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

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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.

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 disproportionally 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

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. 1*A*). 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. 1*A*). 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. 1*A*).

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. 1*B*). 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 forests and scrub (Fig. 1*B*), 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 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 ± SE	P
Intercept	−1.220 ± 0.027	<0.001
Human-made	0.496 ± 0.060	<0.001
Seminatural	0.425 ± 0.051	<0.001
Natural	−2.599 ± 0.140	<0.001
Human-made:natural	1.203 ± 0.271	<0.001
Human-made:seminatural	1.129 ± 0.121	<0.001
Seminatural:natural	−0.057 ± 0.258	ns

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

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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 ± 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 ± SD
Human-made	2,168	904	41.7	43.3 ± 55.3
Seminatural	3,980	1,138	28.6	22.6 ± 36.2
Natural	8,853	1,713	19.4	19.4 ± 31.3
Human-made/natural including human-made and natural combination*	569	369	64.8	34.6 ± 46.0
Human-made and seminatural combination[†]	344	222	64.5	38.2 ± 49.9
Seminatural/natural including seminatural and natural combination	3,644	808	22.2	20.8 ± 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).

A Proportion of species naturalized somewhere

Arable land
Alien-dominated forests and scrub
Perennial ruderal vegetation on mesic soils
Anthropogenic herbaceous vegetation
Freshwater and brackish marshes
Riparian and riverine forests and scrub
Annual semi-terrestrial vegetation
Mesic grasslands and pastures
Inland sand and rock-outcrop grasslands
Sea-grass beds
Hemiboreal birch-pine forests
Mesic broad-leaved deciduous forests
Coastal sand vegetation
Rocks, screes and walls
Mediterranean annual grasslands
Thermophilous broad-leaved deciduous forests
Aquatic vegetation
Alder carrs
Oligotrophic broad-leaved decidous forests
Boreo-continental coniferous forests
Mediterranean dry grasslands
Mediterranean montane xeric woodlands and scrub
Inland saline vegetation
Dry temperate grasslands
Subalpine tall-herb vegetation and scrub
Mediterranean heathlands
Deciduous scrub
Coastal saline vegetation
Mediterranean sclerophyllous forests
Bogs and bog woodlands
Temperate heathlands
Mires, fens and springs
Dry coniferous forests
Laurophyllous forests
Oromediterranean montane grasslands and scrub
Salt-sprayed coastal cliffs
Arctoalpine to subalpine grasslands
Mediterranean garrigue and phrygana
Semi-desert and desert scrub

B Total number of regions where species have naturalized

Anthropogenic herbaceous vegetation
Arable land
Mesic grasslands and pastures
Annual semi-terrestrial vegetation
Mediterranean dry grasslands
Riparian and riverine forests and scrub
Inland sand and rock-outcrop grasslands
Dry temperate grasslands
Coastal sand vegetation
Mediterranean annual grasslands
Perennial ruderal vegetation on mesic soils
Salt-sprayed coastal cliffs
Freshwater and brackish marshes
Coastal saline vegetation
Rocks, screes and walls
Oromediterranean montane grasslands and scrub
Arctoalpine to subalpine grasslands
Mediterranean garrigue and phrygana
Mesic broad-leaved deciduous forests
Subalpine tall-herb vegetation and scrub
Inland saline vegetation
Dry coniferous forests
Thermophilous broad-leaved deciduous forests
Temperate heathlands
Deciduous scrub
Hemiboreal birch-pine forests
Semi-desert and desert scrub
Mediterranean heathlands
Mediterranean sclerophyllous forests
Aquatic vegetation
Mires, fens and springs
Alien-dominated forests and scrub
Laurophyllous forests
Oligotrophic broad-leaved decidous forests
Boreo-continental coniferous forests
Mediterranean montane xeric woodlands and scrub
Alder carrs
Sea-grass beds
Bogs and bog woodlands

■ Human-made habitats ▨ Human-made/Natural habitats ■ Semi-natural habitats ▨ Semi-natural/Natural habitats □ Natural habitats

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.

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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.

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