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Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe

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Summary

1. Although invasions by alien plants are major threats to the biodiversity of natural habitats, individual habitats vary considerably in their susceptibility to invasion. Therefore the risk assessment procedures, which are used increasingly by environmental managers to inform effective planning of invasive plant control, require reliable quantitative information on the extent to which different habitats are susceptible to invasion. It is also important to know whether the levels of invasion in different habitats are locally specific or consistent among regions with contrasting climate, flora and history of human impact.

2. We compiled a database of 52 480 vegetation plots from three regions of Europe: Catalonia (Mediterranean–submediterranean region), Czech Republic (subcontinental) and Great Britain (oceanic). We classified plant species into neophytes, archaeophytes and natives, and calculated the proportion of each group in 33 habitats described by the European Nature Information System (EUNIS) classification.

3. Of 545 alien species found in the plots, only eight occurred in all three regions. Despite this large difference in species composition, patterns of habitat invasions were highly consistent between regions. None or few aliens were found in environmentally extreme and nutrient-poor habitats, e.g. mires, heathlands and high-mountain grasslands. Many aliens were found in frequently disturbed habitats with fluctuating nutrient availability, e.g. in man-made habitats. Neophytes were also often found in coastal, littoral and riverine habitats.

4. Neophytes were found commonly in habitats also occupied by archaeophytes. Thus, the number of archaeophytes can be considered as a good predictor of the neophyte invasion risk. However, neophytes had stronger affinity to wet habitats and disturbed woody vegetation while archaeophytes tended to be more common in dry to mesic open habitats.

5. *Synthesis and applications.* The considerable inter-regional consistency of the habitat invasion patterns suggests that habitats can be used as a good predictor for the invasion risk assessment. This finding opens promising perspectives for the use of spatially explicit information on habitats, including scenarios of future land-use change, to identify the areas of highest risk of invasion.

Key-words: archaeophyte, Catalonia, Czech Republic, exotic species, Great Britain, invasibility, neophyte, non-native, vascular plants, vegetation plots

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Introduction

Invasions by alien plant species is an environmental issue of global significance (Mack *et al*. 2000; Hulme 2006; Pyšek, Richardson & Jarošík 2006; Rejmánek *et al*. 2006; Richardson & Pyšek 2006). However, not all regions, biomes or habitats are invaded to the same extent. It has been demonstrated that temperate regions are invaded more frequently than the tropics (Lonsdale 1999; Rejmánek, Richardson & Pyšek 2005), New World more than the Old World (di Castri 1989; Lonsdale 1999), islands more than the mainlands (Lonsdale 1999; Daehler 2006) and landscapes rich in native species more than landscapes poor in native species (Kühn *et al*. 2003; Stohlgren *et al*. 2005). Within particular regions, the level of invasion usually varies strongly among habitats (Crawley 1987; Rejmánek 1989; Rejmánek, Richardson & Pyšek 2005), suggesting that some habitats are more susceptible to invasions than others. Quantitative comparisons of the level of invasion between habitats have been conducted in some regions (Stohlgren *et al*. 1999; Chytrý *et al*. 2005; Maskell *et al*. 2006; Vilà, Pino & Font 2007), but it is still unclear how far patterns from one region can be generalized or transferred to regions with other climates, historical and biogeographical features and different assemblages of alien plants.

Currently, considerable effort is devoted to modelling spatially explicit scenarios of future climate and land-use change (Sala *et al*. 2000; Settele *et al*. 2005; Rounsevell *et al*. 2006). The risk of invasions by alien species can be projected upon these scenarios, provided there is sufficiently detailed knowledge of the level of invasion typical of different habitats. However, this knowledge is available only for restricted regions. For the development of invasion risk scenarios for large areas such as Europe, it is therefore necessary to test whether the patterns of habitat invasion identified in smaller regions are valid in other regions, particularly in those with contrasting climate.

Earlier attempts to quantify the habitat-specific levels of plant invasion were based usually on the identification of species pools for particular habitats (Crawley 1987; Rejmánek, Richardson & Pyšek 2005; Walter *et al*. 2005). Using this approach, each species of the regional flora was assigned to one or more habitats, based on the expert knowledge of species' habitat preferences. Subsequently, habitats with more species were considered as more invaded or perhaps even more invasible (but see Lonsdale 1999; Chytrý *et al*. 2005). However, habitats with large regional pools of ecologically compatible invasive species may actually not be highly invaded at the local scale. Invasion-resistant habitats may locally contain few or no alien species despite a large pool of ecologically compatible alien species present in the wider region. In contrast, invasion-prone habitats may contain some aliens in most places even though the regional pool of ecologically compatible aliens can be limited.

Large databases of vegetation plots, amassed recently in some European countries (Hennekens & Schaminée 2001), enable comparative analyses of actual level of invasion of different habitats. First analyses based on such data have already appeared for the city of Berlin (Kowarik 1995; 43 habitat types), the Czech Republic (Chytrý *et al*. 2005; 32 habitat types), Great Britain (Maskell *et al*. 2006; eight habitat types) and Catalonia (Vilà, Pino & Font 2007; 32 habitat types). However, no comprehensive data sets of vegetation plots are available so far in most European countries, which prevents an analysis of the level of invasion across habitats in the whole of Europe.

Within the framework of an international project, ALARM (Assessing LArge-scale environmental Risks for biodiversity with tested Methods; Settele *et al*. 2005), we explored three comprehensive data sets of vegetation plots from three regions which represent contrasting climates typical of large parts of southern, central and western Europe: Catalonia (Mediterranean–submediterranean climate), Czech Republic (subcontinental) and Great Britain (oceanic), with the aim to identify (1) whether the composition of alien species found in individual habitats differs between the three regions and if so, to what extent; (2) which are the most common alien plant species; (3) which habitats are most and least invaded; (4) whether the between-habitat pattern in the proportion of alien species is consistent across the three regions; and (5) whether neophytes (post-1500 immigrants) tend to invade the same habitats as archaeophytes (pre-1500 immigrants).

Materials and methods

VEGETATION DATA

The data sets from Catalonia, Czech Republic and Great Britain contained a total of 52 480 vegetation plots (Table 1).

