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Phylogenetic structure of alien plant species pools from European donor habitats

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Abstract

Aim: Many plant species native to Europe have naturalized worldwide. We tested whether the phylogenetic structure of the species pools of European habitats is related to the proportion of species from each habitat that has naturalized outside Europe (habitat's donor role) and whether the donated species are more phylogenetically related to each other than expected by chance.

Location: Europe (native range), the rest of the world (invaded range).

Time period: Last *c.* 100 years.

Major taxa studied: Angiospermae.

Methods: We selected 33 habitats in Europe and analysed their species pools, including 9,636 plant species, of which 2,293 have naturalized outside Europe. We assessed the phylogenetic structure of each habitat as the difference between the observed and expected mean pairwise phylogenetic distance (MPD) for (a) the whole species pool and (b) subgroups of species that have naturalized outside Europe and those that have not. We used generalized linear models to test for the effects of the phylogenetic structure and the level of human influence on the habitat's donor role.

Results: Habitats strongly to moderately influenced by humans often showed phylogenetically clustered species pools. Within the clustered species pools, those species that have naturalized outside Europe showed a random phylogenetic structure. Species pools of less human-influenced natural habitats varied from phylogenetically clustered to overdispersed, with donated naturalized species also often showing random patterns within the species pools. Donor roles in both habitat groups increased with increasing MPD within habitats.

Main conclusions: European human-influenced habitats donate closely related species that often naturalize in disturbed habitats outside their native range. Natural habitats donate species from different lineages with various ecological strategies that allow them to succeed in different habitats in the invaded range. However, the naturalized species donated by most European habitats are phylogenetically random subsets of their species pools.

KEYWORDS

donor habitat, Europe, native range, phylogenetic structure, plant invasion, source-area approach, species pool, vegetation types

1 | INTRODUCTION

Invasive alien species are considered to be a major threat to native ecosystems worldwide (Sala et al., 2000), having adverse environmental and economic impacts (Pimentel et al., 2005; Vilà et al., 2011). To counter these impacts, recent research has focused on the factors leading to the successful establishment and adaptation of alien species (Kolar & Lodge, 2001; Moles et al., 2008; Pyšek, 2001; van Kleunen, Dawson & Maurel, 2015). In this context, information on the evolutionary histories and relationships of alien and native species in plant communities can help understand and predict plant invasions (Procheş et al., 2008). For example, the phylogenetic diversity and structure of invaded plant communities, and the shared evolutionary history between aliens and natives, can inform about underlying ecological mechanisms driving plant invasions and help assess invasibility of plant communities and their habitats (e.g., Junying et al., 2014; Loiola et al., 2018; Lososová et al., 2015).

Invasion success of a species in a community is also affected by the phylogenetic structure of the invaded community, which reflects the evolutionary relatedness across its members (Cavender-Bares et al., 2009), and by the phylogenetic distance between native and alien species (Ricotta et al., 2010; Strauss et al., 2006). Phylogenies can be used to overcome the problem of missing information on traits, assuming that species with shared ancestry are ecologically more similar to each other than to distantly related species (Cavender-Bares et al., 2009). Natives can limit the invasion success of closely related aliens by increased competition between species within the same lineages. However, tests of ‘Darwin’s naturalization hypothesis’ (Diez et al., 2008; Pinto-Ledezma et al., 2020) and of the effects of the phylogenetic distance between native and alien species on alien establishment have so far yielded inconclusive results (Jones et al., 2013). These evolutionary relationships between native and alien species vary among communities occurring in different environmental conditions and experiencing contrasting disturbance regimes (Ng et al., 2019).

Studies of the phylogenetic structure of invaded plant communities consistently show that aliens successfully invade phylogenetically clustered plant communities (Gerhold et al., 2011; Loiola et al., 2018; Lososová et al., 2015). A possible explanation for this consistency might be that phylogenetically clustered communities can be easily invaded because their species are adapted to interact only with their close relatives; hence, they are more vulnerable to competition from distantly related aliens, their pathogens and pests (Gerhold et al., 2011). Also, because many lineages are absent and there is usually more unoccupied niche space in these phylogenetically clustered communities, incoming aliens belonging to distantly related lineages and with complementary ecological strategies may occupy empty niches and coexist with natives (Prinzing et al., 2008). However, these explanations were not supported by recent studies that have found that alien species increased the degree of phylogenetic clustering in many invaded communities (Loiola et al., 2018; Lososová et al., 2015).

