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Where do they come from and where do they go? European natural habitats as donors of invasive alien plants globally

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ABSTRACT

Aim The percentage of alien species found in a given habitat depends on the habitat vulnerability to invasion (invasibility) and the number of species introduced (propagule pressure). However, the global pool of alien species suited to a given habitat also varies. Here, we identify donor habitats of invasive alien plant species originating from Europe, examine the match between habitats they occupy in Europe and recipient areas and test whether donor habitats of invasive plants tend to be vulnerable or resistant to invasions.

Location Europe (source area), North America and the World (recipient areas).

Methods Native European vascular plants invasive in North America and other parts of the World were identified for 35 European natural habitats. Percentages of species invasive outside Europe, of the total number of native species occurring in each European habitat, were used to compare these habitats as donors for invasion. Habitat preferences of European species in their recipient areas were compared with those in Europe.

Results European alluvial forests, alder carrs and coastal sand-dunes harbour the highest percentages of native species that are invasive outside Europe. Outside their native range, European species tend to invade habitats that are similar to their donor habitats in Europe, but species of alluvial and coastal habitats also frequently invade other habitats. European habitats that are important donors of invasive species globally experience the highest levels of invasion by alien species from other regions; this relationship was, however, not confirmed for invasions to North America if considered separately.

Main conclusions Some European habitats are more important donors of invasive plants than others. Therefore, the level of invasion of different habitats is affected also by the differences in the number of invasive species provided by various donor habitats. At a global scale, more important donor habitats are also likely to be more invaded.

Keywords

Biological invasions, colonization pressure, donor habitat, North America, propagule pressure, recipient habitat.

INTRODUCTION

Patterns of incidence of alien species in different habitat types (further habitats) have become an important topic of research, because habitats considerably affect the spread of alien species and they are also convenient units for management and control of plant invasions (Richardson & Pyšek, 2006). Habitats differ in terms of the numbers or percentages of alien or invasive species that have established there (level of invasion; Chytrý *et al.*, 2005; Maskell *et al.*, 2006; Vilà *et al.*, 2007; Kelly *et al.*, 2009; Jauni & Hyvönen, 2010), but the pattern of the mean levels of invasion of

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particular habitats tends to be relatively constant in different biogeographical regions (Chytrý et al., 2008). This indicates that the level of invasion may depend on the same set of factors throughout large geographical areas.

Variation in the level of invasion among habitats is usually explained as a result of habitat vulnerability to invasion and the number of alien species introduced to the site, described as propagule pressure (Lonsdale, 1999; here, this term is understood as the number of arriving species, i.e. colonization pressure *sensu* Lockwood et al., 2009). However, the number of alien species that establish in a particular habitat can also depend on the size of the global pool of species that are able to grow and establish in that habitat. Habitats in the source area (in the native range of species, further called donor habitats) can differ markedly both in the numbers of native species they harbour (Sádlo et al., 2007) and in the ability of these species to become invasive outside their native range (Hejda et al., 2009). Some habitats may select for species with specific life history traits, which are advantageous for their invasion success if these species are introduced to another area (further called recipient area; Pyšek et al., 2009; Schlaepfer et al., 2010). Invasion success may also be higher if the recipient area contains habitats that are similar to those in which the introduced species evolved in their native range (habitats in the recipient area are further called recipient habitats; Facon et al., 2006). As a consequence, some recipient habitats can be more invaded than others just because there are more introduced species that are adapted to these habitats. The level of invasion of particular recipient habitats can be estimated by quanti fying how many species from similar donor habitats are introduced.

Habitats with the highest levels of invasion have several attributes in common (Chytrý et al., 2005, 2008), including high levels of anthropogenic or natural disturbance and temporal fluctuations in nutrient or water supply (Alpert et al., 2000; Davis et al., 2000). Most species adapted to such fluctuating environments have an ability of efficient dispersal and rapid regeneration (Grime, 1979); therefore, they may be overrepresented among introduced aliens. If this is true, recipient habitats with fluctuating resource availability are more likely to be invaded not only because they are easier to invade, but also because a larger proportion of species introduced to the recipient area is adapted to such environments. However, this hypothesis has never been tested, partly because there is still little information on donor habitats of alien species. Sparse studies involving comparisons between source and recipient areas of alien species have mostly focused on climate matching (e.g. Pauchard et al., 2004) and rarely on fine-scale habitat compatibility (Rejmánek et al., 2005). The habitat preferences of species in their source and recipient areas have been rarely compared in studies on individual species (e.g. Sukopp & Starfinger, 1995), while multispecies comparisons are mostly based on floristic regions rather than habitats (Fridley, 2008; but see Hejda et al., 2009).

The pioneering study on the effect of native habitats on plant invasions focused on a set of species invasive in Central Europe (Hejda et al., 2009). It compared a large source area with a very broad range of habitats (the World) with a relatively small recipient area with a restricted range of habitats (Czech Republic). Therefore, many habitats in the source area did not have proper counterparts in the recipient area, and they may have been consequently underestimated as donors of alien species. Although this study offered valuable insights into donor–recipient habitat relationships, it could not provide a more general picture. Hence, we focus here on much larger recipient areas, analyzing the incidence of invasive species from Europe (1) in North America, that is, a continent with broadly similar climates and biomes, and (2) globally. Unlike in Hejda et al. (2009), our habitat delimitation is based on a consistent data source standardized across the whole of Europe.

Our questions are (1) Which European habitats are the main donors of plants that are invasive in North America and the World? (2) Do European species invade similar habitats on other continents as they occupy in Europe? (3) Are the European habitats that are important donors of invasive species to other continents also highly invaded in Europe?

METHODS

Data on European native species and their habitats

The Map of the Natural Vegetation of Europe at the scale 1: 2 500,000 (Bohn et al., 2004) was used to identify habitats of European species in their native range. This map covers the area from the Atlantic coast to the Ural Mountains and includes Iceland, Svalbard and the Caucasus. It is based on hierarchical classification of potential natural vegetation consisting of 19 zonal and azonal vegetation formations divided into 700 basic mapping units representing individual plant communities. We merged these basic mapping units into 35 broader units, further referred to as habitats, according to their geographical, ecological and floristic similarities (see Appendix S1 in Supporting Information). No semi-natural or human-made habitats are included in the map except forested degraded bogs (basic mapping units T4–T7). To make our analysis consistently focused on natural habitats little affected by humans, we excluded this habitat from the analysis. For the same reason, we excluded Atlantic dwarf shrub heaths (basic mapping units E1–E12) that are natural habitats but their species composition broadly overlaps with that of secondary heaths and secondary grasslands.

