

Naturalization of European plants on other continents: The role of donor habitats

Veronika Kalusová^{a,1}, Milan Chytrý^a, Mark van Kleunen^{b,c}, Ladislav Mucina^{d,e}, Wayne Dawson^f, Franz Essl^g, Holger Kreft^h, Jan Perglⁱ, Patrick Weigelt^h, Marten Winter^j, and Petr Pyšek^{i,k,l}

^aDepartment of Botany and Zoology, Masaryk University, 611 37 Brno, Czech Republic; ^bEcology Lab, Department of Biology, University of Konstanz, 78464 Konstanz, Germany; ^cZhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou 318000, China; ^dIluka Chair in Vegetation Science and Biogeography, School of Biological Sciences, The University of Western Australia, Crawley, WA 6009, Perth, Australia; ^eDepartment of Geography and Environmental Studies, Stellenbosch University, Matieland 7602, Stellenbosch, South Africa; ^fDepartment of Biosciences, Durham University, Durham, DH1 3LE, United Kingdom; ^gDivision of Conservation Biology, Vegetation and Landscape Ecology, University of Vienna, 1030 Vienna, Austria; ^hBiodiversity, Macroecology and Conservation Biogeography Group, Faculty of Forest Sciences and Forest Ecology, University of Göttingen, 37077 Göttingen, Germany; ⁱDepartment of Invasion Ecology, Institute of Botany, The Czech Academy of Sciences, 252 43 Průhonice, Czech Republic; ^jSynthesis Centre (sDiv), German Centre for Integrative Biodiversity Research (iDiv) Halle Jena Leipzig, 04103 Leipzig, Germany; ^kDepartment of Ecology, Faculty of Science, Charles University, 128 43 Praha 2, Czech Republic; and ^lCentre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Matieland 7602, South Africa

The success of European plant species as aliens worldwide is thought to reflect their association with human-disturbed environments. However, an explicit test including all human-made, seminatural and natural habitat types of Europe, and their contributions as donor habitats of naturalized species to the rest of the globe, has been missing. Here we combine two databases, the European Vegetation Checklist and the Global Naturalized Alien Flora, to assess how human influence in European habitats affects the probability of naturalization of their plant species on other continents. A total of 9,875 native European vascular plant species were assigned to 39 European habitat types; of these, 2,550 species have become naturalized somewhere in the world. Species that occur in both human-made habitats and seminatural or natural habitats in Europe have the highest probability of naturalization (64.7% and 64.5% of them have naturalized). Species associated only with human-made or seminatural habitats still have a significantly higher probability of becoming naturalized (41.7% and 28.6%, respectively) than species confined to natural habitats (19.4%). Species associated with arable land and human settlements were recorded as naturalized in the largest number of regions worldwide. Our findings highlight that plant species' association with native-range habitats disturbed by human activities, combined with broad habitat range, play an important role in shaping global patterns of plant invasions.

alien species | Europe | native range | naturalization | plant invasion

The role of species habitat association as a factor driving patterns of plant invasions has become a key question in invasion ecology research (1). Comparisons of levels of invasion across multiple different habitats have shown that habitats differ in the number and abundance of alien species (2–5), but analogous habitats in geographically distant regions are invaded to a similar degree (6). Therefore, the most and the least invaded habitats within different regions remain essentially the same (6, 7). The observed patterns suggest that general properties of habitats in the invaded range, such as resource fluctuations and disturbance (8, 9), similarly affect levels of invasion in different parts of the world. In addition, evolutionary adaptations acquired in habitats in the native range are also likely to be important for invasion success (10, 11). Compared with those in the invaded range, the native range habitats (i.e., the donor habitats of potential aliens) have been much less studied in the context of plant invasions (12, 13). However, recent studies indicate that native range habitats differ in the number of invasive species they donate to other regions (14, 15), and the size of habitat specific species pools in the native range affects the levels of invasion in corresponding habitats in the invaded range (16).

Once introduced to a new region, an alien species has to overcome several filters to survive in the local recipient habitats

(17, 18). To match ecologically, the species has to possess traits that enable it to tolerate the range of local environmental conditions present. Since these traits evolved in the native range habitats, conditions in these habitats act as an important factor affecting the invasion success of a species (11, 19–21). Previous studies comparing European natural and seminatural habitats as donors of alien plant species to other parts of the world (15, 16) showed that species with the highest potential for naturalization creating persistent self-sustaining populations in new regions (22) originated from habitats characterized by frequent and severe disturbances and high or fluctuating resource availability. Such conditions also promote the invasibility of habitats in invaded ranges (23). Species from such habitats often have higher probabilities to become successful aliens (10, 24) and are likely to constitute a large component of alien species pools (16). Invasion by alien species often begins in human-disturbed environments, where their propagules are unintentionally introduced or where cultivated species frequently escape (25, 26). Indeed, many early records of alien species come from human-made habitats (27), and these habitats tend to be more invaded than others (6, 28). While this is a well-known phenomenon, the role of human-made habitats as donors of alien plants has not been quantitatively assessed for the whole of Europe, with regard to other habitat types.