Catalonia is located in north-eastern Spain between the Pyrenees and the Mediterranean Sea. It is a region with predominantly Mediterranean–submediterranean climate, although some areas with oceanic and alpine climates occur in the north. The Catalonian data set included vegetation plots (relevés) stored in the FLORACAT database

Table 1. Selected characteristics of the studied regions and numbers of vegetation plots. Numbers of alien species are given with casual species excluded (sources: Bolòs *et al*. 1993; Preston, Pearman & Dines 2002; Pyšek, Sádlo & Mandák 2002; Pino *et al*. 2005)

	Catalonia	Czech Republic	Great Britain
Area (km^2)	32 106	78 865	229 979
Altitude (m a.s.l.)	0–3150	115–1602	0–1343
No. of native species in the region's flora	*c*. 2950	2 256	1 455[1]
No. of archaeophytes in the region's flora	–[2]	258	151
No. of neophytes in the region's flora	264	229	259
No. of plots used in the current study	15 650	20 468	16 362

[1]Including 46 species with doubtful status (native or alien).
[2]Archaeophytes are included among native species.

(Font & Ninot 1995), which were sampled originally for the purpose of phytosociological classification. Only plots assigned to units of phytosociological classification were used in this study. The plots differed in size from 1 m^2 to hundreds of m^2 (Table 2), as is typical for European phytosociological relevés (Chytrý & Otýpková 2003). Further details on the Catalonian data set are given in Vilà, Pino & Font (2007).

The Czech Republic is located in Central Europe and has a subcontinental climate. The Czech data set included vegetation plots sampled with the same aims and methods and using comparable plot sizes as in Catalonia. The source of the data was the Czech National Phytosociological Database (Chytrý & Rafajová 2003), from which a stratified random sample of vegetation plots was taken in order to reduce the effects of local oversampling of some habitats, especially urban areas (Knollová *et al.* 2005). Only plots recorded after 1970 were considered. For further details on the Czech data set see Chytrý *et al.* (2005).

Great Britain is located in a region with oceanic climate. Vegetation plots for the current study were taken from the Countryside Survey database, which includes data from three surveys of British habitats undertaken in 1978, 1990 and 1998 (Smart *et al.* 2003). Countryside Survey plots were located according to the stratified random sampling scheme (Firbank *et al.* 2003) and their size was 4, 10 or 200 m^2. For the purpose of the current analysis, plots from different sites and from all three surveys were selected at random. Although some plots were sampled repeatedly in individual surveys, each plot was selected only once for this analysis.

Alien species found in Czech and British vegetation plots were classified as either archaeophytes (arrived before AD 1500) or neophytes (arrived after AD 1500), based on Pyšek, Sádlo & Mandák (2002) and Preston, Pearman & Dines (2002). Both these national lists of alien species used comparable criteria for classifying species as archaeophyte or neophyte; however, in many cases it is difficult to prove whether a species is archaeophyte or native. As most European archaeophytes originate from southern Europe or the Near East (di Castri 1990), the distinction between archaeophytes and native species is particularly unclear in southern Europe. Therefore Catalonian species were classified only either as neophytes or non-neophytes, the latter containing native species and archaeophytes. The neophyte proportions reported for Catalonia in the present paper are slightly lower than alien proportions reported in Vilà, Pino & Font (2007) because we used a newer version of the FLORACAT database, in which some archaeophytes were removed from the alien species list. Planted crops recorded in arable land plots were excluded from the analysis. Species nomenclature follows Tutin *et al.* (1968–93).

HABITAT CLASSIFICATION

An important part of the current study was the development of a common platform of habitat classification for the three regions. Although the systems of vegetation classification in most European countries are based on the Braun–Blanquet approach (Westhoff & van der Maarel 1973), compatibility of standard vegetation classifications used in different countries is limited. In the current study, this problem was amplified further by a large geographical distance between the studied regions (implying large habitat differences) and different traditions of vegetation classification in the United Kingdom and continental Europe. Therefore, we used broadly delimited habitat types (hereafter called habitats) which reflected environmental features common to the three regions. We adopted the European Nature Information System (EUNIS) Habitats Classification, a standard classification of European habitats developed by the European Environment Agency (http://eunis.eea.europa.eu/habitats.jsp). From the version of this classification, available online from October 2005, we used habitats on hierarchical Level 2, but where these habitats were too heterogeneous with respect to the level of invasion we also used habitats on Level 3. In some cases we merged two or three habitats, because we were not able to assign many plots unequivocally to one of them. In total, we used 33 habitat classes, of which 14 were recorded in all the three regions (Appendix S1 in Supplementary material).

Catalonian and Czech plots were assigned to the EUNIS habitats based on their existing assignments to phytosociological syntaxa, using a syntaxa–EUNIS crosswalk (Rodwell *et al.* 2002; Appendix S2, Supplementary material). Assignment of the Catalonian and Czech plots to habitats differs slightly from the preliminary analyses of the same data sets (Chytrý *et al.* 2005; Vilà, Pino & Font 2007), because the previous analyses used an older version of the EUNIS classification and because some habitats had to be merged or interpreted in a slightly different way in order to achieve compatibility between the three national data sets. In the British data set, plots were assigned to the EUNIS habitats by allocating them to a British National Vegetation Classification community (Rodwell 1991–2000) and Broad Habitat category (www.ukbap.org.uk). These were then matched to EUNIS habitats (Appendix S3, Supplementary material). It is important to note that most vegetation plots included in this study represent homogeneous stands of vegetation rather than ecotonal sites, although the latter can be important habitats of some alien species.

DATA ANALYSIS

For the comparison of the proportion of alien species between habitats and regions, we computed descriptive statistics and univariate tests in the STATISTICA version 7.1 software (www.statsoft.com). In these analyses, we avoided comparing species numbers, because these were affected potentially by different plot sizes. We report mean species numbers per plot for a rough indication, but not for direct comparison, of species richness between habitats. Instead of absolute species numbers, we restricted our between-habitat comparisons to proportions, e.g. the number of aliens divided by the number of all species. The proportions can also be affected to some extent by plot size. For example, Stohlgren *et al.* (2006) reported that the proportion of alien to native species may decrease with increasing plot size. However, our preliminary analyses (e.g. Chytrý *et al.* 2005; Vilà, Pino & Font 2007) showed that the effect of plot size on proportions was negligible. To quantify relationships between archaeophytes and neophytes, we calculated correlation and regression analyses in which species numbers were used instead of proportions, assuming that an increase in plot size would cause the same relative increase in both groups of aliens and native species. Where appropriate, in statistical analyses, variables were square root-transformed after adding 0·5.