Phylogenetic distances between species are assumed to be proxies for evolved ecological differences (Freckleton et al., 2002; Lososová et al., 2016), resulting in the tendency of closely related species to have similar trait characteristics and to be ecologically similar (Losos, 2008). In invaded communities, phylogenetic clustering can be caused by aliens closely related to natives sharing the same niches as those natives. Furthermore, aliens that are closely related to each other might also share some strategies supporting their invasiveness (Cadotte et al., 2009). In particular, traits associated with plant physiological tolerance (Prinzing et al., 2001), growth form, mating system, and habitat preferences (Chazdon et al., 2003) have been shown to be evolutionarily conserved within plant lineages. An increase in phylogenetic clustering of communities in invaded habitats can indicate the existence of a large species pool of closely related alien plants preadapted to the given environments (Lososová et al., 2015). In their native range habitats (or donor habitats), donated alien species may be concentrated in a few lineages forming a distinct group with shared specific traits and effective strategies underpinning their establishment and persistence. Such strategies or traits can determine species' environmental tolerance, effective dispersal, reproduction, and competitive ability, such as fast growth rate, a high number of propagules and fast germination (van Kleunen, Dawson, & Maurel, 2015).

Previous studies have demonstrated that human-disturbed habitats in the native range that have phylogenetically clustered plant communities (Lososová et al., 2015) are important sources of many invasive species (Hejda et al., 2009; Kalusová et al., 2017). Consistent with these observations, comparisons across floras have shown that successful aliens are mainly concentrated in families and genera dominated by ruderal species and agricultural weeds (Lambdon, 2008; Pyšek, 1998). The strong clustering of such plant communities has been repeatedly associated with observed dominance of disturbance-adapted species (Brunbjerg et al., 2012; Helmus et al., 2010). Alien species adapted to disturbances in their native habitats should be preadapted for successful establishment in environments strongly influenced by humans when introduced to new regions. Therefore, the phylogenetic structure of donor habitat communities may also play a role in plant invasions, in addition to the phylogenetic structure of recipient communities. In strongly human-disturbed donor habitats, alien species can be selected randomly depending on stochastic introduction events and establish in similarly disturbed habitats in the invaded range (e.g., Hejda et al., 2015; Loiola et al., 2018). Thus, their phylogenetic structure within the donor habitat species pool should reflect this randomness, although these species should be generally closely related because of the clustering of the entire species pool when compared to other more natural donor habitats. Within species pools of moderately human-disturbed habitats, groups of closely related and disturbance-adapted species may be more likely to establish in similarly human-disturbed areas (Hufbauer et al., 2011) than other species from the habitat species pool. In less disturbed donor habitats supporting phylogenetically random or overdispersed plant communities (Lososová et al., 2015), the phylogenetic relatedness of donated aliens can be random or overdispersed. This is because in the absence of frequent disturbances and the presence of interspecific interactions involving many different lineages, a variety of different strategies other than disturbance adaptation may play a role (see also Supporting Information Figure S1 for a general scheme of the ideas presented here).

Evolutionary and ecological processes favouring plant invasions have often been investigated at the level of communities or individual plots. However, communities are assembled from regional species pools (Jiménez-Alfaro et al., 2018; Zobel, 1997), and some species present in a region may fail to reach the target community just by chance (Blackburn & Gaston, 2001) or due to inherent dispersal constraints. Therefore, studies based on whole species pools tend to provide more robust results (Lososová et al., 2015). The species-pool approach disregards the differences between species in dispersal ability, which affect the probability of species being recorded at different sites (Ozinga et al., 2005). Another common methodological approach of alien plant studies is that usually they only assess the occurrences of aliens in the invaded range. In such cases, alien species originating from various regions are considered jointly, although their characteristics can be influenced by variations in the evolutionary history of source floras or by their dispersal-related variables. Therefore, in our study, we used the source-area approach, which reduces the bias caused by comparing species coming from different regions (Pyšek et al., 2004). We focused on European habitats and their species pools that donate species for naturalization outside Europe (Supporting Information Figure S1). We compared the phylogenetic structure of the whole species pools of these donor habitats and the phylogenetic structure of subgroups of species from these donor habitats that have naturalized outside their native range. To this end, we integrated information on species distribution outside their native range from the Global Naturalized Alien Flora (GloNAF) database (van Kleunen, Dawson, Essl et al., 2015) with the degree to which a given donor habitat is determined or influenced by human activities using habitat naturalness categories. We also tested whether the phylogenetic structure of naturalized species changes from intensively human-influenced and disturbed to less influenced and undisturbed European habitats.