Significance

Understanding which species become successful aliens outside their native range is a fundamental question in ecology, as it informs efforts to mitigate ecological and economic losses from biological invasions. For alien plants of European origin, the association with human-disturbed environments is suggested as a key factor for their establishment success following introduction to other regions, especially to similarly disturbed human-made habitats. By combining a comprehensive list of European habitats and their species composition with a database of plant naturalization records worldwide, we showed that a broad habitat range together with human-induced disturbance experienced in native-range habitats can increase a species' chance of becoming naturalized in other parts of the world.

Author contributions: V.K., M.C., and P.P. designed research; V.K. performed research; V.K. and M.v.K. analyzed data; and V.K., M.C., M.v.K., L.M., W.D., F.E., H.K., J.P., P.W., M.W., and P.P. wrote the paper.

¹To whom correspondence should be addressed. Email: kalveron@tiscali.cz.

To test whether European habitats influenced by human induced disturbances are the major donors of naturalized alien plants worldwide, we combined two recently compiled extensive datasets of unprecedented comprehensiveness: (i) the standardized classification of European vegetation (EuroVegChecklist; ref. 29), which contains the most complete lists available of species associated with different vegetation types in Europe, and (ii) the Global Naturalized Alien Flora (GloNAF) database, the most complete global inventory of naturalized floras (30). We focused on Europe as the source continent because it has donated disproportionately more species to the global naturalized alien flora than expected from the size of its native flora (30). To relate the naturalization probability of European native species to their association with particular habitats in Europe, we grouped European vegetation classes defined in EuroVegChecklist into 39 habitat types. In parallel, vegetation classes were assigned to five naturalness categories: human made (strongly human influenced, $n = 8$ classes), seminatural (moderately human influenced, $n = 10$), natural (not conditioned by human influence, $n = 71$), human made/natural ($n = 6$), and seminatural/natural ($n = 11$). To quantify the naturalization frequency of European native species, we counted the number of regions where each species was recorded as naturalized in GloNAF, also including regions outside their native ranges that were located in other parts of Europe.

Specifically, we asked which European habitats and naturalness categories (i) provide the highest number of species that naturalized outside their native ranges and (ii) donate species that have become established in the highest numbers of the world's regions outside their native ranges.

Results

Habitat Naturalness Categories Affect Species' Naturalization Probability. Among the 9,875 species in our dataset, the ones associated with European habitats classified to the human made and seminatural categories had a significantly higher probability to naturalize outside their native range, compared with the natural habitat category [see generalized linear model (GLM) model; Table 1]. Among species occurring only in habitats of one naturalness category, those from the human made category were most likely to naturalize somewhere (41.7% of species in the cumulative species list of human made habitats), followed by those from the seminatural category (28.6%), while species from the natural habitat category were least likely to naturalize (19.4%). Moreover, species occurring in both human made and natural or human made/natural habitat categories, or in both human made and seminatural habitat categories (i.e., species with a broader habitat range), were even more likely to naturalize than those confined to the human made category only. Of the species found in both

Table 1. Results of a GLM (Bernoulli distribution, $R^2 = 0.156$) examining the effects of the main habitat naturalness categories (human-made, seminatural, natural) and their two-way interactions on global naturalization (yes, naturalized in at least one region outside the native range; no, never naturalized outside the native range) of 9,875 native European species

Model term	Estimate \pm SE	P
Intercept	1.220 \pm 0.027	<0.001
Human made	0.496 \pm 0.060	<0.001
Seminatural	0.425 \pm 0.051	<0.001
Natural	2.599 \pm 0.140	<0.001
Human made:natural	1.203 \pm 0.271	<0.001
Human made:seminatural	1.129 \pm 0.121	<0.001
Seminatural:natural	0.057 \pm 0.258	ns

All explanatory variables were centered to their means to facilitate comparison of model estimates; ns, not significant.

human made and seminatural or natural habitat categories, 64.7% and 64.5% have naturalized (Table 2).