Presence/absence lists for native vascular plant species were compiled for each of the 35 European habitats, based on the descriptions of subordinated basic mapping units in Bohn et al. (2004). These descriptions were compiled by an international team of experts and include dominant, diagnostic (preferential) and other species occurring frequently in each mapping unit. Many species included were not habitat-specific and were listed for more than one habitat. We adopted a broad taxonomic delimitation of species that does not distinguish between infraspecific taxa. Supraspecific taxa such as aggregates or species *sensu lato* (e.g. *Rubus fruticosus* agg.) were excluded, because they may contain both invasive alien and native species. Species alien to Europe, that is, with a native range outside this continent (according to Lambdon *et al.*, 2008; DAISIE, 2009) were removed. The dataset contained 3518 European native plant species. Average number of native species per European natural habitat was 213.9 ± 171.5 (mean ± SD; for total numbers per habitat see Appendix S1). Species nomenclature follows Flora Europaea (Tutin *et al.*, 1968–1993).

Data on distribution of European native species that are invasive elsewhere

In the resulting list of European native species, we identified those that are considered as invasive aliens in two recipient areas: North America and the World. European species invasive in North America were identified using the Floristic Synthesis of North America (Kartesz & Meacham, 1999; using its updated version – J. T. Kartesz, unpublished data). The North American data cover species occurring in the United States (including Alaska and Hawaii), Canada, Greenland, Puerto Rico and other smaller islands. To ensure the same invasion status of species involved, only species marked as invasive or federal- or state-level noxious weeds were considered. Circumpolar or cosmopolitan species occurring in Europe and having both native and alien North American populations were omitted (386 species; e.g. *Phragmites australis* and *Poa pratensis*).

At the global scale, invasive alien species of European origin were identified using the overview of invasive plants of the World (Weber, 2003). Species labelled as invasive in at least one of the 32 regions of the World were considered. Weber's list is limited by the availability of data and therefore unlikely to encompass the whole spectrum of globally invasive species (it contains only 450 species in total). Despite this, we believe that author's effort to compile a comprehensive checklist at the global scale makes it a suitable source of data (Pyšek *et al.*, 2008). For the entire list of European species identified as invasive in North America or globally accompanied by their status and numbers of native European habitats in which they occur, see Appendix S2. It should be noted that native European plant species listed in the Map of Natural Vegetation of Europe represent a subset of European native flora; therefore, some European species invasive in other continents may not be included, especially if they are confined to semi-natural or man-made habitats in Europe.

To describe the habitat preferences of European species in their recipient areas, we used different approaches for North America and the World, adapted to the nature of the available data. European species invasive in North America were assigned to one or more of 11 main terrestrial WWF ecoregions of North America (Olson *et al.*, 2001) included in the updated Floristic Synthesis (J. T. Kartesz, unpublished data). WWF ecoregions are not habitats, but each of them contains a range of habitats that are relatively common within the ecoregion but differ from the habitats prevalent in other ecoregions. Therefore, WWF ecoregions can be used as a proxy for recipient habitats, given that the fine-scale habitat information for the whole of North America is not available. European species invading world-wide were assigned to recipient habitats as indicated by Weber (2003), and also to the regions of the World (Weber, 2003) to indicate their preferences to the main climate types. In total, 17 habitats and 32 World regions were distinguished.

Data analysis

The number of European native species that are invasive outside Europe was used to express their percentage among all the species listed in each European donor habitat. This was calculated separately for species that donor habitats deliver to North America and globally. European habitats differ in the areas they potentially occupy, total numbers of species occurring and the level of detail of their description in the Map of Natural Vegetation of Europe. To remove the potential confounding effects of these factors, we expressed, for each habitat, the number of species that invaded North America or the World as a percentage of all the species listed, rather than their absolute number. For absolute counts of all species and species invading North America or globally that originated from each European habitat, see Appendix S3.

We tested whether habitats that donate more invasive species are also more invaded. Habitats derived from the Map of the Natural Vegetation of Europe were matched to EUNIS habitats used in previous studies of invasions of European habitats (Chytrý *et al.*, 2008, 2009). In total, 13 pairs of matching habitats were identified (see Appendix S4). Levels of invasion for non-forest habitats were taken from the assessment done across contrasting climatic regions of Europe (Chytrý *et al.*, 2008) and those for forests from a subsequent study in which finely delimited forest habitats were used (Chytrý *et al.*, 2009). In both of these studies, the level of invasion of a habitat was calculated as the mean percentage of aliens among all species recorded in vegetation plots taken from national or regional vegetation databases. We used only data on neophytes, that is, alien species that arrived in Europe after AD 1500, because invasions of European species to other continents started after this date. Mean percentages of aliens in European habitats were arcsine-square-root transformed prior to the analyses to normalize the data distribution (Sokal & Rohlf, 1995). To characterize the relationship between the levels of invasion of European habitats and the percentages of European native species that occur in the same habitats and are invasive in North America or globally, we calculated a major axis regression (model II linear regression; Legendre & Legendre, 1998). The significance of the slope (difference against 0) was tested by a randomization with 4999 permutations. For our data, major axis regression is more appropriate than ordinary least-square regression as the independent variables are not fixed. Major axis regression analyses were performed using STATISTICA 9.1 (StatSoft, Inc, 2010).

RESULTS

European habitats that are most important donors of invasive species elsewhere

Of the European native species given in the habitat descriptions of the Map of Natural Vegetation of Europe, 227 were identified as invasive aliens in North America and 100 as invasive aliens globally. The main European donor habitats were similar for species that invaded North America and the World, as indicated by the positive correlation between the percentages of North American and global invaders from Europe present in these habitats ($r = 0.970$, $P < 0.001$). The highest percentages of species invasive outside Europe (Fig. 1) came from alder carrs and alluvial forests across all European macroclimatic zones and from coastal dunes of north-western Europe. In contrast, the lowest percentages of invasive species originated from European arctic, alpine and alti-Mediterranean habitats.