We ask the following questions: (a) Are successfully naturalized alien plant species from Europe more closely related to each other than under random expectation, both across and within the donor-habitat species pools? (b) Does the degree of phylogenetic relatedness among naturalized species depend on the levels of human influence? (c) Is the donor role of European habitats (i.e., the proportion of their native species that have naturalized elsewhere) related to the phylogenetic structure of their species pools? If so, (d) does this relationship depend on the level of human influence on the habitat?

2 | METHODS

2.1 | European donor habitats and their species pools

We derived data on European vegetated habitats from EuroVegChecklist (Mucina et al., 2016), which categorizes European vegetation into 107 vegetation classes, each supplemented by a list of typical/diagnostic plant species. These data covered Europe with the eastern border in the Ural Mountains and the Caspian Sea shore. It also included the Greater Caucasus, Arctic archipelagos and Macaronesian islands.

We merged vegetation classes and their respective species lists into 33 broader categories of European donor habitats. This aggregation was based on the similarities in vegetation physiognomy, dominant life-forms, species composition, ecology, and biogeography following the class descriptions in EuroVegChecklist (see details in Supporting Information Table S1 and Kalusová et al., 2017). We excluded *Robinia* groves (class *Robinietea*) because their species list contained a majority of alien species and seagrass beds (classes *Halodulo wrightii-Thallasietea testudinum*, *Ruppietea maritimae* and *Zosteretea*) to focus on terrestrial and freshwater habitats only. We classified these 33 habitats into five categories of naturalness reflecting the level of human influence and related disturbances (see Supporting Information Table S1 and Kalusová et al., 2017): (a) human-made, that is, the most human-disturbed; (b) transitional human-made/natural; (c) semi-natural, that is, dependent on moderate human influence, moderately disturbed; (d) transitional semi-natural/natural; and (e) natural, that is, existing independently of human intervention, the least human-disturbed.

We merged all subspecies and varieties contained in the source species lists to the species level. We standardized the species nomenclature following The Plant List (TPL, v1.1, www.theplantlist.org) using the R package 'Taxonstand' v1.0 (Cayuela et al., 2012). We restricted our data set to angiosperm species that are native to Europe and have a known association with European habitats. Further, we excluded 401 vascular plant species alien to Europe following the Euro+Med PlantBase (2006–2019), 122 hybrids, and 227 gymnosperms, ferns and fern allies. We analysed 9,636 angiosperm species in total, that is, 83.4% of species listed in Flora Europaea (Tutin et al., 1964–1980). On average, donor habitat species pools contained 375 ± 368 (mean ± *SD*) plant species. Native species counts in each habitat can be found in Supporting Information Figure S2. Within these species lists, and using the GloNAF database (v1.1; Pyšek et al., 2017; van Kleunen, Dawson, Essl, et al., 2015), we identified 2,293 European native plant species that have naturalized outside Europe (106 ± 110 species per habitat). European native species that have naturalized outside Europe are hereafter called *naturalized species*, and those that have not naturalized outside Europe are called *non-naturalized species*.

2.2 | Phylogeny

We linked the names of the 9,636 angiosperm plant species found in the 33 European habitats to the mega-phylogeny implemented in the 'V.PhyloMaker' R package (Jin & Qian, 2019). This mega-phylogeny was derived from two recently published dated mega-trees (Smith & Brown, 2018; Zanne et al., 2014), which are based on molecular markers. We used the 'scenario 3' approach implemented in the same R package to add missing species (*c*. 49%) to the phylogeny (Jin & Qian, 2019; Qian & Jin, 2016). This approach attaches a new genus to the midpoint of the family branch and new species of an existing genus to the basal node of this genus.