European Habitats As Donors of Naturalized Species. When comparing particular habitats, the highest numbers of naturalized species came from anthropogenic herbaceous vegetation and temperate dry and mesic grasslands (Fig. S1). However, when the size of the total species pool of a habitat was accounted for, human made habitats, including arable land and alien dominated forests, had the highest proportion of species naturalized in other regions. These habitats were followed by perennial ruderal vegetation, a habitat containing both human made and natural vegetation types, and anthropogenic herbaceous vegetation (Fig. 1A). Among seminatural and seminatural/natural habitats, mesic grasslands and pastures, and dry sand and rock outcrop grasslands showed the highest proportions of species naturalized in other regions (Fig. 1A). The few natural habitats that had high proportions of naturalized species included riparian forests and riverine scrub, and hemiboreal mixed and temperate mesic deciduous forests. Of nonforest natural habitats, freshwater marshes, sea grass beds, and coastal sand vegetation had the highest proportions. In contrast, natural habitats with the lowest proportions of species that have naturalized were semideserts, various types of coniferous and evergreen forests, and scrub, arcto alpine grasslands, bogs, and mires (Fig. 1A).

Naturalization Frequency of European Species. The naturalization frequency of European species outside of their native range was significantly higher for those species associated with habitats of the human made category (Table 3); on average, they were recorded in the highest number of regions outside their native range compared with other habitat categories (Table 2). In contrast, the association of European species with habitats of the natural category significantly decreased their naturalization frequency (Table 3). Other habitat categories or their combinations showed no significant effect.

Detailed comparison of particular habitats showed that species associated with anthropogenic herbaceous vegetation had the highest naturalization frequency; collectively, they were recorded as naturalized in 83.8% of the GloNAF regions (Fig. 1B). The second most represented were weed species from the arable land that were collectively recorded as naturalized in 73.6% of the regions, followed by species of various types of seminatural grasslands collectively recorded as naturalized in 60.4% of the regions. Species of human made/natural perennial ruderal vegetation have also naturalized in many regions (45.6% of the regions). Species of riparian forests and riverine scrub had the highest collective naturalization frequency among natural habitats (55.6% of the regions). In contrast, species from stressful natural habitats with nutrient poor soils and extremely low or high moisture conditions (29), such as bogs, waterlogged, and dry for ests and scrub (Fig. 1B), have naturalized in the lowest numbers of regions. Species capable of naturalization in the largest numbers of regions originated mainly from European anthropogenic herbaceous vegetation, arable land, or both these habitats and seminatural or natural grasslands (Table S1).

Discussion

Our study provides clear evidence that European species occurring in both human made and other habitat categories are more likely to naturalize in new regions compared with species confined to either human made or seminatural habitat categories alone. However, species of strongly human influenced habitats in the human made category or moderately human disturbed habitats in the seminatural category are also highly likely to naturalize outside their native range. Because Europe is one of the main donors of alien plant species to other parts of the world (19, 30), the association of European species with human activities in their native range may be a major determinant of their

Table 2. Total numbers of native European species assigned to the five categories of habitat naturalness and their combinations, numbers and percentages of those species that have naturalized in at least one region, and mean number \pm SD of regions in which species have naturalized

Habitat naturalness categories and their combination	Total number of native species	Number of native species that have naturalized	Percentage of native species that have naturalized	Mean number of regions where species have naturalized \pm SD
Human made	2,168	904	41.7	43.3 \pm 55.3
Seminatural	3,980	1,138	28.6	22.6 \pm 36.2
Natural	8,853	1,713	19.4	19.4 \pm 31.3
Human made/natural including human made and natural combination*	569	369	64.8	34.6 \pm 46.0
Human made and seminatural combination [†]	344	222	64.5	38.2 \pm 49.9
Seminatural/natural including seminatural and natural combination	3,644	808	22.2	20.8 \pm 33.4

*Species can occur both in vegetation classes that are specifically human made and in vegetation classes that are specifically seminatural, or in vegetation classes that are categorized as human made/natural.

[†]Note that there are no vegetation classes than can be categorized as being human made/seminatural.

success as aliens on other continents (19, 31–33). Our study is among the first to empirically support this long standing but so far untested hypothesis.

Species of Human-Made and Seminatural Habitats Are More Likely to Naturalize. The association of species with human made and seminatural habitats in their native range favors naturalization elsewhere, as indicated by our results. Species associated with these habitats are more likely to naturalize than those confined to natural habitats in their native range. Species of the former habitat categories thus appear to be preadapted to establish populations at human disturbed sites created by human agency around the globe. One possible explanation is that the long term association of species with human disturbed environments in Europe led to the evolution of suitable traits that facilitate establishment in similarly human influenced habitats of the invaded range (19, 33). An alternative explanation could be that human induced disturbance sets strong filters for species arriving in human made habitats of Europe from the regional species pool and thus only those with suitable traits can establish (34, 35). The latter mechanism does not require the evolution of necessary traits in human made habitats; instead, it assumes selection of preadapted species with such traits from the regional flora in the native range.

