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Invasion success of alien plants: do habitat affinities in the native distribution range matter?

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ABSTRACT

Aim To assess how habitat affinities in the native distribution range influence the invasion success of 282 central European neophytes (alien plants introduced after AD 1500).

Location Czech Republic.

Methods Classification trees were used to determine which native habitats donate the most alien species, the correspondence between habitats occupied by species in their native and invaded distribution ranges, and invasion success of species originating from different habitats.

Results The species most likely to naturalize in Central Europe are those associated with thermophile woodland fringes in their native range (81%), cultivated areas of gardens and parks (75%) and broad-leaved deciduous woodlands (72%). The largest proportions of invasive species recruit from those that occur on riverine terraces and eroded slopes, or grow in both deciduous woodland and riverine scrub. When the relative role of habitats in the native range is assessed as a determinant of the probability that a species will become invasive in concert with other factors (the species' residence time, life history, region of origin), the direct effect of habitat is negligible. However, the effect of native habitats on patterns of invasions observed in central Europe is manifested by large differences in the numbers of species they supply to the invaded region. More than 50 neophytes were recruited from each of the following habitats: dry grasslands, ruderal habitats, deciduous woodland, inland cliffs, rock pavements and outcrops, and tall-herb fringes and meadows.

Main conclusions Casual species recruit from a wider range of habitats in their native range than they occupy in the invaded range; naturalized but not invasive species inhabit a comparable spectrum of habitats in both ranges, and successful invaders occupy a wider range of habitats in the invaded than in the native range. This supports the idea that the invasive phase of the process is associated with changes in biological features that allow for extension of the spectrum of habitats invaded.

Keywords

Biological invasions, casual aliens, central Europe, Czech Republic, habitat, invasion, native distribution range, naturalization.

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INTRODUCTION

The quest to determine which habitats are prone to invasions by alien plants has been a focus of research since invasion biology started to develop as a distinct field of ecology. Several studies

have suggested that ecosystems or habitats differ considerably in the number of alien species they harbour (Crawley, 1987; Rejmánek, 1989; Kowarik, 1995; Lonsdale, 1999). With increasing availability of data and development of computing techniques, patterns of invasions with details on invaded habitat have been

described for ranges of habitat types occurring over large areas, from regional (Stohlgren *et al.*, 1999, 2006; Chytrý *et al.*, 2005; Chong *et al.*, 2006; Maskell *et al.*, 2006; Vilà *et al.*, 2007) to continental scales (Chytrý *et al.*, 2008b). Only recently have researchers started to distinguish objectively between invasibility (the inherent vulnerability of a community to invasion when propagule pressure and other confounding factors are held constant; Lonsdale, 1999) and the level of invasion (the number and/or proportion of alien species present; Hierro *et al.*, 2005; Richardson & Pyšek, 2006). The above-mentioned studies have improved our understanding of the role of habitats in plant invasions. They have shown that habitat characteristics, associated availability of resources and specific disturbance regimes, are crucial determinants of the outcome of invasions; in some contexts such factors may be even more important than propagule pressure and climatic factors (Chytrý *et al.*, 2008a).

A poorly understood issue, however, is the extent to which successful alien species arrive pre-adapted to the habitats they invade. May invaded habitats be assumed to be similar to those in which species grow in their native ranges? Surprisingly, this issue has only been given attention in studies targeting individual species (Sukopp & Sukopp, 1988; Sukopp & Starfinger, 1995; Thiele & Otte, 2006), but it is not known which habitats in the native ranges are the main donors of alien plants and whether there is a correspondence between them and habitats invaded in the new region. Yet there are good theoretical reasons to assume that habitat in the native range plays a role in determining invasion success in a new region. Alien plants invade a wide range of habitats, but their niche breadth, in terms of the spectrum of habitats invaded, differs considerably among species (Chytrý *et al.*, 2005; Sádlo *et al.*, 2007; Lambdon *et al.*, 2008). However, conditions under which a species invades may differ from those that typically occur in its native range. During the invasion process there is a rapid selection of individuals best adapted to new conditions, which serve as founders of invasive populations (e.g. Schierenbeck & Aïnouche, 2006; Barret *et al.*, 2008). The invasion success of a species depends on, besides stochastic factors, traits associated with the ability to reproduce and disperse (Pyšek & Richardson, 2007), compete with resident vegetation (Daehler, 2003; Vilà & Weiner, 2004), accommodate and allocate resources or tolerate stressful factors (MacDougall *et al.*, 2006; Muth & Pigliucci, 2007). These traits result from a selection and/or adaptation in the invaded range, but particularly from the long-term adaptive evolutionary processes that took place in the habitats of the native range (Sax & Brown, 2000; Prentis *et al.*, 2008). Therefore, it is likely that species from different habitats in their native ranges differ in their invasion success in the invaded ranges.

This study addresses these issues by using a large number of plant species alien to the temperate region of Europe, and asks the following questions. (1) Which types of habitats in the native distribution range donate most alien species to the invaded region? (2) What is the correspondence between habitats occupied by species in their native and invaded distribution range? (3) What is the invasion success of species originating from different habitats?