Results

COMPARISON OF ALIEN SPECIES COMPOSITION AMONG REGIONS

The pooled data set from the three regions contained 545 alien species (301 neophytes, 228 archaeophytes and 16 species with different status in different regions; Table 3). There were 109 aliens in the Catalonian data set (all neophytes), 390 in the Czech data set (171 neophytes and 219 archaeophytes) and 189 in the British data set (107 neophytes and 82 archaeophytes). The remarkably higher number of aliens in the Czech

Table 2. Descriptive statistics for the vegetation plot size, number of species per plot and percentages of archaeophytes and neophytes relative to the number of all species in plots belonging to different EUNIS habitats. Dash = habitat does not occur in the region or data are not available; Cat = Catalonia, CZ = Czech Republic, GB = Great Britain

	Plot size (interquartile range, m^2)			No. of all species per plot (mean ± SD)			% of neophytes (mean ± SD)			% of archaeophytes (mean ± SD)	
EUNIS habitat	Cat	CZ	GB	Cat	CZ	GB	Cat	CZ	GB	CZ	GB
A2·5 & D6 & E6 Saline habitats	20–50	8–20	4–10	8·0 ± 4·1	16·7 ± 8·8	8·0 ± 4·3	2·2 ± 5·6	1·6 ± 3·4	0·7 ± 2·7	7·4 ± 10·6	1·5 ± 4·6
B1 & B2 Coastal sediments	12–50	–	4–10	10·7 ± 5·8	–	11·6 ± 7·1	3·3 ± 6·4	–	10·0 ± 18·9	–	3·3 ± 7·8
B3 Coastal rocks	20–100	–	4–10	12·0 ± 6·3	–	12·3 ± 6·0	0·7 ± 2·3	–	0·9 ± 4·9	–	0·5 ± 2·2
C1 Standing waters	1–4	10–25	–	11·8 ± 12·0	3·7 ± 2·3	–	0·9 ± 4·3	3·9 ± 12·5	–	0	–
C2 Running waters	4–20	6–20	–	8·6 ± 3·9	10·0 ± 7·3	–	0	1·0 ± 4·1	–	0·2 ± 1·3	–
C3 & D5 Sedge-reed beds	6–44	9–25	4–10	9·8 ± 5·7	10·0 ± 6·8	9·8 ± 6·2	7·1 ± 12·5	2·9 ± 7·2	4·4 ± 14·8	2·5 ± 5·9	1·3 ± 3·1
D1 Bogs	4–18	10–25	10–200	16·1 ± 6·6	9·8 ± 4·9	13·8 ± 7·3	0	0	0·2 ± 1·3	0·1 ± 0·4	0·0 ± 0·3
D2 Poor fens	10–20	10–25	4–10	17·0 ± 5·9	18·3 ± 10·7	14·7 ± 5·2	0	0·1 ± 0·9	0·4 ± 2·4	0·5 ± 1·3	0
D4 Base-rich fens	4–15	10–20	4–10	16·3 ± 5·2	23·8 ± 10·8	22·8 ± 9·4	0	0·2 ± 0·7	0·3 ± 1·0	1·4 ± 2·4	0
E1 Dry grasslands	5–35	14–25	10	29·2 ± 11·8	26·2 ± 12·7	16·6 ± 8·6	0·4 ± 1·4	0·7 ± 3·0	0·4 ± 1·9	6·0 ± 7·7	0·1 ± 1·1
E2 Mesic grasslands	18–50	16–25	10	27·2 ± 12·1	30·3 ± 11·0	18·0 ± 6·9	0·4 ± 1·3	0·7 ± 2·1	1·3 ± 3·2	5·3 ± 6·9	2·5 ± 5·2
E3 & E5·4 Wet grasslands	7–25	15–25	4–10	16·4 ± 7·6	27·0 ± 12·0	16·3 ± 7·0	2·6 ± 7·8	1·2 ± 4·2	1·1 ± 3·5	2·7 ± 5·7	1·0 ± 3·4
E4 Alpine grasslands	10–50	16–25	–	21·5 ± 10·3	13·7 ± 7·7	–	0	0·1 ± 1·1	–	0	–
E5·1 Ruderal vegetation	10–30	10–20	10	17·7 ± 9·4	15·7 ± 7·5	13·1 ± 5·8	5·3 ± 10·6	6·9 ± 8·6	4·5 ± 8·6	35·5 ± 18·8	6·7 ± 10·1
E5·2 Woodland fringes	10–30	10–25	–	24·8 ± 8·7	27·5 ± 9·5	–	0·0 ± 0·3	0·3 ± 1·0	–	4·1 ± 4·4	–
E5·3 Bracken	–	–	10	–	–	10·5 ± 5·4	–	–	0·8 ± 3·1	–	0·5 ± 2·4
E5·5 Subalpine tall forbs	15–75	16–25	4–10	23·0 ± 9·8	16·8 ± 9·1	21·1 ± 7·7	0	0·2 ± 1·7	0·6 ± 1·6	0·7 ± 4·9	0
F2 Subalpine scrub	49–100	100	–	20·6 ± 8·4	23·8 ± 12·7	–	0	0	–	0	–
F3 Temperate scrub	20–50	20–60	10	19·2 ± 10·1	22·3 ± 10·7	15·6 ± 7·2	0·5 ± 2·6	2·3 ± 5·7	1·9 ± 6·7	8·7 ± 10·5	2·3 ± 4·8
F4 Temperate heaths	20–100	10–25	10	23·3 ± 11·7	13·7 ± 7·2	10·8 ± 7·5	0	0·2 ± 1·3	0·3 ± 2·6	0·6 ± 1·8	0·0 ± 0·3
F5 Maquis	50–100	–	–	21·8 ± 8·6	–	–	0·2 ± 1·3	–	–	–	–
F6 Garrigue	25–50	–	–	26·3 ± 9·6	–	–	0·0 ± 0·7	–	–	–	–
F7 Mediterranean heaths	20–50	–	–	20·9 ± 7·4	–	–	0	–	–	–	–
F9 Wet scrub	25–80	38–100	–	18·9 ± 10·9	14·6 ± 7·8	–	3·1 ± 6·5	2·0 ± 4·2	–	1·4 ± 3·4	–
FA Hedgerows	–	–	10	–	–	6·7 ± 5·5	–	–	2·8 ± 8·3	–	1·7 ± 5·8
G1 & 4 Deciduous woodlands	75–100	150–400	4–10	27·7 ± 11·3	26·3 ± 12·8	14·9 ± 8·5	0·2 ± 1·7	1·0 ± 2·4	3·1 ± 7·9	0·7 ± 2·0	0·9 ± 4·3
G2 Evergreen woodlands	40–100	–	–	22·8 ± 10·3	–	–	0·1 ± 0·6	–	–	–	–
G3 Coniferous woodlands	100–150	25–50	10–200	24·8 ± 8·5	15·6 ± 10·5	9·9 ± 8·2	0	0·4 ± 1·6	24·8 ± 29·7	0·6 ± 2·8	0·3 ± 1·9
G5 Disturbed woodlands	10–30	25–50	–	21·1 ± 8·4	20·2 ± 9·6	–	0·2 ± 1·1	2·8 ± 4·8	–	4·2 ± 8·8	–
H2 Screes	10–60	9–24	–	13·0 ± 5·9	16·5 ± 8·3	–	0·7 ± 3·2	1·4 ± 3·3	–	10·7 ± 9·5	–
H3 Cliffs and walls	4–20	1–9	–	10·2 ± 5·3	8·0 ± 5·0	–	0·3 ± 2·4	7·0 ± 14·1	–	9·5 ± 17·2	–
H5·6 Trampled areas	5–20	4–15	–	15·7 ± 8·6	12·0 ± 6·5	–	6·2 ± 11·2	6·0 ± 7·2	–	21·8 ± 21·0	–
I1 Arable land	30–90	15–100	10–200	21·6 ± 9·0	26·2 ± 9·5	11·7 ± 7·9	7·3 ± 9·8	5·6 ± 5·2	14·3 ± 25·6	55·5 ± 13·5	16·2 ± 16·0