Many species of European anthropogenic or weed vegetation are, within Grime's CSR (competitive, stress tolerant, and ruderal) life strategy framework (36), R strategists that can withstand frequent disturbances by having persistent seed banks and fast regeneration. They are likely to require recipient habitats with regular disturbances that decrease competition with established native plants. Human made and natural perennial ruderal vegetation in Europe mainly consists of herbs with C or CR strategies with vegetative reproduction that enables survival under moderate levels of disturbance (37, 38), but these species are also successful competitors in natural habitats. Many of them are effectively dispersed by humans or wind, which supports their spread outside their native ranges (37, 39). Species of human made habitats are also associated with naturally nutrient rich or anthropogenically nutrient enriched sites (40). The ability to utilize high resource levels for fast growth is considered typical of successful alien species (18, 41).

The greater naturalization frequency of European species associated with human made habitats may further be attributed to the fact that species frequently occurring in densely human populated areas in their native range are more likely to be introduced to new regions (12, 41). This applies to species restricted to human made habitats and the ones that also occur in more natural habitats, but the latter are more likely to be dispersed by humans because they tend to be more widespread in their native range (42). Also, species restricted to human made habitats that often occur in the vicinity of

transportation systems or that are directly utilized by humans have a high chance of human assisted long distance dispersal (43, 44). It is likely that the observed pattern of donor habitats results from a combination of species traits gained or filtered in strongly or moderately human influenced habitats, and a higher introduction rate leading to greater propagule pressure. However, understanding their relative contributions requires further research.

Many species of various types of European seminatural mesic and dry grasslands were identified as naturalized in many regions worldwide. These European grasslands have been used by humans for a long time (45), and their species pools are thus adapted to human disturbances, which may facilitate the initial phase of spread in strongly or moderately human influenced habitats in new regions. While some species of dry grasslands were introduced as contaminants of seeds and crops (44), others were introduced intentionally to improve pastures (45) and were grown at high population densities on grazing land, which could unintentionally have increased the propagule pressure and facilitated escape from cultivation and subsequent naturalization (46). However, higher naturalization frequency is not associated with the seminatural category as a whole. Other seminatural habitats such as mires or heathlands that are confined to sparsely populated, high elevation areas decrease the chance that species are picked up and transported, thus reducing the contribution of naturalized species from this habitat category.

Species Confined to Natural Habitats in Their Native Range Are Less Likely to Naturalize. Compared with human made and seminatural habitats, natural habitats are generally moderate to poor donors of naturalized species. However, many naturalized alien species were also donated by habitats that frequently experience natural disturbance, by nutrient rich and highly productive riparian forests and riverine scrub, and by eutrophic forests. This indicates the importance of alien species adaptation to conditions induced by natural disturbance processes that are similar to those in human made habitats in new regions. Indeed, disturbances and nutrient enrichment factors selecting for species that are able to successfully establish in new regions together with increased probability of species transport have been previously suggested as causes of high numbers of alien species coming from European riparian forests (14–16). Coastal habitats including sea grass beds and coastal dunes have also been shown to be important donors of alien species that can profit from adaptation to frequent natural disturbances in dynamic environments (15). Moreover, these habitats are usually found in lowlands and close to coastal regions that are more densely populated, where increased opportunities for effective species transport can play a role (15, 16).



Fig. 1. A comparison of 39 European habitats as donors of native plant species that have naturalized outside the native range. (A) Proportion of species naturalized in any of the world's regions studied and (B) naturalization frequency as the number of world's regions where any of the species are recorded as naturalized are shown. Habitat naturalness categories are indicated by different filling patterns.

In contrast, poor donors of naturalized alien species include natural habitats with nutrient poor soils and stressful site conditions at both ends of the moisture gradient, such as bogs and bog woodlands, mires, saline vegetation, heathlands, xeric scrub, and semideserts. This is also in accordance with previous findings that only few invaders are adapted to stressful conditions (47) indicating low importance of S strategy for plant naturalization compared with R and C or CR strategies. Some of these habitats are small and isolated, often at high elevations, while others cover vast areas. Nevertheless, in all of them the human influence is negligible because of low human population densities in these areas. Therefore, it is difficult to distinguish between the effect of adaptation to stressful conditions that prevent establishment in human disturbed productive habitats (8, 47) and a lower probability of species introduction to new regions.