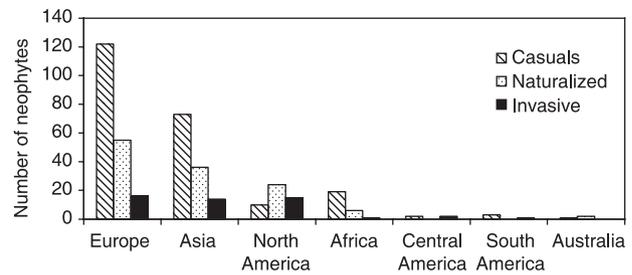


Figure 1 The geographical origins of the studied neophytes ($n = 282$) and numbers of species from particular regions that are casual, naturalized but not invasive, and invasive in the Czech Republic.

DATA AND METHODS

The species analysed

Information on alien plant species occurring in the Czech Republic was taken from Pyšek *et al.* (2002); only neophytes (species introduced after AD 1500; see Pyšek *et al.*, 2004) were used for analyses. The species were classified as casual, naturalized or invasive in the study region. Casual alien plants are those that do not form self-reproducing populations in the invaded region and whose persistence depends on repeated introductions of propagules; naturalized plants sustain self-reproducing populations without direct intervention by people; and invasive plants are a subset of naturalized plants that produce reproductive offspring, often in very large numbers, at considerable distances from the parent plants and which have the potential to spread over large areas (see Richardson *et al.*, 2000, and Pyšek *et al.*, 2004, for detailed definitions).

For each species, information was obtained on the occurrence in habitats in both native (Fig. 1) and invaded (Czech Republic) distribution ranges, number of habitats occupied in the native range (primary niche breadth), region of origin, life-form, time of introduction to the Czech Republic and planting history. Data on these attributes were obtained from the working database of the alien flora of the Czech Republic (Pyšek *et al.*, 2002). The information was complete for all attributes ($n = 282$), except for time of introduction, which was available for only 213 species.

Classification of habitats in the native and invaded range

The data on species habitat affiliations in the native distribution range were obtained from the literature, using regional floras from areas of species native distribution, national flora of the Czech Republic and other relevant sources. As habitat descriptions in the literature were often vague, only species for which detailed information was found were considered. This screening yielded 282 species, which were subjected to analysis. We did not focus on natural habitats only, but screened for complete habitat spectra of species in their native ranges. This decision was based on the assumption that during the long period of human influence

in native ranges, habitat spectra of most species also include human-made habitats to which successful colonizers have become adapted (di Castri, 1989), and from which they spread to new regions.

Based on verbal descriptions in the above sources, habitats in the native range were classified using a slightly modified version of the European Nature Information System (EUNIS) (Davies & Moss, 2003; available at <http://eunis.eea.europa.eu/habitats.jsp>). EUNIS is a comprehensive hierarchical pan-European system of habitat classification, covering all types of habitats from natural to artificial, from terrestrial to freshwater and marine. Habitat types are based on plant and animal communities, together with abiotic factors. A combination of EUNIS levels 2 and 3 was used to achieve comparable ecological breadth of the habitats considered. For example, at level 2 the category 'woodland fringes and clearings and tall forb stands' (category E5 of EUNIS) comprises a much broader scale of habitats than dry grasslands (E1), therefore hierarchical level 3 was used to differentiate habitats included in E5. Moreover, some habitats frequently encountered in species native ranges, such as newly emerged substrata (riverine terraces, eroded banks and slopes) or frequently disturbed human-made habitats were difficult to fit into the EUNIS system. EUNIS uses a category 'miscellaneous inland habitats with sparse or no vegetation' (H5), which merges habitats exposed to natural disturbance regimes with those disturbed by human activities. To achieve better resolution and distinguish between these two ecologically distinct habitat types, this category was divided into two *ad hoc* introduced level 3 categories: (1) H5a, riverine terraces, gravel banks, eroded river edges, slopes and avalanche tracks (natural newly emerged or frequently disturbed substrata); (2) H5b, trampled areas and newly emerged habitats in the surroundings of settlements and industrial facilities. Other human-made habitats were classified as 'anthropogenic forb-rich habitats' (E5.1) and 'lines of trees, small anthropogenic woodlands, recently felled woodland, early-stage woodland and coppice' (G5). Finally, the remaining anthropogenic habitats were classified in the category 'constructed, industrial and other artificial habitats' (J), following Chytrý *et al.* (2005).

For each native-range habitat, the number of species that occur as casual, naturalized or invasive (further termed as 'invasion status categories') in the invaded range in the Czech Republic was calculated.

To make the habitat data in native and invaded ranges comparable, the same classification system was used for the Czech Republic, with a slight modification in classification of C3 and H5 habitat categories. This was necessary in order to take into account the greater variation within the habitats in a wide range of geographical regions, from which species alien to the Czech Republic originate. For each species, information on the occurrence in habitats in the invaded range (Czech Republic) was taken from a database that contains the assignment of species to a complete range of 88 habitat types representative of the diversity of Czech vegetation (Sádlo *et al.*, 2007). The information from the database was translated into categories of the EUNIS system. In both native and invaded ranges, most species were assigned to more than one habitat.