Table 3. Numbers of neophytes and archaeophytes recorded in all vegetation plots from individual regions, including those found in a single region only, in two regions only and in all the three regions. Sixteen species with different status (archaeophyte or neophyte) in different regions are included in both groups. CZ = Czech Republic, GB = Great Britain

	Neophytes	Archaeophytes
Total	317	244
Catalonia total	109	–
Czech Republic total	171	219
Great Britain total	107	82
Catalonia only	74	–
Czech Republic only	113	162
Great Britain only	67	25
Catalonia + CZ only	23	–
Catalonia + GB only	5	–
CZ + GB only	28	57
Catalonia + CZ + GB	7	–

data set was not due to more plots included in this data set: we conducted a few trials in which we deleted 4818 plots randomly from the Czech data set in order to make its size equal to the Catalonian (smallest) data set, but these trials led to a decrease in the total number of aliens by only 14–19 species.

Of 301 neophytes, only seven were recorded in vegetation plots in all three regions: *Calendula officinalis*, *Conyza canadensis*, *Helianthus tuberosus*, *Juncus tenuis*, *Chamomilla suaveolens*, *Phalaris canariensis* and *Solidago canadensis*. In addition, *Panicum miliaceum* also occurred in all three regions, but it is considered as an archaeophyte in the Czech Republic and neophyte in the other two regions. A further 56 neophytes were found in two regions. Species compositions of neophytes in Czech and British habitats were more similar to each other than to the species composition of neophytes in Catalonian habitats. Of 228 archaeophytes, 57 occurred in both the Czech Republic and Britain. In addition, 12 occurred in both regions with reversed status.

Although the region's lists of top aliens contain some species common to two regions, overall they are somewhat dissimilar (Tables 4 and 5; see also Appendix S4 in Supplementary material for the lists of the most common aliens in particular habitats). Interestingly, the British list of the most common neophytes (Table 4a) contains 40% woody plants. However, woody plants are absent from the corresponding Catalonian list, and represented by a single species, *Robinia pseudacacia*, in the Czech list.