Species Occurring in Multiple Habitat Categories Are More Likely to Naturalize. We show that European species associated with both human made habitats and natural or seminatural habitats in their native range are more likely to naturalize outside their native range than species associated exclusively with human made or seminatural habitats. According to the concept of anthropogenically induced adaptation to invade (48), two types of adaptation to human disturbances can evolve in the native range. First, habitat generalists that adapted to both natural and human influenced habitats in the native range that is, having broad habitat ranges can naturalize

more easily in the new region regardless of how the invaded habitats are influenced by humans. Second, habitat specialists that are adapted to strongly human influenced habitats (48) are less likely to invade habitats that are little affected by human activities. Our results indicate that high invasion success is to be expected for those generalist species (12, 49) with multiple native range habitats

Table 3. Effects of the main habitat naturalness categories (human-made, seminatural, natural) and their two-way interactions on the number of regions worldwide in which native European species associated with the given naturalness habitat category have naturalized (linear model; $R^2 = 0.099$)

Model term	Estimate ± SE	P
Intercept	2.167 ± 0.043	<0.001
Human made	0.793 ± 0.092	<0.001
Seminatural	0.036 ± 0.080	ns
Natural	0.393 ± 0.106	<0.001
Human made:natural	0.247 ± 0.243	ns
Human made:seminatural	0.166 ± 0.181	ns
Seminatural:natural	0.476 ± 0.249	ns

Numbers of regions were ln transformed, and species that have not naturalized anywhere were excluded. All explanatory variables were centered to their means to facilitate interpretation of model estimates; ns, not significant.

including those that are human made. Indeed, the importance of a broad native habitat range has been reported for naturalization of Central European plants in North America (11). Species that have a broad habitat range are likely to tolerate a broad range of conditions, both biotic and abiotic, and may develop better competitive abilities through interactions with various species (50). Thus, naturalized species have probably benefited from a broad habitat range as well as the association with human made or seminatural habitats, making them preadapted for establishment in human influenced habitats outside their native ranges. Although habitats are complex units defined by many underlying factors, those that are the most important donors of naturalized species share one property, which is frequent disturbance, often human induced. Other factors that could influence naturalization probability are mentioned in *SI Discussion*.

Species of European Human-Made Habitats Are Able to Naturalize in Many Regions. Our results show that alien species associated with human made habitats in Europe invaded the majority of regions included in the GloNAF database (up to 84% of the regions for species of anthropogenic herbaceous vegetation). The strong human alteration of environmental conditions renders human made habitats similar in many respects across the world, despite their different biogeographical locations (51). High levels of invasion in human made habitats (6) can be caused by larger alien species pools or by a higher chance for species to be transported to new regions (49). More incoming species results in higher colonization pressure in such habitats (52), and species that successfully establish increase their abundance and produce more propagules, facilitating their further spread (53).

We predicted that the specific nature of human made habitats contributes to a wider geographic range of alien species adapted to them. Indeed, we found that species of human made habitats are naturalized in many regions worldwide. However, it is important to note that the number of regions is only an approximation of the invaded range size, because GloNAF regions differ in their sizes, and it remains unclear to what extent particular regions have been colonized. Also, we have no information on the representation of different habitats in invaded regions. If the origin of species in strongly human influenced habitats facilitates their establishment in similarly disturbed habitats elsewhere, then a higher abundance of those habitats in the invaded region can increase the probability that species are recorded there (see also the note on perennial ruderal vegetation in *SI Discussion*). Nonetheless, the number of regions in which a species was recorded as naturalized is the best proxy of naturalization frequency available at a global scale and strongly correlates with the cumulative area of these regions (54).

Conclusions

Our study represents, so far, the most comprehensive analysis of the role of native range habitats on worldwide naturalization probability and extent of alien plants of European origin. European species that occur in human made and other habitats at the same time, or in human made and seminatural habitats alone, have higher probabilities to naturalize outside Europe than species confined to natural habitats only. Therefore, broad habitat range and association with disturbed, human influenced habitats in the native range belong among important factors contributing to species' naturalization success. Further work is needed to gain a more detailed insight into the effect of donor habitats on the various invasion outcomes of species at the global scale.