Statistical analysis

The data were analysed using classification trees (Breiman *et al.*, 1984; Steinberg & Colla, 1995; De'ath & Fabricius, 2000). The invasion status (1, casual; 2, naturalized but not invasive; 3, invasive) was the response variable, and either the identity of habitats only, or the habitats plus life-form, geographical origin, mode of introduction, primary niche breadth (number of habitats occupied in the native distribution range) and residence time were the explanatory variables. The trees were constructed by binary recursive partitioning in CART version 6.0 (Breiman *et al.*, 1984; Steinberg & Colla, 1995), which uses the most reliable pruning strategy of over-growing trees, ensuring that any important tree structure is not overlooked. To find the optimal tree, a sequence of nested trees of decreasing size, each of them being the best of all trees of its size, was constructed, and the resubstitution relative errors were estimated for each tree in such a way that their estimated cross-validated relative error rates were within one standard error of the minimum (1 SE rule; Breiman *et al.*, 1984). Ten-fold cross-validation was used to obtain estimates of the cross-validated relative errors of these trees. These estimates were then plotted against tree size, and the optimal tree was chosen based on the 1-SE rule (Steinberg & Colla, 1995). Following De'ath & Fabricius (2000), a series of 50 cross-validations were run, and the modal (most likely) single tree was chosen for interpretation and presentation. The quality of the best single classification tree was evaluated by its misclassification rate, i.e. by comparing the misclassification rate of this best model with the misclassification rate of the null model (De'ath & Fabricius, 2000).

The best trees were represented graphically, with the root node 1 standing for undivided data at the top, and the terminal nodes, describing the groups of data, at the bottom of the hierarchy. The quality of each split was expressed by the value of improvement, corresponding to the misclassification rate at each node. Surrogates of each splitter variable, i.e. explanatory variables closely mimicking the action of the primary splitter, were assessed and ranked according to their association values, with the highest possible value of 1.0 corresponding to the surrogate producing exactly the same split as the primary split. To prevent the explanatory variable residence time, with missing values, from having an advantage as a splitter, this variable was penalized in proportion to the degree to which its values were missing, and treated by back-up rules that closely mimicked the action of the primary splitters. To reduce the splitting power of categorical variables with many categories (the identity of habitats had 34 categories in our case), these were also adjusted to have no inherent advantage over quantitative variables, following penalization rules described by Steinberg & Colla (1995).

RESULTS

Of the 282 neophytes analysed, 38 (13.5%) are invasive, 90 (31.9%) naturalized but not invasive and 154 (54.6%) casual in the Czech Republic; this represents 55.1%, 56.2% and 18.8% of the total numbers of alien species assigned to the respective

Table 1 EUNIS (European Nature Information System) habitat categories distinguished in the native distribution range and the numbers of species, classified according to invasion success (Cas, casual; Nat, naturalized but not invasive; Inv, invasive), that recruit from these habitats and occur as aliens in the Czech Republic. The percentage of naturalized species includes invasive. See text for details on habitat classification. Habitats donating at least eight alien species are shown in bold.

Category	Definition	Cas	Nat	Inv	Total	% Nat	% Inv
B1	Coastal dunes and sandy shores	13	4	0	17	23.5	0.0
B2	Coastal shingle	5	1	0	6	16.7	0.0
B3	Rock cliffs, ledges and shores, including the supralittoral	4	2	1	7	42.9	14.3
C1	Surface standing waters	1	0	1	2	50.0	50.0
C2	Surface running waters	1	0	1	2	50.0	50.0
D5	Sedge and reedbeds, normally without free-standing water	6	2	1	9	33.3	11.1
D6	Inland saline and brackish marshes and reedbeds	7	0	0	7	0.0	0.0
E1	Dry grasslands	55	27	7	89	38.2	7.9
E2	Mesic grasslands	16	9	3	28	42.9	10.7
E3	Seasonally wet and wet grasslands	5	6	0	11	54.5	0.0
E4	Alpine and subalpine grasslands	6	4	3	13	53.8	23.1
E5.1	Anthropogenic herb stands	49	21	11	81	39.5	13.6
E5.2	Thermophile woodland fringes	3	10	3	16	81.3	18.8
E5.4	Moist or wet tall-herb and fern fringes and meadows	27	16	13	56	51.8	23.2
E5.5	Subalpine moist or wet tall-herb and fern stands	4	1	4	9	55.6	44.4
E6	Inland saline grass and herb-dominated habitats	6	1	0	7	14.3	0.0
E7	Sparsely wooded grasslands	2	1	0	3	33.3	0.0
F2	Arctic, alpine and subalpine scrub	3	2	2	7	57.1	28.6
F3	Temperate and mediterranean-montane scrub	10	8	2	20	50.0	10.0
F4	Temperate shrub heathland	1	1	2	4	75.0	50.0
F9.1	Riverine scrub	12	7	6	25	52.0	24.0
F9.2	[<i>Salix</i>] carr and fen scrub	1	0	0	1	0.0	0.0
G1	Broadleaved deciduous woodland	16	30	12	58	72.4	20.7
G2	Broadleaved evergreen woodland	0	2	1	3	100.0	33.3
G3	Coniferous woodland	1	0	0	1	0.0	0.0
G4	Mixed deciduous and coniferous woodland	13	9	2	24	45.8	8.3
G5	Lines of trees, small anthropogenic woodlands, recently felled woodland, early-stage woodland, coppice	5	4	1	10	50.0	10.0
H2	Screes	6	7	0	13	53.8	0.0
H3	Inland cliffs, rock pavements and outcrops	32	20	4	56	42.9	7.1
H5a	Riverine terraces, eroded slopes and banks, avalanche tracks	11	4	10	25	56.0	40.0
H5b	Trampled habitats and other intensively disturbed habitats with a sparse vegetation	9	4	4	17	47.1	23.5
H6	Recent volcanic features	2	0	0	2	0.0	0.0
I1	Arable land and market gardens	17	13	6	36	52.8	16.7
I2	Cultivated areas of gardens and parks	2	3	3	8	75.0	37.5
J	Constructed, industrial and other artificial habitats	51	21	11	83	38.6	13.3