Recipient ecoregions and habitats of invasive species from European habitats

In North America, most invasive species of European origin occurred in the ecoregion of temperate broad-leaved or mixed forests and grasslands (222 species in total) and along shorelines (219 species), and less in the ecoregions of boreal forests (187 species), tundra (184 species) and Mediterranean savannas (145 species). At the global scale, invasive species from Europe occupied habitats similar to those predominating in the most invaded North American ecoregions: alluvial and coastal habitats (78 species), grasslands (60) and forests and woodlands (47). The lowest numbers of European species were recorded in ecoregions and habitats related to climates that are different from European, such as tropical broad-leaved forests of North America (51) or mangroves (1) and deserts of the World (1).

Shorelines of North America (Table 1), and riparian and coastal habitats globally (Table 2) were invaded by species from a wide spectrum of European donor habitats, but species from the corresponding habitats, European alluvial forests (up to 24.1% of species invading North America and 13.3% globally) and coastal sand-dunes of NW Europe (15.6% in North America and 8.3% globally), prevailed. Species of European coastal and alluvial habitats were the most numerous invaders in the majority of both the North American ecoregions and many World's habitats: they delivered more than 10% of invaders for six North American ecoregions and more than 4% of invaders for six global habitats. Other European species tended to invade habitats similar to those in their native range. For example, boreal forest ecoregion of North America was invaded mainly by species of European boreal forests (up to 13.7% of invaders), oligotrophic forests (11.0%) and subalpine woodlands (10.2%). Grassland-dominated ecoregions and grassland habitats of both recipient areas were invaded by species of European coastal dunes (11.1% of invaders invading ecoregions and 10.1% global habitats), forest-steppes (6.7 and 5.2%) and open halophilous vegetation (6.0 and 4.0%). There are many species from various types of European forests and scrub in North American forests in temperate regions and forests world-wide. In the Mediterranean-type climatic region of North America (e.g. California), the invasive species originated mainly from open habitats of warm and dry or summer-dry parts of Europe.

World regions as recipients of invasive species from European habitats

If particular regions of the World are compared (Table 3), those with warm and dry or a summer-dry climate, such as in the south-western USA, Australia and South Africa, are invaded by species from deserts (14.7% of invaders), dry coniferous forests and scrub (up to 9.8%) and steppes in southern and Eastern Europe (5.5%). Conversely, in the wetter and colder regions (e.g. Canada and Alaska), species of European bogs (up to 4.9% of invaders) and boreal alluvial forests (4.3%) are more common.

Habitats as donors and recipients of invasive species

There was a significant positive relationship between the percentage of species originating from European habitats and invasive globally and the level of invasion in the same European habitats ($R^2 = 0.685$; slope = 0.019; 95% confidence interval of slope = 0.010, 0.0275; $P < 0.001$; Fig. 2b). This indicates that the European habitats from which many species invasive in other parts of the World have come are also among the most invaded by alien species. However, no significant relationship was found if European species invasive in North America were used as a measure (Fig. 2a).

DISCUSSION

Important donor habitats and their properties

Our results show that habitats vary widely in their significance as donors of invasive alien plants. Most European species that invade other continents originate from two different habitats: (1) alluvial forests and alder carrs across all macroclimatic zones and (2) coastal dunes of north-western Europe. In general, the main differences between these and other European habitats are their high dynamics, incidence of either natural or human-induced disturbance events and the probability of species transport.

Alluvial forests in Europe are characterized by frequent disturbances and nutrient enrichment by periodical flooding

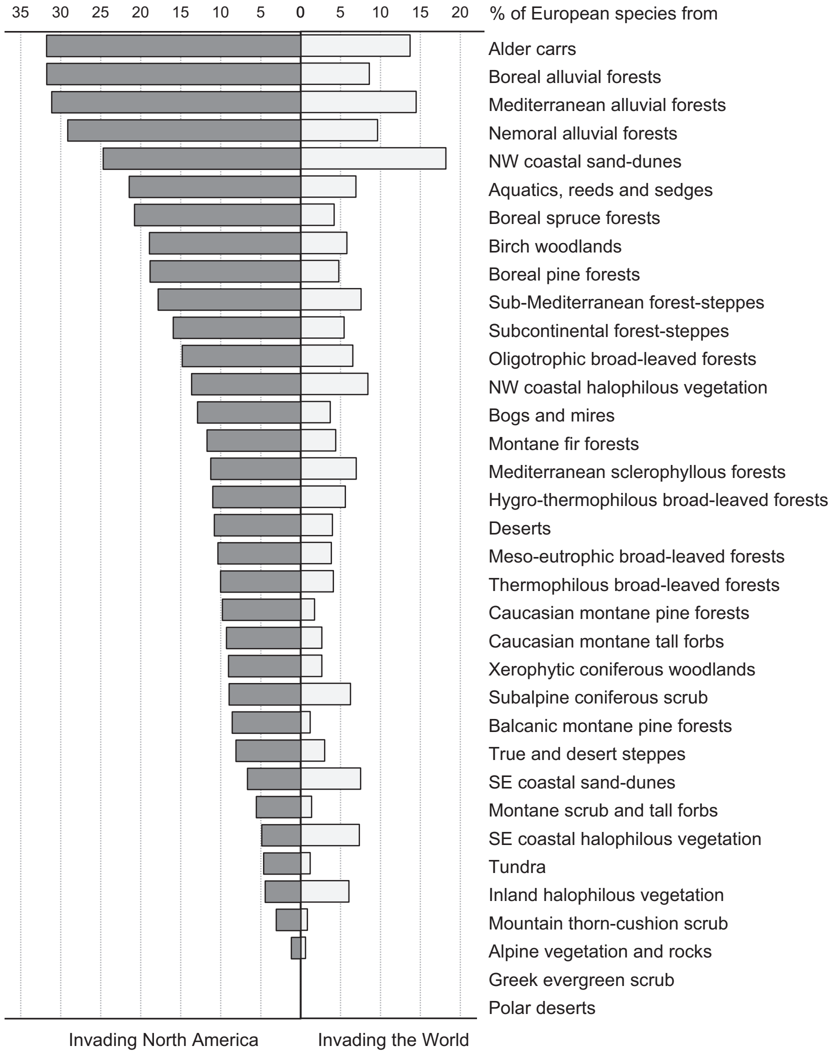

Figure 1 Main European donor habitats of invasive alien plant species in North America and in the World. European habitats plotted in descending order based on the percentage of their species that are invasive in North America.