2.3 | Data analyses

We identified nodes in the phylogeny of native European species that encompassed significantly more naturalized species than the rest of the tree using the *nodesig* function adapted for R by Abellán et al. (2016). This function allowed us to determine the position of phylogenetic clustering by testing each node of the phylogenetic tree for an overabundance of naturalized species. We carried out this analysis for all the species in the European data set and compared the observed patterns with 999 random samples of equal size drawn from the phylogeny.

We converted the phylogenetic tree of the European species to an interspecific phylogenetic distance matrix using the *cophenetic* function in the R package 'stats'. We calculated the phylogenetic structure of three different species groups in each of the donor European habitats: (a) all native species, (b) naturalized species of European origin, and (c) non-naturalized species of European origin. We used the mean pairwise phylogenetic distance (MPD; Webb et al., 2002), which expresses the average phylogenetic distance between all pairs of species. We also calculated the mean nearest taxon distance (MNTD; Webb et al., 2002), which considers, for each species, only the distance to its phylogenetically nearest species. Because MPD and MNTD were significantly correlated across habitats (for naturalized species: $r_s = .53$, $p < .001$; for non-naturalized species, $r_s = .53$, $p < .001$), we only present the results for MPD. As MPD considers all the pairwise phylogenetic distances in the habitat, including deeper branching in the tree, it is more informative for testing hypotheses about the mean relatedness of species in communities under environmental filtering (Tucker et al., 2017).

To investigate whether the phylogenetic structure of species that have their native range in Europe and have naturalized elsewhere was significantly more clustered or overdispersed than expected by chance, we randomized the data by reshuffling the tip labels of the phylogeny 999 times, keeping the species richness and the frequency of naturalized species constant. We calculated the standardized effect size of mean pairwise phylogenetic distance (SES MPD) for all species in the data set as (observed MPD – mean expected MPDs)/standard deviation (*SD*) of expected MPD. We tested the significance of SES MPD by comparing the observed MPD values with the distributions of random matrices using two-tailed *p*-values. Positive SES MPD values and high quantiles (SES MPD > 0, $p > .975$) indicate overdispersion, that is, a greater phylogenetic distance among species than expected by chance, whereas negative SES MPD values and low quantiles (SES MPD < 0, $p < .025$) indicate clustering, that is, smaller phylogenetic distances among species than expected by chance. Zero or near-zero values indicate a random phylogenetic pattern (Kembel et al., 2010).

While SES MPD can be used to assess the significance of phylogenetic clustering or overdispersion within a given habitat, comparing this metric among habitats is problematic because it is sensitive to species richness (Sandel, 2018). Therefore, to measure the deviation from the random phylogenetic structure of habitat species pools and their subsets of naturalized and non-naturalized species, we additionally calculated the difference between the observed MPD and expected MPD (ΔMPD) values derived from the randomizations. Previous studies have suggested using the rarefied SES MPD as a metric of phylogenetic structure when comparing communities with different species richness (Sandel, 2018). This metric reduces the dependence of SES MPD on species richness of different assemblages, but rarification comes at the cost of reducing certainty of estimates because the variance of MPD expected from randomizations is higher in species-poor samples. We note that because the source pool is the same for all habitats (i.e., the entire European flora), the median ΔMPD provides a metric equivalent to rarefied SES MPD without reducing statistical power ($r = .999$; $p < .001$; Supporting Information Figure S5). Negative values of ΔMPD indicated phylogenetic clustering, near-zero values indicated random phylogenetic pattern and positive values indicated phylogenetic overdispersion compared to the null expectations. The deviation of the phylogenetic structure from the random expectation was considered significant if more than 97.5% of randomizations resulted in negative ΔMPD values in the case of phylogenetic clustering or positive values in the case of overdispersion. We additionally tested whether the species pools of each habitat, regardless of the species naturalization status, were phylogenetically clustered or overdispersed compared to null expectations by repeating the randomization process while keeping the number of species in each habitat constant. Finally, we tested whether the naturalized and non-naturalized species of European origin within each habitat showed a non-random phylogenetic structure. For these analyses, the phylogeny was trimmed to the habitat-specific species pool and the tip labels were reshuffled in each randomization while maintaining the number of naturalized species. Only species capable of growing in each particular habitat were thus included in the random habitat pool (de Bello, 2012; Kraft & Ackerly, 2010). All calculations were performed using the *ses.mpd* and *mpd* functions in the R package 'picante', v1.8 (Kembel et al., 2010).