categories (69, 160 and 817) in that country (Pyšek *et al.*, 2002). Most species have their native distribution range in other parts of Europe (193 species, 68.4%; Fig. 1). The following habitats in the native range donated more than 50 neophytes to the Czech Republic: dry grasslands (E1), ruderal and anthropogenic habitats (J, E5.1), deciduous woodland (G1), inland cliffs, rock pavements and outcrops (H3) and tall-herb fringes and meadows (E5.4). The same habitats donated large numbers of invasive species (7–13), which is also the case for riverine terraces, eroded slopes and banks and avalanche tracks (H5a, 10 species; Table 1).

To assess the relative invasion success (defined as the ratio of casual, naturalized or invasive neophytes to all neophytes recorded),

only those habitats from which at least eight neophytes recruit were considered (because proportions for these habitats are less likely to be influenced by random factors). Coastal dunes and sandy shores (B1), sedge and reedbeds (D5), dry grasslands (E1), ruderal and anthropogenic habitats (J, E5.1) and inland cliffs, rocks pavements and outcrops (H3) exhibited the highest proportion of casual species among all neophytes, ranging between 57.1% and 76.5% in these habitats (Table 1). In contrast, species associated in their native range with thermophile woodland fringes (E5.2), broadleaved deciduous woodland (G1) and cultivated areas of gardens and parks (I2), were most likely to naturalize in the Czech Republic; their proportion in these habitats is 81.3%, 75.0% and 72.4%, respectively (Table 1).

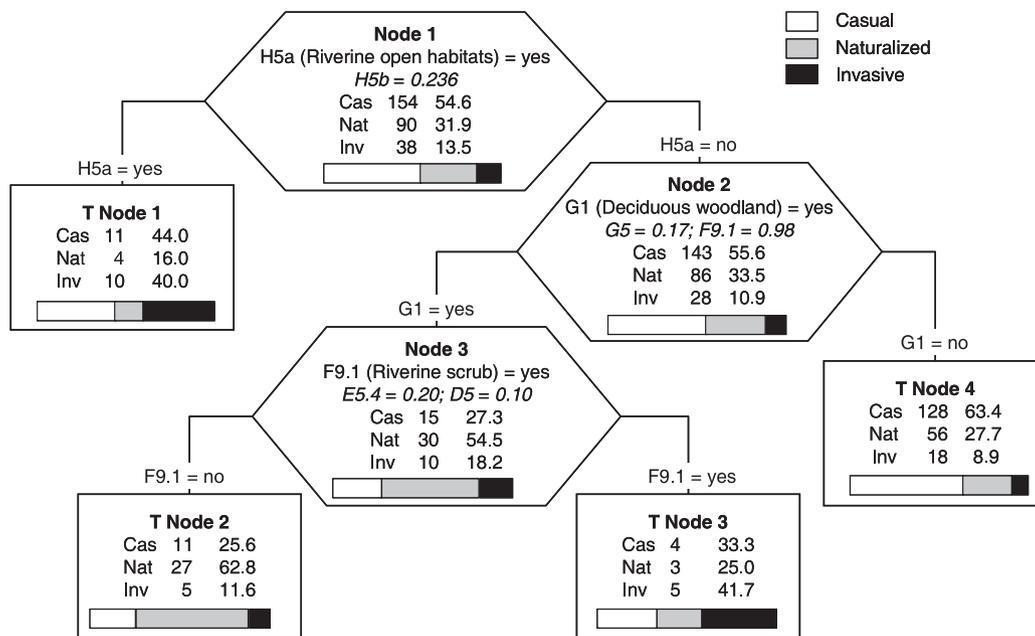


Figure 2 Classification tree showing the effect of habitat in the native range on invasion success of alien species in the Czech Republic (Cas, casual; Nat, naturalized but not invasive; Inv, invasive). Each node (polygonal table) and terminal node (rectangular table, T) shows node number, splitting variable name, split criterion (surrogates of primary splitters with an association value > 0.1 are shown in italics) and number of cases (with percentage listed and shown graphically) in the three groups. The misclassification rate of the model is 39.2%, compared with 66.7% for the null model (estimated with the initial class assignment 1, casual). See Table 1 for habitat codes.