Materials and Methods

Species and Habitat Data. Our dataset included European habitat types and a list of their associated vascular plant species, derived from the hierarchical vegetation classification system EuroVegChecklist (version October 2014; ref. 29). In total, the list (*Dataset S1*) comprised 9,875 native European species, a significant proportion of the total European native flora (c. 12,500 species; ref. 55). For nomenclature standardization, see *SI Methods*. Phytosociological classes of European vegetation recognized in the EuroVegChecklist were hierarchically grouped into (i) 39 habitat types, also called habitats in this paper, and (ii) five habitat categories according to the degree of naturalness, including (a) human made habitats, (b) seminatural, and (c) natural habitats. However, because some phytosociological classes can develop at both natural and human influenced sites, we defined two other categories: (d) human made/natural habitats and (e) seminatural/natural habitats. The merging criteria are described in *SI Methods*, and a list of vegetation classes assigned to habitats and categories is available in *Table S2*.

Within the species list, 2,250 species were identified to be naturalized outside their native range, irrespective of whether it was inside or outside of Europe, using the GloNAF database (version 1.1; refs. 30 and 54). Naturalized aliens included those species that create self sustaining populations in a given region without human intervention and recruit freely but do not necessarily spread over large areas (22). Only naturalized species known as neophytes were considered that is, those introduced outside their native range after AD 1500 (54). The number of regions worldwide in which each species was recorded as naturalized was obtained from GloNAF (843 regions in total; see *SI Methods* for details).

Data Analysis. To test whether species from the habitat naturalness categories differed in their probability of naturalization somewhere in the world (irrespective of the number of regions where they are naturalized), we applied a GLM with the Bernoulli distribution. Because some species occur in two habitat categories at the same time, we converted the habitat categories into three dummy variables, each with two levels (56): human made, seminatural, and natural. Species from combined habitat categories (human made/natural or seminatural/natural) were assigned to the two corresponding habitat categories (for coding, see *SI Methods*). As main effects, we included three dummy variables: human made (yes, no), seminatural (yes, no), and natural (yes, no). To test whether the effect of a habitat type on naturalization of a species also depends on the species occurrence in another habitat type, we also included all two way interactions between the dummy variables (human made:natural, human made:seminatural, and seminatural:natural). We also tested the effect of species association with main habitat naturalness categories and their two way interactions in Europe on the number of GloNAF regions in which the species have naturalized that is, naturalization frequency. Numbers of regions were \ln transformed. To facilitate interpretation of the model estimates, each of the dummy variables was centered to its mean value (56). Total variation explained by the model was calculated following Nakagawa and Schielzeth (57). The analyses were performed using the `glm` function in R (version 3.1.2; ref. 58).

At the scale of individual habitats, we calculated the proportion of species native to Europe that have become naturalized somewhere, relative to the number of all species assigned to the given habitat to account for the size of the habitat species pool. To compare the frequency of naturalization, we also calculated, for each habitat, the total number of regions where at least one representative of that habitat has been reported as naturalized.

ACKNOWLEDGMENTS. We highly appreciate the critical comments of three anonymous reviewers, who helped to improve the manuscript. V.K., M.C., J.P., and P.P. were supported by the Czech Science Foundation (Centre of Excellence Pladias Grant 14 36079G); J.P. and P.P. by long term research development project RVO 67985939 and a Praemium Academiae award from The Czech Academy of Sciences; M.v.K. by Deutsche Forschungsgemeinschaft (DFG) Grant KL 1866/9 1; L.M. by the Iluka Chair established by an agreement between Iluka Resources Ltd (Pty) and The University of Western Australia; F.E. by the Austrian Science Fund (FWF) Grant I2096 B16; and M.W. by DFG Grant FZT 118.

1. Pyšek P, Chytrý M (2014) Habitat invasion research: Where vegetation science and invasion ecology meet. *J Veg Sci* 25:1181–1187.
2. Stohlgren TJ, Barnett D, Flather C, Kartesz J, Peterjohn B (2005) Plant species invasions along the latitudinal gradient in the United States. *Ecology* 86:2298–2309.
3. Chytrý M, Pyšek P, Tichý L, Knollová I, Danihelka J (2005) Invasions by alien plants in the Czech Republic: A quantitative assessment across habitats. *Preslia* 77:339–354.
4. Vilà M, Pino J, Font X (2007) Regional assessment of plant invasions across different habitat types. *J Veg Sci* 18:35–42.

5. Medvecká J, Jarolimek I, Senko D, Svitok M (2014) Fifty years of plant invasion dynamics in Slovakia along 2,500 m altitudinal gradient. *Biol Invasions* 16:1627–1638.
6. Chytrý M, et al. (2008) Habitat invasions by alien plants: A quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. *J Appl Ecol* 45: 448–458.
7. Kalusová V, Chytrý M, Peet RK, Wentworth TR (2015) Intercontinental comparison of habitat levels of invasion between temperate North America and Europe. *Ecology* 96: 3363–3373.