(Naiman & Décamps, 1997). In such environments, species that are highly competitive and good at regenerating have an adaptive advantage. Species in alluvial habitats are also very effectively dispersed by wind or water (Johansson *et al.*, 1996). Species with these traits are likely to be at an advantage in terms of their ability to spread and survive at disturbed sites and compete with native plants in a new region. Alder carrs also often occur on European floodplains (Ellenberg, 1988) and they share almost all of their species identified as invasive aliens with alluvial forests. Hejda *et al.* (2009) found a similar pattern for species invading Central Europe, the majority of which originate from alluvial habitats of other continents.

European coastal sand-dunes affected by strong wind, sand movement and grazing are another continually changing habitat (Castillo & Moreno-Casasola, 1996). The majority of the species of European coastal dunes that are invasive outside Europe are clonal perennials (e.g. *Ammophila arenaria* and *Elymus repens*) and shrubs (e.g. *Ulex europaeus*). Clonal growth is one of the plant traits associated with high invasiveness (Pyšek, 1997). Clonality enables species to occupy both productive and infertile, disturbed habitats or sites with fine-scale environmental variation, where spatial division of labour among ramets may be advantageous (Price & Marshall, 1999). Other invasive alien species that originate from coastal dunes are short-lived herbaceous plants. Their invasion is more habitat-limited as they survive better in habitats where there is little competition from other species (Lake & Leishman, 2004).

In contrast, few or no invasive species originated from arctic and alpine habitats. The nutrient availability in these habitats is very low and the climatic conditions extreme. Stress-tolerant species dominating such habitats are not able to invade frequently disturbed or productive environments because they cannot compete with resident species (Alpert *et al.*, 2000; Rejmánek *et al.*, 2005). Also, their ability to invade stressed habitats outside their native range is low, most likely because of their intrinsically low relative growth rate and limited seed production (Grime, 1979).

Environmental conditions and associated species traits are not the only plausible explanation of why particular habitats are the main donors of invasive species. Humans over the last thousands years have had an immense influence on

Table 1 Percentages of invasive alien species originating from different European donor habitats occurring in the recipient North American WWF ecoregions. Numbers are percentages of species invading particular ecoregions, relative to the total number of native species recorded in particular European habitats. European 'Polar deserts' and 'Greek evergreen scrub' are not included, because no species invasive in other continents were recorded there. Values > 5% (light grey) and > 10% (dark grey) are highlighted to visualize the pattern.

	Percentages of species invasive in North American WWF ecoregions											
European habitats	Total North America	Shorelines	Tropical moist broad-leaved forests	Tropical dry broad-leaved forests	Temperate broad-leaved and mixed forests	Temperate coniferous forests	Temperate grassland, savanna, scrub	Flooded grasslands	Mediterranean scrub and savanna	Xeric shrubland, deserts	Boreal forests	Tundra
Tundra	4.7	1.2	0.6	0.6	0.6	0.6	0.6	–	1.2	0.6	1.2	1.2
Alpine vegetation and rocks	1.2	1.0	0.3	0.3	0.6	0.3	0.6	–	0.6	0.6	1.0	1.0
Birch woodlands	18.9	8.8	2.9	2.9	7.3	2.9	3.7	0.7	3.7	3.7	10.2	8.8
Montane scrub and tall forbs	5.6	4.6	0.5	0.5	3.7	0.9	1.9	–	0.5	0.9	4.6	4.6
Subalpine coniferous scrub	9.0	8.1	2.7	2.7	5.4	2.7	5.4	–	2.7	2.7	8.1	6.8
Caucasian montane tall forbs	9.3	8.7	–	–	6.0	2.7	2.0	–	3.3	1.3	8.7	8.7
Boreal spruce forests	20.8	12.6	1.6	1.6	6.3	4.2	5.3	–	2.6	3.2	13.7	13.2
Montane fir forests	11.7	8.5	1.0	1.0	4.8	2.1	3.8	–	3.1	2.7	8.9	8.9
Boreal pine forests	18.8	12.2	0.5	0.5	6.9	3.2	4.3	–	3.2	4.3	13.3	12.8
Caucasian montane pine forests	9.8	8.8	–	–	5.3	1.8	1.8	–	3.5	–	7.0	7.0
Balcanic pine forests	8.6	7.2	–	–	4.8	3.6	1.2	–	0.0	1.2	7.2	7.2
Oligotrophic broad-leaved forests	14.8	11.4	1.5	1.7	6.3	3.9	5.1	–	5.1	2.7	11.0	10.7
Meso-eutrophic broad-leaved forests	10.4	9.4	1.1	1.1	5.0	2.4	3.7	0.1	3.8	2.8	8.7	8.1
Thermophilous broad-leaved forests	10.0	8.6	1.2	1.2	4.1	2.5	3.5	0.2	3.8	1.5	8.0	7.7
Hygro-thermophilous broad-leaved forests	11.0	9.4	4.7	4.7	6.5	1.9	4.7	–	8.4	6.5	7.5	7.5

Table 1 Continued.