The proportion of invasive species among all donated neophytes exceeded 20% in eight habitats. Of neophytes from subalpine moist or wet tall-herb and fern habitats (E5.5), 44.4% were invasive in the Czech Republic, as were 40.0% of neophytes from riverine terraces, eroded slopes and banks and avalanche tracks (H5a), 37.5% from cultivated areas of gardens and parks (I2), 24.0% from riverine scrub (F9.1), 23.5% from trampled and other intensively disturbed habitats (H5b), 23.2% from moist or wet tall-herb and fern fringes and meadows (E5.4), 23.1% from alpine and subalpine grasslands (E4) and 20.7% from deciduous woodland (G1) (Table 1).

The classification tree model with the identity of habitats as the only explanatory variable provides an insight into which combinations of habitats in the native range lead to invasion success (Fig. 2). The highest proportion of invasive species recruits from species that grow on riverine terraces, eroded banks and slopes, and avalanche tracks (H5a, terminal node 1). Species that do not occur in these habitats are invasive if they occur in deciduous woodland (G1) and, at the same time, in riverine scrub (F9.1; terminal node 3). Naturalized species are most likely to recruit from deciduous woodland (G1, node 3) or its surrogate with an association value of 0.98 – riverine and lakeshore scrub (F9.1). The affinity of casuals was less obvious, but they tend to recruit from habitats other than riverine terraces and deciduous woodland (terminal node 4). Other habitats appeared only as surrogates for primary splitters with rather low association values (Fig. 2).

When species affinity to habitats in the native range was assessed in concert with other species attributes, it appeared that the effect of habitats on invasion status is minor. None of the native range habitat categories was selected as a primary splitter for the classification tree model or appeared as an important surrogate (only two anthropogenic habitats, J and E5.1, were surrogates for annual life-form but both with a low association value of 0.130). Whether a species becomes casual, naturalized or invasive depends on the time of introduction, region of origin and life history (Fig. 3). Species are mostly casuals either if introduced after 1955 (terminal node 4), or, if earlier, when they are annuals of European origin (terminal node 2). In contrast, they tend to be naturalized or invasive if they were introduced before 1955 and were of non-European origin (terminal node 3) or European non-annuals (terminal node 1).

Correspondence between habitats in the native and invaded distribution range differs among species in the three categories of invasion success (Fig. 4). Casual alien species recruit from a wide range of native habitats ($n = 34$) but occur in a narrower range of habitats after introduction ($n = 23$, Fig. 4a). Species that successfully naturalized but did not become invasive inhabit a comparable spectrum of habitats in both ranges (with 29 habitats occupied both in the native and invaded range, Fig. 4b) and those that became invasive did so in a wider range of habitats ($n = 28$) than occupied in the native range ($n = 25$; Fig. 4c).

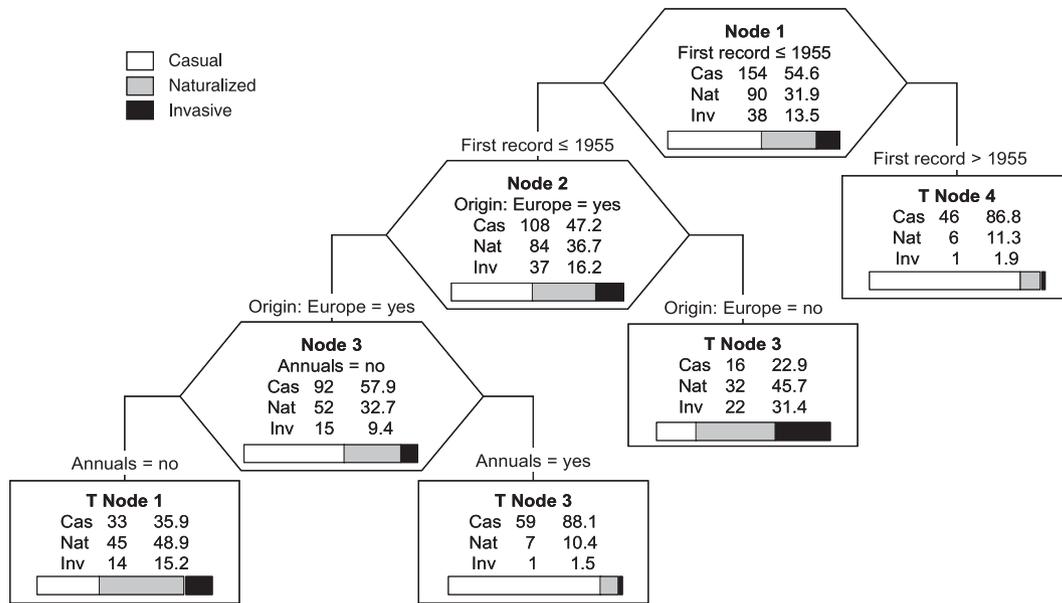


Figure 3 Classification tree showing factors that determine the invasion status of alien species in the Czech Republic (Cas, casual; Nat, naturalized but not invasive; Inv, invasive). Habitat in the native distribution range, time of introduction (expressed as the first record in the Czech Republic), life-form, geographical origin, mode of introduction and primary niche breadth (number of habitats occupied in the native distribution range) were used as explanatory variables. Each node (polygonal table) and terminal node (rectangular table, T) shows node number, splitting variable name, split criterion and number of cases (with percentage listed and shown graphically) in the three groups. The misclassification rate of the model is 39.0%, compared with 66.7% for the null model (estimated with the initial class assignment 1, casual).