8. Alpert P, Bone E, Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspect Plant Ecol Evol Syst* 3:52–66.
9. Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: A general theory of invasibility. *J Ecol* 88:528–534.
10. Hejda M, Chytrý M, Pergl J, Pyšek P (2015) Native-range habitats of invasive plants: Are they similar to invaded-range habitats and do they differ according to the geographical direction of invasion? *Divers Distrib* 21:312–321.
11. Pyšek P, et al. (2015) Naturalization of central European plants in North America: Species traits, habitats, propagule pressure, residence time. *Ecology* 96:762–774.
12. Prinzing A, Durka W, Klotz S, Brandl R (2002) Which species become aliens? *Evol Ecol Res* 4:385–405.
13. Hierro JL, Maron JL, Callaway RM (2005) A biogeographical approach to plant invasions: The importance of studying exotics in their introduced and native range. *J Ecol* 93:5–15.
14. Hejda M, et al. (2009) Invasion success of alien plants: Do habitat affinities in the native distribution range matter? *Global Ecol Biogeogr* 18:372–382.
15. Kalusová V, Chytrý M, Kartesz JT, Nishino M, Pyšek P (2013) Where do they come from and where do they go? European natural habitats as donors of invasive alien plants globally. *Divers Distrib* 19:199–214.
16. Kalusová V, Chytrý M, Peet RK, Wentworth TR (2014) Alien species pool influences the level of habitat invasion in intercontinental exchange of alien plants. *Global Ecol Biogeogr* 23:1366–1375.
17. Blackburn TM, et al. (2011) A proposed unified framework for biological invasions. *Trends Ecol Evol* 26:333–339.
18. Knapp S, Kühn I (2012) Origin matters: Widely distributed native and non-native species benefit from different functional traits. *Ecol Lett* 15:696–703.
19. di Castri F (1989) History of biological invasions with special emphasis on the Old World. *Biological Invasions: A Global Perspective*, eds Drake JA, et al. (John Wiley, Chichester, UK), pp 1–30.
20. Bossdorf O, Lipowsky A, Prati D (2008) Selection of preadapted populations allowed *Senecio inaequidens* to invade Central Europe. *Divers Distrib* 14:676–685.
21. Lee CE, Gelembiuk GW (2008) Evolutionary origins of invasive populations. *Evol Appl* 1:427–448.
22. Richardson DM, et al. (2000) Naturalization and invasion of alien plants: Concepts and definitions. *Divers Distrib* 6:93–107.
23. Chytrý M, et al. (2008) Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology* 89:1541–1553.
24. Richardson DM, Pyšek P (2006) Plant invasions: Merging the concepts of species invasiveness and community invasibility. *Prog Phys Geogr* 30:409–431.
25. Pyšek P (1998) Alien and native species in Central European urban floras: A quantitative comparison. *J Biogeogr* 25:155–163.
26. Hulme PE (2005) Nursery crimes: Agriculture as victim and perpetrator in the spread of invasive species. *Crop Science and Technology, Proceedings of an International Congress Held in Glasgow, 31st October - 2nd November 2005* (British Crop Protection Council, Alton, UK), pp 733–740.
27. Botham MS, et al. (2009) Do urban areas act as foci for the spread of alien plant species? An assessment of temporal trends in the UK. *Divers Distrib* 15:338–345.
28. Lambdon P, et al. (2008) Alien flora of Europe: Species diversity, temporal trends, geographical patterns and research needs. *Preslia* 80:101–149.
29. Mucina L, et al. (2016) Vegetation of Europe: Hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. *Appl Veg Sci* 19:3–264.
30. van Kleunen M, et al. (2015) Global exchange and accumulation of non-native plants. *Nature* 525:100–103.
31. Crosby AW (1986) *Ecological Imperialism: The Biological Expansion of Europe, 900–1900* (Cambridge Univ Press, Cambridge, UK).
32. Pyšek P, Prach K, Mandák B (1998) Invasions of alien plants into habitats of Central European landscape: An historical pattern. *Plant Invasions: Ecological Mechanisms and Human Responses*, eds Starfinger U, Edwards K, Kowarik I, Williamson M (Backhuys, Leiden, The Netherlands), pp 23–32.
33. La Sorte FA, Pyšek P (2009) Extra-regional residence time as a correlate of plant invasiveness: European archaeophytes in North America. *Ecology* 90:2589–2597.