We calculated each European habitat's donor role as the proportion of species from the habitat that have naturalized outside Europe. Then, we used generalized linear models (GLMs) with binomial error distribution and logit link function (Dobson, 1990) to model the habitat donor role as a function of the phylogenetic structure of species pools (i.e., all native species of the habitat), the level of human-influence, and the interaction between the two. Generalized linear models with binomial error distribution are recommended for analysing proportions derived from counts (Douma & Weedon, 2019). For all GLMs, the level of human-influence included two states: human-influenced (n = 14; including human-made with semi-natural habitats and their transitions) and natural (n = 19). As a measure of phylogenetic structure for each habitat, we used the median value of ΔMPD from the randomizations described above, that is, the median model. We also calculated repeated GLMs, a series of models in which we successively introduced each ΔMPD from the randomizations to obtain the distribution of estimates and their p-values across all randomizations. We determined the overall significance of the explanatory variables when > 97.5% of estimates from the repeated model had the same direction (positive or negative) as the estimates from the median model and reached $p < .05$. We tested the significance of the terms within GLMs using the likelihood-ratio test. We calculated the percentage of deviance explained [D2 = (null deviance − model deviance)/null deviance corresponding to the proportion of variation explained; Nakagawa & Schielzeth, 2013] using the *glm* and *ANOVA* functions in the R package 'stats'. To separate simple effects of the two human-influence categories from the interaction with the phylogenetic structure, we applied post-hoc tests using the *simple_slopes* function from the R package 'reghelper' v0.3.5 (Hughes, 2020). All analyses were performed in R v4.0.3 (R Core Team, 2020).

3 | RESULTS

3.1 | Phylogenetic structure of naturalized species of European origin across habitats

Species native to Europe and naturalized outside this continent showed a random phylogenetic pattern (n = 2,293; SES MPD z = 0.569; p = .69) across the entire data set in which species pools of all habitats were merged (SES MPDs for each European habitat with species numbers are available in Supporting Information Figures S2–S4). However, some families such as Amaranthaceae, Polygonaceae, Fabaceae, Geraniaceae, Papaveraceae and Poaceae, and genera such as *Chenopodium*, *Atriplex*, *Rumex* and *Trifolium* had a significantly higher concentration of naturalized species of European origin than under random expectation (Figure 1; Table 1). In total, the 2,293 naturalized species of European origin belonged to 682 genera (64.6% of all genera in the data set).

3.2 | Phylogenetic structure of plant species within human-influenced and natural European habitats

The phylogenetic structure of the species pools was habitat-specific, ranging from clustered through random to overdispersed (Figure 2a). Strongly and moderately human-influenced (human-made to semi-natural) habitats most often showed phylogenetic clustering (78.5%), while none of them was significantly overdispersed. Natural habitats showed phylogenetic clustering less often (47.4%) and also included habitats with significant phylogenetic overdispersion (26.3%).

Relative to all species within their habitats, the subgroups of plant species that have naturalized outside Europe most often showed random phylogenetic patterns in both human-influenced (85.7%) and natural habitats (89.5%) (Figure 2b). This was true for two of the most important donor habitats of naturalized plant species of European origin: arable land and anthropogenic herbaceous vegetation (human-made). The third most important donor habitat of European naturalized species, perennial ruderal vegetation on mesic soils (human-made/natural), provided naturalized species that were significantly more related to each other than expected based on random draws. In contrast, deciduous scrub (semi-natural/natural) provided more distantly related naturalized species than expected based on random draws. Among natural habitats, the exceptions