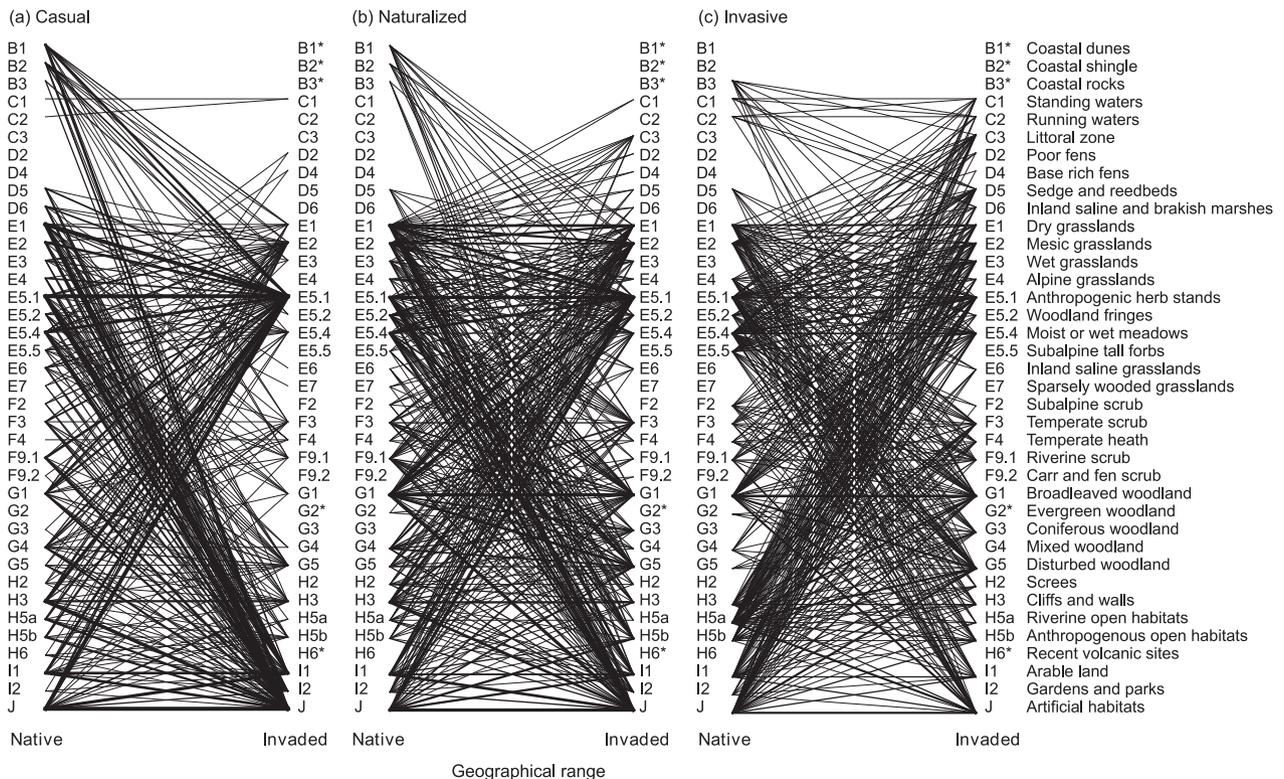


Figure 4 Correspondence between habitats in native (left) and invaded (right) distribution range shown for species that occur as (a) casual ($n = 154$), (b) naturalized but not invasive ($n = 90$) and (c) invasive in the Czech Republic ($n = 38$). Lines connect habitat of a species in the native range (left) with that in the invaded range (right). For species occurring in multiple habitats each combination of native/invaded habitats is displayed separately. The thickness of the line reflects number of species. Habitats that do not occur in the Czech Republic are indicated by asterisk. Habitat names are shortened; see Table 1 for full names.

DISCUSSION

From native to invaded range, from habitat to habitat

An invasion from one region to another is associated with translocation from a spectrum of habitats the species occupies in its native range to habitats that are available in the region of introduction. Recent studies show that characteristics of habitats in which invasions occur (Chytrý *et al.*, 2008b), disturbance regime and availability of free resources in particular (Davis *et al.*, 2000) are crucial for the outcome of invasions. The present study is the first to elucidate the role of habitats in native distribution ranges of introduced species on invasion success. It shows that individual habitats differ in how many species they supply and how successful these species are after the introduction.