European habitats	Total North America	Shorelines	Tropical moist broad-leaved forests	Tropical dry broad-leaved forests	Temperate broad-leaved and mixed forests	Temperate coniferous forests	Temperate grassland, savanna, scrub	Flooded grasslands	Mediterranean scrub and savanna	Xeric shrubland, deserts	Boreal forests	Tundra
	Percentages of species invasive in North American WWF ecoregions											
Mediterranean sclerophyllous forests	11.3	10.0	2.4	1.9	4.6	4.0	5.7	0.8	6.7	2.7	7.5	7.8
Xerophytic coniferous woodlands	9.0	7.8	1.6	1.3	5.4	1.8	2.5	0.5	3.4	2.2	6.7	6.5
Subcontinental forest-steppes	15.9	13.7	2.1	2.1	7.9	4.5	5.8	0.3	6.9	5.5	14.0	11.3
Sub-Mediterranean forest-steppes	17.8	14.0	2.7	2.4	10.0	5.5	6.7	1.8	8.8	5.5	14.0	12.2
True and desert steppes	8.1	7.6	1.9	1.1	4.6	2.3	4.9	1.1	4.9	3.8	7.2	5.7
Mountain thorn-cushion scrub	3.1	3.0	0.9	0.4	1.3	0.4	1.3	0.4	0.9	1.3	2.6	2.6
Deserts	10.8	10.7	2.7	2.7	5.3	2.7	5.3	–	10.7	8.0	10.7	8.0
NW coastal sand-dunes	24.7	15.6	3.7	3.7	5.5	7.3	11.1	2.8	11.9	6.4	15.6	13.8
SE coastal sand-dunes	6.7	6.5	4.3	4.3	3.2	3.2	3.2	2.2	6.5	4.3	5.4	5.4
NW coastal halophilous vegetation	13.6	8.4	1.2	1.2	4.8	2.4	6.0	1.2	7.2	6.0	8.4	6.0
SE coastal halophilous vegetation	4.9	4.2	1.1	1.1	3.2	1.1	2.1	–	3.2	2.1	4.2	4.2
Inland halophilous vegetation	4.4	4.0	1.0	1.0	3.0	3.0	3.0	–	4.0	4.0	4.0	3.0
Aquatics, reeds and sedges	22.4	10.9	1.0	–	7.9	5.0	5.9	2.0	5.9	5.0	12.9	10.9
Bogs and mires	12.9	5.2	–	–	3.7	0.8	1.5	–	0.8	2.2	5.2	4.5
Alder carrs	31.8	19.4	1.6	0.8	10.5	1.6	7.3	0.8	11.3	8.1	19.4	16.9
Boreal alluvial forests	31.8	17.2	2.2	2.2	14.0	4.3	7.5	–	7.5	9.7	20.4	16.1
Nemoral alluvial forests	29.1	22.1	2.5	2.2	13.4	5.5	11.2	1.6	11.8	7.7	21.9	20.0
Mediterranean alluvial forests	31.1	24.1	5.4	3.6	12.7	6.6	13.3	3.0	18.1	8.4	19.9	19.3

Table 2 Percentages of invasive alien species originating from different European donor habitats with respect to recipient habitats they invade in the World (Weber, 2003). Numbers are percentages of species invading particular world-wide habitats relative to the total number of native species in European habitats. European 'Polar deserts' and 'Greek evergreen scrub' are not included, because no species invasive in other continents were recorded there. Values > 2% (light grey) and > 5% (dark grey) are highlighted to visualize the pattern.

	Percentages of species invasive in different habitats world-wide																	
European habitats	Total in the World	Forest edges	Forests	Woodlands	Sclerophyllous forests	Shrubland	Heathland	Grassland and pastures	Riparian habitats	Freshwater wetlands	Saltwater marshes	Coastal scrub, dunes and beaches	Coastal estuaries and mudflats	Mangrove	Deserts and desert scrub	Rock outcrops	Disturbed sites and damps	Bog edges
Tundra	1.1	0.6	–	–	–	–	1.2	1.2	0.6	0.6	–	0.6	–	–	–	–	–	0.6
Alpine vegetation and rocks	0.6	0.3	–	–	–	–	0.6	0.6	0.3	0.3	–	0.3	–	–	–	–	–	0.3
Birch woodlands	5.8	0.7	2.9	0.7	–	2.2	2.2	3.7	3.7	2.2	–	2.2	–	–	–	–	1.5	0.7
Montane scrub and tall forbs	1.4	–	0.5	0.5	–	–	0.5	0.9	0.9	0.5	–	0.5	–	–	–	–	–	0.5
Subalpine coniferous scrub	9.2	–	5.4	1.4	–	1.4	2.7	6.8	5.4	2.7	–	4.1	–	–	–	1.4	2.7	1.4
Caucasian montane tall forbs	2.7	1.3	2.0	1.3	–	–	–	1.3	2.7	0.7	–	0.7	–	–	–	–	0.7	–
Boreal spruce forests	4.2	2.1	2.6	1.1	–	1.1	0.5	1.1	1.1	–	–	–	–	–	–	0.5	1.1	0.5
Montane fir forests	4.4	1.7	3.8	1.4	–	1.4	0.7	1.7	2.1	–	–	0.7	–	–	–	–	1.0	0.3
Boreal pine forests	4.8	1.1	2.1	0.5	–	1.1	2.1	0.5	3.2	–	–	1.6	–	–	–	0.5	2.1	0.5
Caucasian montane pine forests	2.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Balcanic pine forests	1.2	–	1.2	–	–	–	–	1.2	–	–	–	1.2	–	–	–	–	–	–
Oligotrophic broad-leaved forests	6.6	1.5	3.2	1.2	0.2	1.2	1.2	3.2	4.1	1.7	–	1.2	–	–	–	0.2	0.7	0.2
Meso-eutrophic broad-leaved forests	3.9	1.6	2.9	1.0	0.1	0.7	0.6	2.3	2.8	0.7	–	1.0	–	–	–	0.4	0.6	0.1
Thermophilous broad-leaved forests	4.1	1.3	2.8	1.0	0.2	0.6	1.0	2.5	3.0	0.9	0.2	1.2	–	–	–	0.2	0.6	0.2

Table 2 Continued.

European habitats	Total in the World	Forest edges	Forests	Woodlands	Sclerophyllous forests	Shrubland	Heathland	Grassland and pastures	Riparian habitats	Freshwater wetlands	Saltwater marshes	Coastal scrub, dunes and beaches	Coastal estuaries and mudflats	Mangrove	Deserts and desert scrub	Rock outcrops	Disturbed sites and damps	Bog edges
	Percentages of species invasive in different habitats world-wide																	
Hygro-thermophilous broad-leaved forests	5.6	2.8	4.7	0.9	–	0.9	1.9	1.9	4.7	0.9	–	1.9	–	–	–	–	–	–
Mediterranean sclerophyllous forests	7.0	1.3	4.0	1.6	0.8	1.1	3.0	4.8	4.8	1.3	0.3	3.2	–	–	–	0.8	–	0.3
Xerophytic coniferous woodlands	2.7	0.7	1.6	0.7	–	0.7	1.1	1.6	1.3	0.5	–	0.5	–	–	–	–	0.2	0.2
Subcontinental forest-steppes	5.5	1.4	3.4	1.0	–	–	0.7	3.4	3.8	1.7	–	1.0	–	–	–	0.3	0.3	–
Sub-Mediterranean forest-steppes	7.6	1.5	2.7	0.9	0.3	0.9	1.8	5.2	6.1	3.0	0.3	3.0	–	–	–	0.9	0.9	–
True and desert steppes	3.0	0.4	1.5	0.8	–	–	0.4	2.7	1.5	1.1	–	1.1	–	–	–	–	0.8	–
Mountain thorn-cushion scrub	0.9	–	–	–	–	0.4	–	0.4	–	–	–	0.4	–	–	0.4	–	0.4	–
Deserts	4.0	–	1.3	1.3	–	2.7	–	2.7	1.3	–	–	–	–	–	–	–	1.3	–
NW coastal sand-dunes	18.2	4.6	5.5	–	–	2.8	5.5	10.1	8.3	1.8	0.9	6.4	0.9	–	–	1.8	3.7	0.9
SE coastal sand-dunes	7.5	–	–	1.1	1.1	1.1	2.2	3.2	3.2	–	1.1	4.3	1.1	–	–	1.1	–	–
NW coastal halophilous vegetation	8.4	–	–	–	–	1.2	1.2	3.6	4.8	3.6	2.4	4.8	2.4	1.2	–	–	1.2	–
SE coastal halophilous vegetation	7.4	–	1.1	–	–	–	–	2.1	5.3	2.1	3.2	2.1	2.1	1.1	–	–	2.1	–
Inland halophilous vegetation	6.1	–	1.0	1.0	–	–	1.0	4.0	3.0	3.0	–	2.0	–	–	–	1.0	2.0	–
Aquatics, reeds and sedges	6.9	–	0.0	–	–	–	–	1.0	5.0	5.9	–	1.0	2.0	–	–	–	–	–