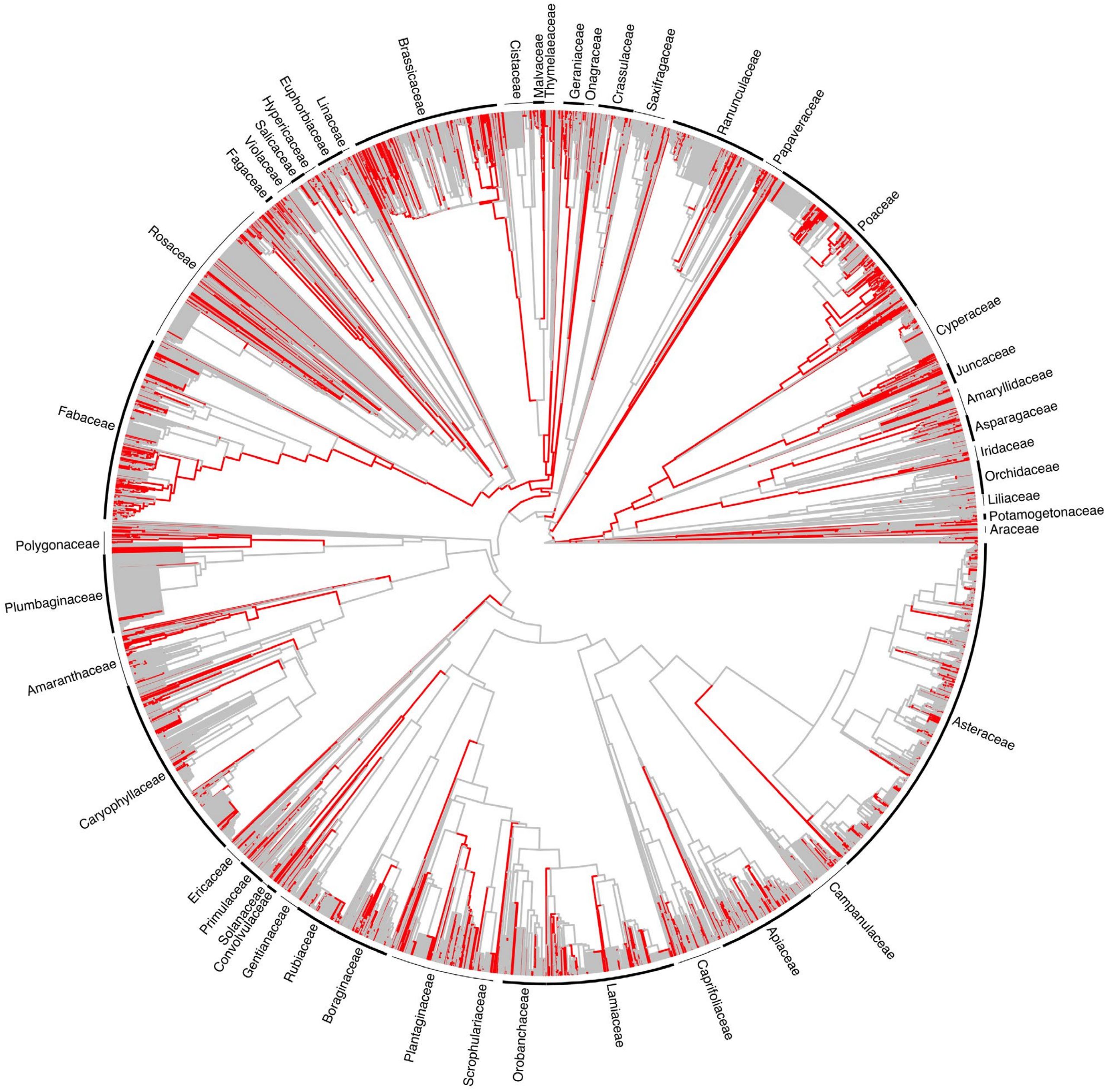


FIGURE 1 Phylogeny of the 9,636 studied species native to Europe. The red tips indicate European species naturalized elsewhere, and red branches indicate the lineages that encompass more naturalized descendant taxa than expected by chance

to random phylogenetic patterns included coastal and inland saline vegetation and salt-sprayed cliffs that both provided naturalized species that were more distantly related than expected.

Plant species that have not naturalized outside Europe also often showed random phylogenetic patterns in human-influenced habitats (78.5%; Figure 2c). The exceptions to this pattern included rocks, screes and walls (human-made/natural), mesic grasslands and pastures (semi-natural) and deciduous scrub (semi-natural/natural). Non-naturalized species in these habitats were more closely related than expected based on random draws. A random phylogenetic structure for non-naturalized species also prevailed in natural habitats (63.2%). Exceptions to this were coastal sand vegetation, coastal and inland saline vegetation, freshwater marshes, laurophyllous forests, mesic broad-leaved forests, riparian forests and salt-sprayed coastal cliffs. In these habitats, species that have not naturalized outside Europe were also more closely related than expected.