Our study shows marked differences in the number of central European neophytes donated by individual habitats from other parts of the world (mostly Asia, North America and Africa; Fig. 1); these numbers vary from 1 to 89 species (Table 1). Dry grasslands (E1), ruderal and anthropogenic habitats (J, E5.1), deciduous woodland (G1), wet tall-herb fringes and meadows (E5.4) and rock pavements and outcrops (H3) in the native distribution ranges supply the highest numbers of neophyte species to the Czech Republic. This suite of habitats suggests a significant role of propagule pressure from native to invaded regions. Species from human-made habitats (including the category of rock pavements and outcrops, which also comprises human-made habitats of similar ecological conditions, e.g. walls and ruins) are likely to be transported by human vectors for obvious reasons, and those of dry grasslands as seed or crop contaminants (Hulme *et al.*, 2008). Another reason may be that woodlands are the most frequent type of habitat in those areas of North America that have climatic conditions comparable to central Europe. In general, the total geographical areas of individual habitats in the native range are likely to influence the numbers of species they supply to central Europe. However, it was impossible to include them as an explanatory variable because data on land cover are not available for the native ranges of the species analysed. The above-mentioned native habitats that supply high numbers of neophytes are also responsible for donating many species that are invasive (*sensu* Richardson *et al.*, 2000; Pyšek *et al.*, 2004) in central Europe. The large number of species coming from wet tall-herb fringes and deciduous woodland probably results from their competitive ability acquired in plant communities of the native distribution range; wet tall-herb fringes and deciduous woodlands are highly productive habitats, which harbour many competitively strong plant species (Grime, 1979).

Classification tree analysis of the relative invasion success, expressed as the proportion of all neophytes recruiting from a given habitat and that became invasive in the Czech Republic, identified riverine terraces, eroded slopes and avalanche tracks, and also riverine scrub, as the most likely source habitats of invasive plant species (Fig. 2). Riparian habitats are among the most invaded in many regions of the world (Pyšek & Prach, 1993; Planty-Tabacchi *et al.*, 1996; Chytrý *et al.*, 2005, 2008b; Richardson *et al.*, 2007); invasions of species recruiting from riparian habitats

hence seem to profit from a good match between ecological conditions of native and invaded habitats. Therefore, riparian habitats act both as a source of and a target for invasive neophytes. An 'ideal invader' recruiting from a riparian habitat in the native range is likely to be adapted to both natural and human-induced disturbances and effective dispersal by water and humans; such species also have a good competitive ability, which allows them to suppress, by vigorous growth, quickly developing vegetation in nutrient rich, wet riparian habitats in the invaded range. Since riparian habitats are generally rich in nutrients (Naiman & Décamps, 1997; Richardson *et al.*, 2007), this competitive ability is manifested via fast growth and a high production of biomass.

Species from native habitats other than riverine terraces are only successful if they occur in deciduous woodland and riverine scrub. There is an ecological link between these three native range habitats. During succession, riverine terraces and other newly emerged substrata develop into riverine scrub and then, depending on the intensity and frequency of disturbances, into alluvial deciduous woodlands (Ellenberg, 1988). All of these habitats can be therefore seen as different stages of succession in one site. Species that are able to colonize riparian open habitats immediately after a disturbance, e.g. a flood, and survive when succession results in the formation of vegetation cover, are likely to become successful invaders if they colonize analogous habitats following introduction to a new region.

In contrast, none of the neophytes recruiting from wet grasslands, screes and coastal sand dunes, and a low proportion of those from dry grasslands (7.9%) and inland cliffs, rock pavements and outcrops (7.1%), become invasive, despite rather large proportion, 23–55%, becoming naturalized (Table 1). Interestingly, although most invasions occur or at least start in human-disturbed environments, a low proportion of neophytes that colonize human-made habitats in their native ranges become invasive in central Europe. These species can be adapted for effective dispersal but not for competition. A possible reason for this could be the inability to compete with resident vegetation. Species of disturbed habitats are often annuals; this life-form was found to be associated with low invasion success in most habitats of the invaded range (Fig. 3).

Effects of native habitats versus other factors

Our analysis also shows that whether a species invades or remains at the stage of casual or naturalized but not invasive is, to a large extent, determined by factors other than the type of habitat occupied in the native range. When residence time, region of origin and life history were used as explanatory variables for invasion success in the same model with native habitat identity (Fig. 3), it appeared that the direct role of habitat in determining invasion success is negligible (habitat categories only appeared as surrogates of the primary splitter with a low association value). That a species only survives as a casual and does not become naturalized or invasive is associated with short residence time, European origin and annual life form. It is well documented that species with longer residence times are more widespread (e.g. Rejmánek, 2000; Castro *et al.*, 2005; Wilson *et al.*, 2007) and more likely to

be invasive (Pyšek & Jarošík, 2005). However, disappearance of the direct effect of habitat in the native range when tested together with other factors does not preclude habitats from being important co-determinants of invasion patterns observed in invaded regions. There are two reasons for this. First, the above model tested relative success measured as the proportion of species in the three categories of invasion status, a measure which is not related to vastly different numbers of neophytes recruited from individual habitats. Two native habitats may not differ with respect to the probabilities of species they supply to becoming casual, naturalized or invasive, yet their contributions to the level of invasion (in the terms of Hierro *et al.*, 2005, Chytrý *et al.*, 2005, and Richardson & Pyšek, 2006) in the invaded range can be very different in terms of the number of resulting invasions, because of the different numbers of species donated by each of the habitats. Second, an indirect effect that habitat in the native range has on the outcome of invasion elsewhere can be seen in habitat being an important evolutionary force under which species traits are selected (Sax & Brown, 2000).