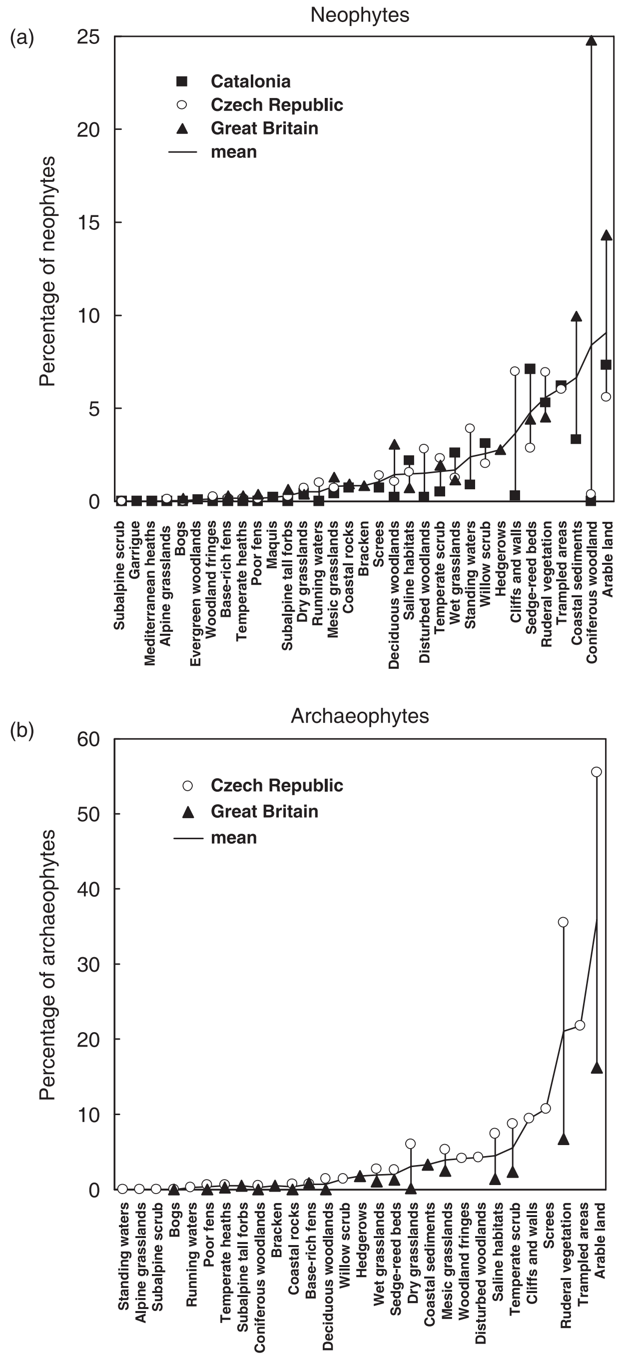

Fig. 1. Percentages of neophytes and archaeophytes occurring in vegetation plots in different EUNIS habitats in Catalonia, Czech Republic and Great Britain. Habitats are ranked by increasing mean percentages. Some habitats are only represented or documented in one or two countries. See Table 2 for EUNIS habitat codes and Appendix 1 for full habitat names.

PROPORTION OF ALIENS IN DIFFERENT HABITATS

Mean proportions of alien species per plot were compared among different habitats (Table 2). Generally, similar habitats were found with high or low alien proportions in different regions, which indicates that the patterns in the proportion of alien species are consistent even across regions with rather different alien floras (Fig. 1).

The habitats with the lowest proportions of neophytes (Table 2, Fig. 1a) are those on soils with constantly low nutrient availability. They include mires (bogs, poor fens, base-rich fens), some grasslands (alpine grasslands, woodland fringes), heathlands and scrub (subalpine scrub, temperate heaths) and evergreen Mediterranean vegetation (maquis, garrigue, Mediterranean heaths, evergreeen woodland).

Table 4. Twenty most common neophytes (a, measure of occurrence frequency in the landscape) and neophytes occurring in most habitats (b, measure of ecological range) in each region. Numbers are percentages. Percentages in (a) express the number of occurrences in the plots of each habitat relative to the total number of plots in that habitat, averaged across habitats. Percentages in (b) are the numbers of habitats in which the species was found in at least one plot, relative to the total number of habitats considered in this study for the particular region. Species included in the lists of two or three regions are in bold type

Catalonia		Czech Republic		Great Britain	
(a) Mean percentage occurrence in vegetation plots of different habitats					
Aster squamatus	2·3	*Impatiens parviflora*	3·8	*Picea sitchensis*	5·1
Xanthium strumarium ssp. *italicum*	1·7	***Veronica persica***	2·3	***Chamomilla suaveolens***	3·0
Amaranthus retroflexus	1·3	***Chamomilla suaveolens***	2·0	*Acer pseudoplatanus*	3·0
Conyza bonariensis	0·7	***Conyza canadensis***	1·7	***Veronica persica***	1·8
Amaranthus blitoides	0·6	***Epilobium adenocaulon***	1·5	*Brassica napus* ssp. *napus*	1·5
Sorghum halepense	0·6	*Trifolium hybridum*	1·4	*Lolium multiflorum*	0·9
Conyza canadensis	0·6	*Robinia pseudacacia*	0·9	*Pinus contorta*	0·7
Conyza sumatrensis (Retz.) E. Walker	0·5	***Amaranthus retroflexus***	0·9	***Impatiens glandulifera***	0·6
Cyperus eragrostis	0·5	*Agrostis gigantea*	0·8	*Picea abies*	0·4
Carpobrotus edulis	0·4	*Elodea canadensis*	0·7	***Epilobium adenocaulon***	0·4
Bidens frondosa	0·4	*Galinsoga ciliata*	0·6	*Epilobium brunnescens*	0·3
Sporobolus indicus	0·4	*Galinsoga parviflora*	0·6	*Cardaria draba*	0·3
Bromus willdenowii	0·4	***Bidens frondosa***	0·6	*Pinus nigra*	0·3
Amaranthus hybridus	0·4	***Impatiens glandulifera***	0·5	*Claytonia perfoliata*	0·2
Chenopodium ambrosioides	0·4	*Solidago canadensis*	0·4	*Aesculus hippocastanum*	0·2
Euphorbia prostrata	0·3	*Medicago sativa*	0·4	*Claytonia sibirica*	0·2
Artemisia verlotiorum	0·3	*Juncus tenuis*	0·4	*Pseudotsuga menziesii*	0·2
Xanthium spinosum	0·2	*Solanum tuberosum*	0·4	*Rhododendron ponticum*	0·2
Echinochloa colonum	0·2	*Oxalis europaea*	0·3	*Vicia faba*	0·2
Amaranthus albus	0·2	*Acorus calamus*	0·3	*Brassica rapa*	0·2
(b) Percentage of habitats in which the species was recorded					
Aster squamatus	45	***Epilobium adenocaulon***	72	*Acer pseudoplatanus*	74
Conyza canadensis	45	*Impatiens parviflora*	68	*Picea sitchensis*	68
Conyza bonariensis	35	*Agrostis gigantea*	52	*Brassica napus* ssp. *napus*	58
Conyza sumatrensis (Retz.) E. Walker	35	***Conyza canadensis***	52	*Lolium multiflorum*	58
Xanthium strumarium ssp. *italicum*	32	***Robinia pseudacacia***	48	***Veronica persica***	58
Amaranthus retroflexus	29	*Trifolium hybridum*	48	***Epilobium adenocaulon***	53
Artemisia verlotiorum	29	***Bidens frondosa***	44	*Impatiens glandulifera*	53
Sorghum halepense	29	*Erigeron annuus*	44	***Chamomilla suaveolens***	53
Amaranthus blitoides	26	*Juncus tenuis*	40	*Aesculus hippocastanum*	47
Chenopodium ambrosioides	26	*Medicago sativa*	40	*Picea abies*	47
Robinia pseudoacacia	26	*Solidago canadensis*	40	*Epilobium brunnescens*	42
Amaranthus hybridus	23	*Aster novi-belgii* group	36	*Senecio viscosus*	42
Cyperus eragrostis	23	*Cytisus scoparius*	36	*Brassica rapa*	37
Euphorbia nutans	23	*Lupinus polyphyllus*	36	*Claytonia perfoliata*	37
Euphorbia prostrata	23	***Chamomilla suaveolens***	36	*Claytonia sibirica*	37
Sporobolus indicus	23	*Oxalis fontana*	36	*Geranium pyrenaicum*	37
Bidens frondosa	19	*Acorus calamus*	32	*Cardaria draba*	37
Bromus willdenowii	19	*Galinsoga parviflora*	32	*Rhododendron ponticum*	37
Coronopus didymus	19	*Rumex thyrsiflorus*	32	*Veronica filiformis*	37
Datura stramonium	19	***Veronica persica***	32	*Castanea sativa*	32
Kochia scoparia	19			*Cotoneaster microphyllus*	32
Oenothera biennis	19			*Reynoutria japonica*	32
Paspalum dilatatum	19			*Mimulus guttatus*	32
				Veronica polita	32