Table 2 Continued.

European habitats	Total in the World	Percentages of species invasive in different habitats world-wide																
		Forest edges	Forests	Woodlands	Sclerophyllous forests	Shrubland	Heathland	Grassland and pastures	Riparian habitats	Freshwater wetlands	Saltwater marshes	Coastal scrub, dunes and beaches	Coastal estuaries and mudflats	Mangrove	Deserts and desert scrub	Rock outcrops	Disturbed sites and damps	Bog edges
Bogs and mires	3.7	0.8	1.5	0.8	–	–	0.8	1.5	2.2	1.5	–	1.5	–	–	–	0.8	–	0.8
Alder carrs	13.7	2.4	4.8	1.6	–	0.8	0.8	2.4	12.1	8.9	–	3.2	–	–	–	–	0.8	–
Boreal alluvial forests	8.6	1.1	4.3	1.1	–	–	–	2.2	7.5	6.5	–	2.2	–	–	–	–	–	–
Nemoral alluvial forests	9.5	1.9	4.9	1.6	0.3	0.8	0.8	4.1	7.1	3.3	0.3	1.6	0.8	–	–	0.6	1.4	–
Mediterranean alluvial forests	14.5	4.2	7.8	1.8	0.6	1.2	1.8	6.0	13.3	4.2	0.6	2.4	–	–	–	0.6	3.6	–

European alluvial and coastal areas (Décamps *et al.*, 1988; Castillo & Moreno-Casasola, 1996). The introduction of species to the other parts of the World was facilitated by human activities serving as a transport vector (Hulme *et al.*, 2008). Therefore, species characteristic of strongly disturbed habitats have a higher chance of being carried long distances, either deliberately or unintentionally, than species in inland and upland habitats. As a consequence, species of alluvial and coastal habitats have a greater chance of becoming invaders even though they may not differ in their traits from those in other habitats.

Habitat preferences in the recipient area

Several studies have shown that many species invade alluvial and coastal habitats (e.g. Planty-Tabacchi *et al.*, 1996; Chytrý *et al.*, 2005, 2008; Maskell *et al.*, 2006; Pyšek *et al.*, 2010). These habitats occur in all macroclimatic regions, and their vegetation is azonal, determined mainly by local factors; therefore, their species composition is more similar across different climatic zones than that of zonal habitats. Local factors occurring in these habitats, namely frequent natural disturbances, also facilitate establishment of invaders (Richardson *et al.*, 2007). In our study, these habitats contained the highest numbers of invasive species of European origin. Moreover, our results suggest that alluvial habitats may act as nearly universal recipients of invasive species originating from various donor habitats. Still the highest percentage of invasive species in riparian habitats world-wide and shoreline ecoregion of North America originated from the corresponding alluvial forest and coastal habitats of Europe. We also demonstrate that alluvial habitats are not only highly invasible but also species native to these habitats tend to become successful invaders in a broad range of recipient habitats and ecoregions. Their success may be due to some of their traits evolved in alluvial habitats, namely their ability to establish in disturbed habitats and successfully compete with other species. They were reported as frequent in North American forests that have experienced a human-induced or natural disturbance (McDonald *et al.*, 2008).

Apart from alluvial and coastal habitats, we showed that North American ecoregions and habitats globally tend to be invaded by species from similar habitats as proposed by the habitat compatibility hypothesis (Rejmánek *et al.*, 2005). We identified relatively high percentages of European species that invade boreal forests and tundra of North America, although the North American boreal zone contains fewer invasive alien species than the temperate zone. In the boreal regions, most invaded sites are those disturbed by human activities, such as urban areas and land along pipelines (Cody *et al.*, 2000), roads and railways (Rose & Hermanutz, 2004). Thus, disturbance together with human-assisted propagule input support invasions of the otherwise unfavourable boreal landscapes, and these habitats contain a large proportion of invasive alien species of European origin. The surprisingly high number of European species invading the tundra ecoregion,

Table 3 Occurrences of European species in other regions of the World (Weber, 2003). Numbers are percentages of species invading particular recipient regions relative to the total number of native species in European donor habitats. European 'Polar deserts' and 'Greek evergreen scrub' are not included, because no species invasive in other continents were recorded there. Values > 2% (light grey) and > 5% (dark grey) are highlighted to visualize the pattern.