Niche breadth in the native and invaded range: implications for the invasion process

Comparison of niche breadth, defined as the spectrum of habitats invaded, in the native and invaded distribution range reveals a consistent pattern. Casual neophytes in the Czech Republic recruit from a wider range of habitats in the native range than they occupy in the invaded range; naturalized but not invasive neophytes occur in a comparable number of habitats in both ranges; and invasive neophytes occur in a wider range of habitats in the invaded range than they occupy in their native range (Fig. 4). We suggest an interpretation based on the nature of the invasion process (Richardson *et al.*, 2000), also termed the naturalization–invasion continuum (Richardson & Pyšek, 2006).

Casual alien species depend for their persistence on the repeated introduction of propagules by humans, because they do not reproduce in the wild in the invaded region due to various constraints (Richardson *et al.*, 2000; Pyšek *et al.*, 2004); their invasiveness is generally low compared to naturalized and invasive species. It is reasonable to assume that the same constraints limit them from even a short-term persistence in some habitats in the invaded range. Naturalized species reproduce in the wild without human assistance, which requires a good match between climatic and ecological conditions in both ranges; these species need to arrive well adapted to the new conditions. The pattern observed can be interpreted by different factors acting at each stage of the invasion. At import, release or escape, which relates to the casual stage, propagule pressure is crucial. For naturalization, biogeographical and ecological factors are most important. For invasion mainly ecological and evolutionary factors need to be considered (Williamson, 2006). This implies that the last stage of the process (invasion) is often associated with changes in the genetic make-up of the populations of invading species that occur in the new range, or with a high level of phenotypic plasticity. Both phenomena have been repeatedly documented (e.g. Lee, 2002; Daehler, 2003; Bossdorf *et al.*, 2005) and could

explain why the highly successful species invade a wider range of habitats than they occupy in their native range.

Incorporating habitat information into screening systems: on the way to better prediction?

Our study was performed in central Europe. The spectrum of habitats in the native range that supplied many species alien to the invaded range may differ between the Czech Republic and other target regions, depending on the spectrum of habitats in each region and their specific features. Nevertheless, it seems to be a generally valid assumption that the character of the native habitat induces pre-adaptations that are likely to influence the performance of the species in its invaded range. In the same vein, it is probable that general features of habitats donating invasive species, i.e. a good supply of moisture and nutrients, fluctuations of these resources and exposure to human-made and/or natural disturbance, would hold for other regions as well, since these features seem to be generally associated with habitat invasibility (Davis *et al.*, 2000; Chytrý *et al.*, 2008a,b).

The result of our study that different native habitats donate different numbers of invasive species to invaded regions therefore seems to be rather robust. However, the native habitats seem to have little relative explanatory power, in terms of invasion success, if assessed together with other species attributes analysed. The question thus arises whether the information on native habitat affinities can be used to improve our ability to predict the probability of an introduced species becoming invasive? We believe there are practical implications. Current weed risk assessment schemes, based on the original work of Pheloung *et al.* (1999) and developed further to be applicable in other situations and regions (Daehler *et al.*, 2004; Krivánek & Pyšek, 2006) use information on a taxon's current weed status in other parts of the world, climatic and environmental preferences and biological traits, but do not take into account its habitat context. Pheloung *et al.* (1999) were aware of this limitation; they point out that expert systems designed for particular biomes (e.g. Tucker & Richardson, 1995) are likely to be more accurate in their predictions of weediness, because successful invaders are strongly habitat dependent. Our study indicates that habitats in source regions, from which evaluated species originate, can be scored with respect to the quantity of successful invaders they are likely to supply.

The classification tree using only native habitats provided very similar results, in terms of categorizing species by their invasion success, to that including other species attributes, and comparison of misclassification rates of the two models indicates that including species attributes did not improve the performance of the latter model. If individual species are mapped on the classification trees their positions are very similar regardless of whether only native habitats, or native habitats plus other attributes, are used as explanatory variable. Moreover, it needs to be borne in mind that attributes such as the time of introduction, region of origin and life history perform better in explaining invasion success, but from a practical point of view their use is often constrained by a lack of data. However, practical decisions need to be

based on prediction. For managers responsible for decisions about introductions of new species, the information on habitat affinity in the native range is likely to be readily available and its predictive value is emphasized by the fact that the time of introduction, a variable with the greatest explanatory power, is irrelevant when the decision about new introduction to a country is to be made. Incorporating the information on the range of habitats that a species subject to screening occupies in its native range could therefore improve the accuracy of predictions made by systems that are currently in use.

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BIOSKETCH

The research team at the Institute of Botany (<http://www.ibot.cas.cz/invasions/>) focuses on various aspects of plant invasions (e.g. species invasiveness, habitat invasibility, impact of invasions, large-scale invasion patterns). The members of the group were recently involved in the ALARM and DAISIE projects of FP6 of the European Union. Within the framework of the former project, a series of studies focused on the invasibility of European habitats were conducted and the importance of factors that determine invasibility at various spatial scales was analysed. Author contributions: P.P. and M.C. conceived the ideas; M.H. and J.S. collected the data; V.J., M.H. and J.P. analysed the data; and P.P., M.H. and M.C. contributed to the writing.

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