there are no aliens at all. Similar results have been obtained by Pyšek et al. (2002a), Pino et al. (2005), Simonová and Lososová (2008), Chytrý et al. (2009) and Gassó et al. (2009).

In general, we did not find any significant associations between altitude and the measures of invasion for habitats with a small number of analysed relevés (e.g. Temperate shrub heathland), the small number of relevés with no alien species (e.g. Permanent mesotrophic and eutrophic lakes, ponds and pools) or for habitats that occur over a short range of altitudes (e.g. Open non-Mediterranean dry acid and neutral grassland, including inland dune grassland and artificial broadleaved deciduous forestry plantations occurred only from 120 to 270 m a.s.l.).

The decrease in the relative alien richness with altitude is most interesting for the anthropogenic habitats, which are, in general, highly disturbed, rich in nutrients and close to the potential sources of propagules, such as urban areas and communication networks (Vilà et al. 2007). One possible explanation for this observation is that at higher altitudes, climatic conditions, especially temperature, negatively affect the establishment of many alien species, which originate from warmer regions and are often found in the warmer areas of lower altitudes (Pyšek 1998; Lososová et al. 2004; Pyšek et al. 2005; Simonová and Lososová 2008). This is especially the case for archaeophytes that are predominantly of Mediterranean and Sub-Mediterranean origin. According to Alexander et al. (2011), there is a progressive loss of species with narrow ecological amplitudes with increasing altitude; therefore, the species found at high altitudes are also those with the widest ranges at low elevations. However, Becker et al. (2005) observed in the Swiss Alps that the altitudinal maxima of alien species are increasing over time. In the neighbouring Czech Republic, Pyšek et al. (2011) has shown that higher altitudes were increasingly invaded by alien species in the last 250 years as a consequence of increasing anthropogenic disturbances, higher propagule pressure and climate change manifested in elevated temperatures. Therefore, we may presume that as long as human influence in higher altitudes does not decrease, the spread of alien species to higher altitudes will continue.

Long-term trend in the level of invasion

There is an observable trend of archaeophytes shifting from anthropogenic towards more natural habitats. A

significant downward trend in the relative richness of archaeophytes was observed in anthropogenic habitats (anthropogenic herb stands of annuals and trampled mesophilous grasslands with annuals, Fig. 3). Among natural or semi-natural vegetation, Scots pine woodland south of the taiga, screes, water-fringing reedbeds and tall helophytes other than canes, permanent mesotrophic pastures and aftermath-grazed meadows and shady woodland edge fringes, are notable in that they also show decreases in the relative archaeophyte richness. This could be caused either by a simultaneous increase in the relative richness of neophytes in the case of the last three habitats or in the case of the Scots pine woodland south of the taiga and water-fringing reedbeds and tall helophytes other than canes by a general decrease in the number of archaeophytes, which is also indicated by the decrease in cover of archaeophytes with time. On the other hand, a significant increase in the relative archaeophyte richness was observed in other natural habitats (e.g. perennial calcareous grassland and basic steppes; thermophilous deciduous woodland; inland cliffs, rock pavements and outcrops; seasonally wet and wet grasslands; inland salt steppes, Fig. 3), as well as in the anthropogenic habitat of arable lands. These results indicate that even though archaeophytes have been present in the region for centuries and have occurred frequently in anthropogenic habitats for a long time, some of them are recently gaining more important roles in natural habitats. This is also supported by the relatively high number of habitats in which the total cover of archaeophytes significantly increases with time, especially in the natural and semi-natural habitats.

The general increase in the relative richness and total cover of neophytes in many habitats with time is not surprising. According to Lambdon et al. (2008), an average of 6.2 new species, capable of naturalization arriving each year to Europe, and approximately 5.3 European species capable of naturalization are newly found in parts of the continent outside their native range each year. Botham et al. (2009) observed an increase in the number of archaeophytes and neophytes between the years 1997 and 2004 in Great Britain; however, they suggest this might have resulted from changes in the recording convention as the number of native species increased as well. Importantly, the relative neophyte richness is increasing predominantly not in anthropogenic (except for the

anthropogenic herb stands of perennials and arable lands) but in semi-natural and natural habitats. Habitats that are being gradually invaded include habitats of European importance e.g. Perennial calcareous grassland and basic steppes, Meso- and eutrophic oak, hornbeam, ash, maple, lime, elm and related woodland, and Thermophilous deciduous woodland (Fig. 3). In two of the semi-natural habitats and natural habitats, inland sand and rock with open vegetation and seasonally wet and wet grasslands, a significant increase in all four evaluated categories was observed. These findings together with the significant increase in the relative archaeophyte richness in some natural habitats should be considered as a signal for activities in conservation and the restoration of natural habitats.

In New Zealand, broad patterns in the invasion level dynamics were fairly consistent among all evaluated habitats: the number of alien species recorded in both anthropogenic and natural habitats has increased over the last 50 years (Aikio et al. 2012). The significant increase in the relative neophyte richness in natural and semi-natural habitats may indicate the occurrence of a lag phase for many neophytes. Essl et al. (2012) suggest that low levels of invasion in forests in Central Europe that are situated farther from settlements may turn out to be an ephemeral phenomenon, and the lag phase caused by dispersal limitation, heterogeneity in species' local residence time as well as increases in local levels of propagule pressure may lead to invasion debts at both the landscape and habitat levels. According to the results of González-Moreno et al. (2013) alien species are rarely in equilibrium with their environment and their spread in forest edges depends heavily on constant propagule pressure from the nearby landscape. Martin et al. (2009) suggests two main causes of lag phases in the invasion of forest habitats. First is the structure of available alien flora, which is usually dominated by early successional species with little or no shade tolerance due to horticultural preference of heliophilous and fast growing plants. The second is forest dynamics, which is based on a trade-off between high survivorship under low light versus rapid growth under high light, and therefore the scarcity of shade-tolerant, mid- to late-successional exotic tree species means that all but highly disturbed forests appear resistant to exotic tree invasion.

The significant increase in the relative archaeophyte richness in some natural habitats in Slovakia has not yet been observed in the forests of neighbouring

Austria (Essl et al. 2012). This may indicate more complex changes of habitats and be an early warning sign of ecological degradation, since due to their long presence in Central Europe archaeophytes are likely close to their optimal distribution at both the landscape and habitat levels (Essl et al. 2012).

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