The habitats with the greatest proportion of aliens belong to two groups, anthropogenic habitats (arable land, ruderal vegetation, trampled areas) and coastal, littoral and riverine habitats (coastal sediments, sedge-reed beds, wet scrub). Some habitats are among the most invaded in single regions only, e.g. coniferous woodland only in Britain and cliffs and walls only in the Czech Republic.

The pattern of habitat invasion by archaeophytes in the Czech Republic and Britain (Fig. 1b) is similar to the corresponding pattern for neophytes. The habitats with the highest and lowest proportions of aliens are generally the same for both neophytes and archaeophytes, although there are some exceptions (see the next section). Czech habitats contain on average higher proportion of archaeophytes than British habitats.

INVASIONS BY ARCHAEOPHYTES AND NEOPHYTES

If habitat mean values are compared, there is a strong positive correlation between the numbers of archaeophytes and

Table 5. Twenty most common archaeophytes and archaeophytes occurring in most habitats in the Czech Republic and Britain. See Table 4 for further explanation

Czech Republic		Great Britain	
(a) Mean percentage occurrence in vegetation plots of different habitats			
Arrhenatherum elatius	9·0	*Bromus sterilis*	3·9
Cirsium arvense	7·0	*Lamium album*	2·0
Matricaria perforata	5·4	***Capsella bursa-pastoris***	1·6
Polygonum aviculare group	5·4	*Avena fatua*	1·3
Fallopia convolvulus	4·6	***Lamium purpureum***	1·3
Convolvulus arvensis	4·4	*Geranium dissectum*	1·2
Capsella bursa-pastoris	4·1	*Viola arvensis*	1·0
Echium vulgare	3·1	*Artemisia vulgaris*	1·0
Mentha arvensis	3·0	***Fallopia convolvulus***	1·0
Lapsana communis	2·9	***Myosotis arvensis***	0·9
Myosotis arvensis	2·5	*Sisymbrium officinale*	0·8
Thlaspi arvense	2·3	*Alopecurus myosuroides*	0·6
Medicago lupulina	2·3	*Picris echioides*	0·6
Chelidonium majus	2·2	*Papaver rhoeas*	0·6
Lamium purpureum	2·1	*Aegopodium podagraria*	0·5
Veronica arvensis	1·9	*Silene latifolia*	0·5
Vicia hirsuta	1·8	*Conium maculatum*	0·5
Sonchus oleraceus	1·8	*Ballota nigra*	0·5
Anagallis arvensis	1·7	*Sinapis arvensis*	0·5
Atriplex patula	1·6	*Malva sylvestris*	0·5
(b) Percentage of habitats in which the species was recorded			
Arrhenatherum elatius	76	*Bromus sterilis*	68
Cirsium arvense	64	*Aegopodium podagraria*	63
Cirsium vulgare	60	***Ballota nigra***	63
Convolvulus arvensis	60	*Geranium dissectum*	63
Echium vulgare	60	*Agrostis gigantea*	58
Lapsana communis	60	*Artemisia vulgaris*	58
Linaria vulgaris	60	***Lamium album***	58
Medicago lupulina	60	***Myosotis arvensis***	58
Silene latifolia	60	*Picris echioides*	58
Tanacetum vulgare	60	*Avena fatua*	53
Lamium album	56	*Conium maculatum*	53
Mentha arvensis	56	*Lamium purpureum*	53
Fallopia convolvulus	52	***Silene latifolia***	53
Lactuca serriola	52	*Viola arvensis*	53
Myosotis arvensis	52	***Fallopia convolvulus***	47
Sonchus oleraceus	52	*Malva sylvestris*	47
Vicia hirsuta	52	*Alopecurus myosuroides*	42
Ballota nigra	48	***Capsella bursa-pastoris***	42
Capsella bursa-pastoris	48	*Fumaria officinalis*	42
Carduus acanthoides	48	*Chamomilla recutita*	42
Cheloniumsat majus	48	*Sinapis arvensis*	42
Pastinaca sativa	48	*Sisymbrium* officinale	42
Matricaria perforata	48	*Smyrnium olusatrum*	42