European habitats	Percentages of invasive species in different global regions															
	S Africa	Temperate Asia	Tropical Asia	Australia and New Zealand	Canada, Alaska	SE USA	W USA	Remaining USA	Chile, Argentina	Canary Isles, Madeira	S Atlantic Isl.	Azores	Mascarenes	Micronesia	Hawaii	Melanesia, Polynesia
Tundra	–	–	–	1.2	–	–	–	–	0.6	–	–	–	0.6	0.6	0.6	–
Alpine vegetation and rocks	–	–	–	0.6	–	–	–	–	0.3	–	–	–	0.3	0.3	0.3	–
Birch woodlands	–	–	–	5.8	0.7	0.7	–	0.7	0.7	–	–	–	0.7	0.7	0.7	–
Montane scrub and tall forbs	–	–	–	1.4	–	–	–	–	–	0.5	–	–	–	–	0.5	–
Subalpine coniferous scrub	–	–	–	9.5	–	–	4.1	1.4	–	–	–	–	–	–	–	–
Caucasian montane tall forbs	–	–	–	1.3	–	–	0.7	–	–	–	–	–	–	–	–	–
Boreal spruce forests	–	–	–	2.6	1.1	–	0.5	1.6	–	–	–	–	–	–	–	–
Montane fir forests	–	–	–	3.4	0.3	–	0.3	1.0	–	0.3	–	–	–	–	–	–
Boreal pine forests	–	–	–	3.2	1.6	0.5	–	2.7	–	–	–	–	–	–	0.5	–
Caucasian montane pine forests	–	–	–	9.8	–	–	2.4	1.2	1.2	–	–	–	2.4	1.2	3.7	–
Balcanic pine forests	–	–	–	1.2	–	1.2	–	–	–	–	–	–	–	–	–	–
Oligotrophic broad-leaved forests	0.1	–	–	3.3	0.4	0.1	–	–	–	–	–	–	–	–	–	–
Meso-eutrophic broad-leaved forests	0.2	–	–	3.2	0.4	0.3	0.7	0.9	0.2	–	–	–	0.2	0.2	0.3	0.2
Thermophilous broad-leaved forests	–	–	–	4.7	–	–	0.9	–	–	–	–	–	–	–	0.9	–
Hygro-thermophilous broad-leaved forests	0.8	0.3	0.3	6.7	0.3	0.3	1.9	0.8	0.3	–	0.3	–	0.3	–	1.1	0.3
Mediterranean sclerophyllous forests	0.5	–	–	2.2	0.2	0.2	0.2	0.2	0.2	–	–	–	–	–	0.5	–

Table 3 Continued.

European habitats	Percentages of invasive species in different global regions															
	S Africa	Temperate Asia	Tropical Asia	Australia and New Zealand	Canada, Alaska	SE USA	W USA	Remaining USA	Chile, Argentina	Canary Isles, Madeira	S Atlantic Isl.	Azores	Mascarenes	Micronesia	Hawaii	Melanesia, Polynesia
Xerophytic coniferous woodlands	0.3	–	–	3.1	2.1	–	0.3	2.4	0.3	0.3	–	0.3	–	0.3	0.7	–
Subcontinental forest-steppes	–	–	–	5.5	2.4	0.6	0.3	1.8	–	–	–	–	–	–	0.9	–
Sub-Mediterranean forest-steppes	–	–	0.4	1.5	1.1	0.4	0.8	0.8	–	–	–	–	–	–	0.8	–
True and desert steppes	–	–	0.4	0.9	–	–	0.0	–	–	–	–	–	–	–	–	–
Mountain thorn-cushion scrub	1.3	–	–	2.7	–	–	4.0	–	–	–	–	–	–	–	–	–
Deserts	2.8	0.9	0.9	14.7	1.8	0.9	2.8	2.8	–	–	0.9	–	0.9	–	0.9	–
NW coastal sand-dunes	2.2	–	–	7.5	–	–	2.2	–	–	–	–	–	–	–	2.2	–
SE coastal sand-dunes	1.2	–	–	4.8	2.4	1.2	3.6	1.2	–	–	–	–	–	–	–	–
NW coastal halophilous vegetation	1.1	–	–	8.4	2.1	2.1	2.1	2.1	–	–	–	–	–	–	–	–
SE coastal halophilous vegetation	–	–	–	4.0	1.0	0.0	–	2.0	–	–	–	–	–	–	–	–
Inland halophilous vegetation	–	–	–	5.0	3.0	2.0	1.0	2.0	–	–	–	–	–	–	–	–
Aquatics, reeds and sedges	–	–	–	2.2	1.5	0.8	–	1.5	–	–	–	–	–	–	–	–
Bogs and mires	1.6	–	–	10.5	4.9	1.6	1.6	3.2	–	–	–	–	–	–	–	0.8
Alder carrs	–	–	–	11.8	4.0	1.3	4.0	4.0	1.3	–	–	–	1.3	1.3	1.3	–
Boreal alluvial forests	1.1	–	–	6.5	4.3	1.1	–	3.2	–	–	–	–	–	–	–	–
Nemoral alluvial forests	0.8	–	–	6.8	3.0	0.8	1.6	2.5	–	0.3	–	–	–	–	0.3	0.3
Mediterranean alluvial forests	1.8	–	–	10.8	3.0	0.6	3.6	2.4	–	–	0.6	–	–	–	0.6	0.6