34. Knapp S, Kühn I, Schweiger O, Klotz S (2008) Urbanization causes shifts in species' trait state frequencies. *Preslia* 80:375–388.
35. Ricotta C, Di Nepi M, Guglietta D, Celesti-Grapo L (2008) Exploring taxonomic filtering in urban environments. *J Veg Sci* 19:229–238.
36. Grime JP (1979) *Plant Strategies and Vegetation Processes* (John Wiley, Chichester, UK).
37. Lososová Z, et al. (2006) Patterns of plant traits in annual vegetation of man-made habitats in central Europe. *Perspect Plant Ecol Evol Syst* 8:69–81.
38. Wittig R (2005) The origin and development of the urban flora of Central Europe. *Urban Ecosyst* 7:323–339.
39. Prach K, Pyšek P (1999) How do species dominating in succession differ from the others? *J Veg Sci* 10:383–392.
40. Williams NSG, Hahs AK, Vesik PA (2015) Urbanisation, plant traits and the composition of urban floras. *Perspect Plant Ecol Evol Syst* 17:78–86.
41. Dostál P, Dawson W, van Kleunen M, Keser LH, Fischer M (2012) Central European plant species from more productive habitats are more invasive at a global scale. *Glob Ecol Biogeogr* 22:64–72.
42. Pyšek P, Richardson DM, Williamson M (2004) Predicting and explaining plant invasions through analysis of source area floras: Some critical consideration. *Divers Distrib* 10:179–187.
43. Booth BD, Murphy SD, Swanton CJ (2003) *Plant Invasions: Weed Ecology in Natural and Agricultural Systems* (CABI Publishing, Wallingford, UK).
44. Hulme PE, et al. (2008) Grasping at the routes of biological invasions: A framework for integrating pathways into policy. *J Appl Ecol* 45:403–414.
45. Poschold P, Baumann A, Karlik P (2010) Origin and development of grasslands in central Europe. *Grasslands in Europe of High Nature Value*, eds Veen P, Jefferson R, de Smidt J, van der Straaten J (KNNV Publishing, Zeist, The Netherlands), pp 15–25.
46. Driscoll DA, et al. (2014) New pasture plants intensify invasive species risk. *Proc Natl Acad Sci USA* 111:16622–16627.
47. te Beest M, Elschot K, Olf H, Etienne RS (2013) Invasion success in a marginal habitat: An experimental test of competitive ability and drought tolerance in *Chromolaena odorata*. *PLoS One* 8:e68274.
48. Hufbauer RA, et al. (2012) Anthropogenically induced adaptation to invade (AIAI): Contemporary adaptation to human-altered habitats within the native range can promote invasions. *Evol Appl* 5:89–101.
49. Pyšek P, et al. (2009) The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. *Divers Distrib* 15: 891–903.
50. Sax DF, Brown JH (2000) The paradox of invasion. *Glob Ecol Biogeogr* 9:363–371.
51. Kowarik I (2011) Novel urban ecosystems, biodiversity, and conservation. *Environ Pollut* 159:1974–1983.
52. Lockwood JL, Cassey P, Blackburn TM (2009) The more you introduce the more you get: The role of colonization pressure and propagule pressure in invasion ecology. *Divers Distrib* 15:904–910.
53. Williamson M (1996) *Biological Invasions* (Chapman & Hall, London).
54. Pyšek P, et al. (2017) Naturalized alien flora of the world: Species diversity, taxonomic and phylogenetic patterns, geographic distribution and global hotspots of plant invasion. *Preslia* 89:203–274.
55. Tutin TG, et al. (1964–1980) *Flora Europaea* (Cambridge Univ Press, Cambridge, UK), Vol 1–4.
56. Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. *Methods Ecol Evol* 1:103–113.
57. Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol Evol* 4:133–142.
58. R Core Team (2014) *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna), Version 3.3.2.
59. Wagner V, et al. (2017) Alien plant invasion in European woodlands. *Divers Distrib* 23: 969–981.
60. Cayuela L, Granzow-de la Cerda Í, Albuquerque FS, Golicher DJ (2012) Taxonstand: An R package for species names standardisation in vegetation databases. *Methods Ecol Evol* 3:1078–1083.
61. Davies CE, Moss D (2003) *EUNIS Habitat Classification, August 2003* (European Topic Centre on Nature Protection and Biodiversity, Paris).
62. Janssen JAM, et al. (2016) *European Red List of Habitats: Part 2. Terrestrial and Freshwater Habitats* (Publication Office of the European Union, Luxembourg).
63. Bohn U, et al. (2004) *Interactive CD-ROM to the Map of the Natural Vegetation of Europe. Scale 1:2 500 000. Explanatory Text, Legends, Maps* (Landwirtschaftsverlag, Münster, Germany).