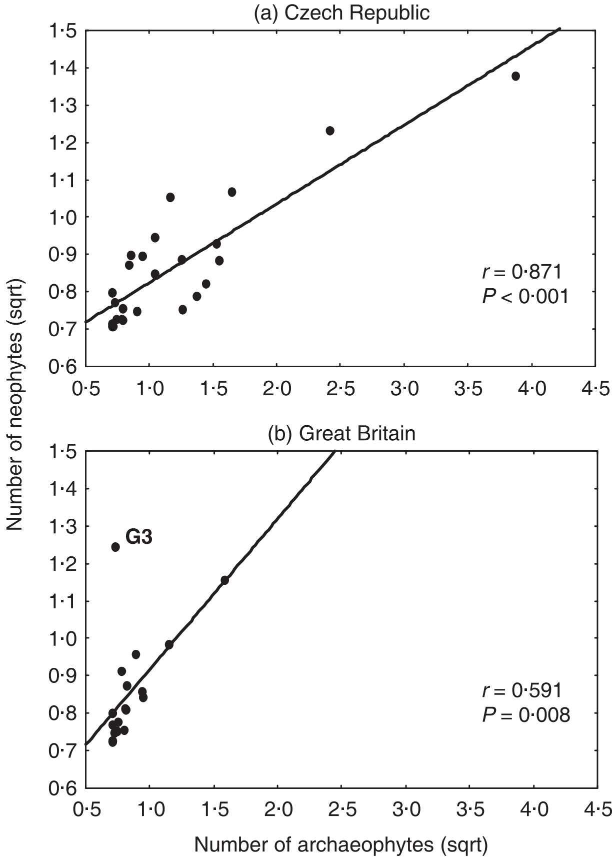

Fig. 2. Relationships between numbers of neophytes and archaeophytes in individual habitats in the Czech Republic and Great Britain. Each point represents habitat mean values. G3 = coniferous woodland.

neophytes in Czech and British habitats (Fig. 2). Positive relationships also prevail within individual habitats in separate analyses using individual plots of each habitat as data points (Table 6). For 16 Czech and 11 British habitats there are positive relationships and for nine Czech and eight British habitats the relationships are not significant. There is no negative relationship.

Apart from this general trend, it appears that some habitats tend to support a higher proportion of neophytes and others of archaeophytes (Table 6). Both in the Czech Republic and Britain proportion of neophytes to all aliens is high for woodlands and nutrient-rich wet habitats, while it is low for nutrient-poor habitats, dry and mesic grasslands, heathlands and scrub, and also for anthropogenic habitats.

Discussion

ALIEN SPECIES OF THE THREE REGIONS

In the Czech Republic the total numbers of both archaeophytes and neophytes found in all plots were the highest, while Catalonia and Britain did not differ greatly in the total numbers of neophytes (Table 3). This may reflect both the slightly different nature of the three data sets and real differences. The British data set did not involve urban habitats while these were contained in the other national data sets, so the total pool of aliens in the British data set may be underrepresented (Roy, Hill & Rothery 1999). The low number of archaeophytes in British compared to Czech habitats also reflects the differences in total pools of archaeophytes in the two countries. If casuals are excluded, the Czech flora contains 258 and the British flora 151 archaeophytes (Table 1). This pattern probably reflects the climatic match of archaeophytes in their secondary range. Most archaeophytes in central and western Europe originate from drier and warmer

Table 6. Within-habitat correlations between archaeophytes and neophytes (a) and ratios of the number of neophytes to the number of all aliens (archaeophytes + neophytes; b), in the Czech Republic and Britain. Dash = habitat does not occur in the region or data are not available. In (a), numbers are correlation coefficients between the number of archaeophytes and neophytes in vegetation plots of each habitat (*** $P < 0{\cdot}001$, ** $P < 0{\cdot}01$, * $P < 0{\cdot}05$, NS = not significant). 'No arch' and 'no neo' means that the habitat contains no archaeophytes or no neophytes, respectively. In (b) ratios for those habitats that contain on average less than 0·1% of neophytes or archaeophytes in vegetation plots are put into brackets, because such values may be unstable

	(a) Arch-neo correlations		(b) Ratio neophytes/all aliens	
EUNIS habitat	CZ	GB	CZ	GB
A2·5 & D6 & E6 Saline habitats	0·18*	NS	0·20	0·33
B1 & B2 Coastal sediments	–	0·25***	–	0·59
B3 Coastal rocks	–	NS	–	(0·53)
C1 Standing waters	no arch	–	1·00	–
C2 Running waters	NS	–	(0·75)	–
C3 & D5 Reedbeds	0·48***	NS	0·43	0·61
D1 Bogs	no neo	0·07*	(0)	(0·87)
D2 Poor fens	0·14**	no arch	0·16	(1·00)
D4 Rich fens	NS	no arch	0·16	(1·00)
E1 Dry grasslands	0·16***	0·08***	0·08	(0·73)
E2 Mesic grasslands	0·33***	0·23***	0·10	0·34
E3 & E5·4 Wet grasslands	0·22***	0·22***	0·27	0·50
E4 Alpine grasslands	no arch	–	(1·00)	–
E5·1 Ruderal vegetation	0·27***	0·21***	0·16	0·36
E5·2 Woodland fringes	NS	–	0·06	–
E5·3 Bracken	–	0·11*	–	0·60
E5·5 Subalpine tall forbs	NS	no arch	(0·33)	1·00
F2 Subalpine scrub	no aliens	–	no aliens	–
F3 Temperate scrub	0·31***	0·13***	0·17	0·38
F4 Temperate heaths	NS	NS	0·18	(0·86)
F9 Wet scrub	0·46***	–	0·57	–
FA Hedgerows	–	0·09***	–	0·48
G1 & 4 Deciduous woodlands	0·27***	0·09**	0·55	0·76
G3 Coniferous woodlands	0·28***	n.s.	0·35	0·97
G5 Disturbed woodlands	0·45***	–	0·41	–
H2 Screes	0·52***	–	0·13	–
H3 Cliffs and walls	0·36***	–	0·40	–
H5·6 Trampled areas	0·31***	–	0·22	–
I1 Arable land	0·15***	0·25***	0·09	0·29

areas of southern Europe and the Near East (di Castri 1990), which makes them better adapted to the subcontinental Czech climate than to the wet British climate. It is probable that the lower number of archaeophytes in British habitats does not result from the greater distance from their native range (thus a lower probability of immigration), because many archaeophytes arrived in both countries very soon after the beginning of Neolithic agriculture (Pyšek & Jarošík 2005).

The analysis of alien species composition in vegetation plots revealed a considerable dissimilarity between the Mediterranean–submediterranean, subcontinental and oceanic regions of Europe. Generally, compositions of alien floras are more similar among different habitats of the same region than between the same habitats of different regions. A similar pattern was found by Weber (1997) in his analysis of alien plant occurrence in European countries and by Lloret *et al.* (2004), who found more than 400 aliens on eight large Mediterranean islands, but only four of them were present on all islands.