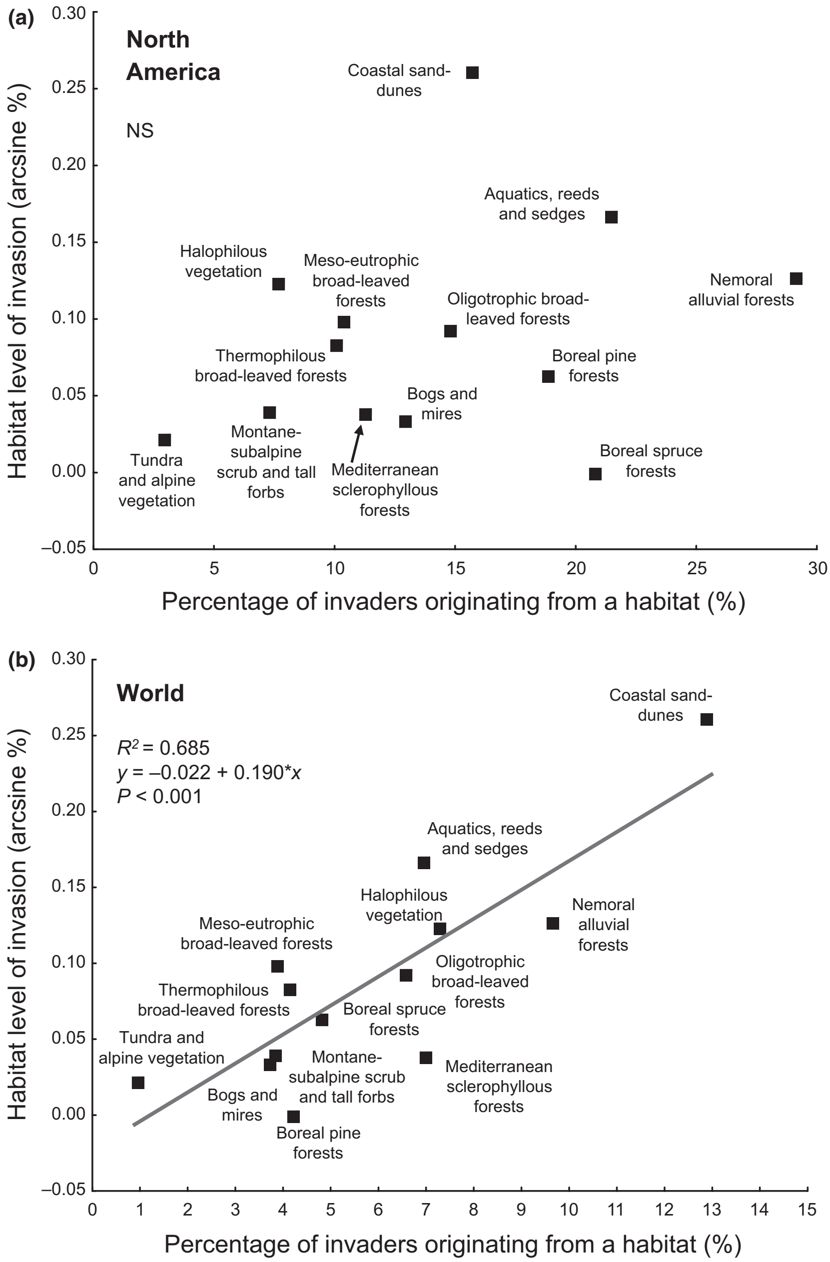

Figure 2 Major axis regression of the level of invasion of European habitats and percentages of species originating from the same habitats those are invasive alien in (a) North America and (b) in the World. Data on the level of invasion (Chytrý *et al.*, 2008, 2009) were arcsine-square-root transformed; NS non-significant.

found in our dataset, may represent an artefact of recording species occurrences rather than evidence that tundra is particularly vulnerable to invasion by species from Europe. In the Floristic Synthesis database, species occurrences were recorded for particular states or counties, and their boundaries were overlapped with the ecoregion boundaries to obtain species lists for ecoregions. Thus, all invasive species recoded in low-latitude states or counties with small areas of alpine tundra were assigned to the tundra ecoregion. Proper tundra belongs to the regions with a low level of invasion because of its harsh environment, limited resource fluctuation, low productivity and low human disturbance (Alpert *et al.*, 2000). Indeed, there are only scattered occurrences of alien invasive species reported for the wilderness areas of Alaska (Marler, 2000) and even when tundra habitats are re-seeded with alien species they usually fail to become established (Loope, 1992).

Do more invaded habitats provide more invasive species to other regions?

We hypothesized that European habitats that are most invaded by species originating outside Europe (Chytrý *et al.*, 2008, 2009) tend to be the main donors of species that are invasive on other continents, and conversely, European habitats containing few invasive species are a poor donor of species that are invasive elsewhere. We found support for this hypothesis in the case of European species invading globally, but not for those invading North America. In spite of this equivocal result, this hypothesis is worthy of further testing using better data on species occurrence in habitats in both source and recipient areas.

Data limitations and avenues for future research

We studied continental and global-scale patterns of invasive plant species in donor and recipient habitats. Such studies are dependent on the availability of high-quality data covering large areas, but the first comprehensive databases enabling such analyses become available only in the last decade. The European data we used were compiled from the Map of Natural Vegetation of Europe (Bohn *et al.*, 2004), which contains a unique overview of vegetation types and their species composition across the whole of Europe. This dataset can be used to identify patterns over large areas, but it has some limitations. First, the map only covers the potential natural vegetation. We are aware that semi-natural and human-made habitats usually contain higher numbers of invasive species than natural habitats. They may serve as an important source of potential invaders because of their association with human activity. However, there is no comprehensive overview of the species composition of human-made habitats at the European scale. In addition, the map gives no identification of the abundance of the different species, thus it is not possible to assess whether frequency of species in habitats affects their probability of becoming invasive on other continents. Moreover, the species listed for individual mapping units were selected by the authors of this map using expert judgement; they are incomplete records of the species composition, and the quality of these species lists varies among mapping units. Therefore, species lists cannot be used for assessing absolute numbers of species or of invasive species, which we solved by focusing the analysis on percentages of all the species that are invasive outside Europe.

Another problem is the match between habitat classifications used in Europe and on other continents. Owing to the long history of vegetation classification, there is a detailed syntaxonomical system in Europe (Rodwell *et al.*, 2002), but a lack of compatible systems for other continents. We used a habitat classification that reflects the main differences in the environmental conditions, climate, regional species pools and levels of disturbance of European vegetation and matched it to available data for North America and the World. We tried to achieve the best possible match with the data available, but especially in the case of ecoregions, the match cannot be perfect because each ecoregion contains many different habitat types. We believe that in the future, increasing availability of new comprehensive datasets of species habitat affinities over large areas will enable to carry out more accurate studies of the relationships between donor and recipient habitats as one of the determinants of plant invasions.

CONCLUSIONS

This study is one of the first attempts to assess the role of donor habitats in plant invasion. We demonstrate that donor habitats of invasive species do matter. There are distinct differences in the percentages of species that have originated in different European habitats among species invading other continents. Species from some European habitats, especially alluvial and coastal, are more likely to become invasive than others. This pattern is distinct enough to be worthy of incorporating into risk assessment systems for determining the invasive potential of European species. The results also give some support to the hypothesis that habitats that are characterized by frequent disturbances and fluctuating resources are not only vulnerable to invasion by alien species, but also a source of many invasive species. Thus, the level of invasion of these habitats seems to be influenced not only by habitat properties and propagule pressure per se but also by a relatively high number of species that are adapted to these habitats among all aliens.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Habitat types based on the Map of the Natural Vegetation of Europe.

Appendix S2 List of European species invasive in North America and globally.

Appendix S3 Absolute numbers of European native species non-invasive and invasive to North America or the World and donor habitat area.

Appendix S4 Crosswalk between the European habitats used and the EUNIS habitats.

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BIOSKETCH

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