This is important for the interpretation of the habitat invasion patterns. As the alien floras found in vegetation plots of the same habitats differ strongly between regions, patterns of habitat invasions in each region seem to be determined mainly by properties of the habitats rather than the identity of particular alien species.

LEVEL OF INVASION IN DIFFERENT HABITATS

Between-habitat patterns in the proportion of aliens are very similar among the Mediterranean–submediterranean, subcontinental and oceanic regions. Generally, similar habitats have high or low proportions in each of these regions. For neophytes, there are two exceptions which result from artefacts in the data (Fig. 1a). Firstly, coniferous woodland has a very high proportion of neophytes in Britain but a low proportion in the other regions. This is due to most British coniferous woodlands being plantations of alien conifers, whereas natural coniferous woodlands are poor in aliens (Crawley 1987). Secondly, the higher proportion of aliens on cliffs and walls in the Czech Republic is due to many Czech plots being sampled on urban walls.

Our study suggests that the habitat-specific proportions of alien species between the contrasting climatic regions are consistent for neophytes and archaeophytes. The habitats with the lowest proportion of aliens in all regions include bogs and mires, alpine–subalpine grasslands and different kinds of nutrient-poor heathlands (i.e. alpine, temperate and Mediterranean). In contrast, the highest proportions were in man-made and coastal habitats. Neophytes are also found in high proportions in fresh-water and littoral habitats while this is also true of archaeophytes on screes. Similar patterns have also been confirmed by the analyses of habitat-specific species pools of aliens in other parts of Europe, e.g. Austria (Walter *et al*. 2005) or Berlin (Kowarik 1995).

The relative constancy of the habitat invasion patterns across regions, occurring in spite of the large differences in species composition, suggests the existence of general mechanisms that make a habitat either resistant or susceptible to invasion. Common attributes of habitats with a low proportion of aliens include environmentally stressful conditions (e.g. low temperature or pronounced drought), low nutrient availability and infrequent disturbance. In contrast, habitats with higher proportions of aliens are usually developed on nutrient-rich soil and experience frequent disturbances, both anthropogenic and natural (e.g. coastal sediments or riverine vegetation). In addition, all the habitats with high proportions of aliens experience short periods of strongly increased nutrient availability, e.g. fertilization on arable land, deposition of nutrient-rich mud from flood waters or disturbance of resident vegetation, which causes lower nutrient uptake. These observations are consistent with the theory of fluctuating resource availability (Davis, Grime & Thompson 2000), which suggests that occurrence of rapid pulses in resource availability is the key process determining habitat invasibility by enabling new species to establish in the community (see also Shea & Chesson 2002).

ARCHAEOPHYTES AND NEOPHYTES

Generally, habitats with more archaeophytes also have more neophytes (Fig. 2) and the same is true when individual sites are compared within particular habitats (Table 6). This observation made on Czech and British vegetation plots corresponds to the observation made by Deutschewitz *et al*. (2003) in larger sampling units – grid cells of 32 km^2 in Germany. The evidence of this positive relationship on different spatial scales is important for risk assessment of habitat invasions, because it predicts that the habitats and areas currently highly invaded by archaeophytes hold a higher risk of future invasions by new neophytes. This is also interesting from the theoretical point of view because it suggests that, through time, basically the same mechanisms can be responsible for higher susceptibility of habitats to invasion, in spite of different taxa, origin, residence time and invasion event characteristics.

However, apart from this general trend and from the fact that nearly all habitats contain a larger proportion of archaeophytes than neophytes, some habitats tend to host more archaeophytes and less neophytes than others and vice versa (Table 6; see also the deviations of data points from the regression lines in Fig. 2). Neophytes show a higher affinity to wet habitats and woodlands, while archaeophytes to open vegetation at dry or mesic sites. This general trend, valid across a broad range of different habitats in two contrasting climatic regions, is consistent with previous Central European studies which compared habitat affinities of these two groups of aliens within a single broad habitat such as arable land (Pyšek *et al*. 2005) or across a landscape (Deutschewitz *et al*. 2003). The most probable explanation is the habitat compatibility of aliens in their primary and secondary range. Most archaeophytes of temperate Europe originate from southern Europe and the Near East, i.e. rather dry areas with a high representation of dry treeless vegetation. In contrast, most neophytes originate from wetter areas with deciduous broad-leaved woodlands of North America or Eastern Asia. Thus, each of these two groups of aliens matches the prevailing habitat conditions in their native range.

TOWARDS A RISK ASSESSMENT OF PLANT INVASIONS

We demonstrated that similar patterns of habitat invasion emerge in different regions of Europe, which have contrasting climate and considerably different composition of alien floras. Independently of the available pool of potential invaders, habitats with high proportions of aliens are frequently disturbed with intermittent increases of nutrient availability, while those with low proportions are infrequently disturbed habitats with constantly low nutrient availability, many of them occurring in harsh climatic conditions. Moreover, recently spreading aliens are generally present in the same habitats that have been invaded by historically earlier aliens, although there are some deviations reflecting habitat compatibility of different species in their native and secondary range.

These robust patterns make habitats a promising predictor of biological invasions at the regional level. For planning effective monitoring and management of alien plants, nature conservationists and land managers use risk assessment tools (Daehler *et al*. 2004; Maguire 2004), which are so far based mainly on traits of the potentially invasive species. Our study demonstrates that the quality of risk assessment can benefit greatly from incorporating the information on the identity of receptor habitats. Many maps of habitat distribution are currently available in Europe and such maps can help identify areas with high invasion risk. Furthermore, in order to estimate major trends in the future spread of alien plants, the habitat-specific proportions of aliens could be projected onto spatially explicit scenarios of future land-use changes (Rounsevell *et al*. 2006). Due to consistent patterns of habitat invasion between different climatic regions, such scenarios may have a broad potential for extrapolation to wider areas of Europe.

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Overview of the EUNIS habitats used.

Appendix S2. Crosswalk phytosociological syntaxa–EUNIS.

Appendix S3. Crosswalk British NVC communities–EUNIS.

Appendix S4. List of most common alien species in Catalonian, Czech and British habitats.

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