3.3 | The effect of habitat phylogenetic structure and human influence on the habitat donor role

Habitats with distantly related species played a slightly more important donor role than the habitats with closely related species

TABLE 1 Plant families (a) and genera (b) with their associated number of species across the European native species data set

(a) Family	Standardized randomization rank	Number of species in the data set	(b) Genus	Standardized randomization rank	Number of species in the data set
Amaranthaceae	1,000.0	177	*Chenopodium*	1,000.0	19
Polygonaceae	1,000.0	79	*Cuscuta*	1,000.0	8
Fabaceae	1,000.0	644	*Atriplex*	1,000.0	25
Geraniaceae	1,000.0	73	*Rumex*	1,000.0	40
Papaveraceae	1,000.0	66	*Trifolium*	1,000.0	98
Poaceae	1,000.0	658	*Medicago*	1,000.0	31
Lythraceae	999.5	12	*Trigonella*	1,000.0	6
Malvaceae	999.0	40	*Melilotus*	1,000.0	14
Brassicaceae	998.0	510	*Lathyrus*	1,000.0	40
Hydrocharitaceae	997.5	6	*Ornithopus*	1,000.0	4
Araceae	997.0	23	*Thlaspi*	1,000.0	19
Oleaceae	995.5	14	*Sisymbrium*	1,000.0	18
Verbenaceae	994.0	3	*Geranium*	1,000.0	39
Betulaceae	990.0	13	*Phalaris*	1,000.0	8
Apocynaceae	988.0	19	*Elymus*	1,000.0	13
Grossulariaceae	986.5	6	*Bromus*	1,000.0	27
Juncaceae	986.0	75	*Juncus*	1,000.0	42
Amaryllidaceae	985.0	98	*Salvia*	999.5	28
Iridaceae	985.0	52	*Lepidium*	999.5	14
Araliaceae	983.0	8	*Glyceria*	999.0	6

Note: The standardized randomization rank was obtained from the *nodesig* function. The higher the standardized randomization rank, the higher the chance that the family/genus contains more species that have naturalized outside Europe than under random expectation. Twenty families and genera with the highest standardized randomization rank are shown. In all cases, the standardized randomization ranks corresponded to $p < .05$.

(Table 2, Figure 3a). This relationship was significant in the median ΔMPD value model and consistent in the majority of repeated regressions. We found positive effects of the higher median ΔMPD on the donor role in both habitat groups regardless of the level of human influence (human-influenced versus natural habitats; Figure 3b,c). In the median ΔMPD model, the effect of the phylogenetic structure of habitat species pool on the habitat donor role differed between human-influenced and natural habitats. However, this result appeared to be sensitive to the uncertainty in the expected MPD values in the repeated models (70.7% of models were significant).

4 | DISCUSSION

4.1 | Naturalized plants from European human-influenced habitats are random selections from phylogenetically clustered species pools

The species pools of human-influenced (i.e., human-made to semi-natural and transitional) European habitats are often phylogenetically clustered, regardless of whether their plant species naturalize elsewhere or not. Within these phylogenetically clustered habitat species pools, subgroups of naturalized and non-naturalized species usually show random phylogenetic patterns. The clustered pattern of the whole habitat species pool indicates that the lineages occurring in human-influenced habitats are likely to contain species with strategies that facilitate their establishment in disturbed sites. Such species have a higher chance of succeeding when introduced to similarly disturbed habitats in a new area (Hufbauer et al., 2011; Kalusová et al., 2017). However, our analyses show that species that naturalize outside their native range are selected from these species pools randomly with respect to their phylogenetic position.

The most human-influenced habitats, such as anthropogenic herbaceous vegetation consisting mainly of weedy species, are generally assembled under strong environmental filters imposed by human-induced disturbances and fluctuating resources (Davis et al., 2000). Such filters select for lineages preadapted to human-made environments, including species that are annuals, grow rapidly, are selfers, produce many seeds, and have persistent seed banks (Lososová et al., 2006). In our data set, species of human-made habitats that naturalized outside Europe were significantly over-represented, for example, in the genera *Atriplex*, *Chenopodium* and *Sisymbrium*. These species are introduced mostly unintentionally to strongly human-influenced sites. Here, environmental filtering by human-induced disturbances is probably the most important factor shaping species composition (Grime, 2006; Turner, 2010). Interspecific competition from the resident species can be low in early successional vegetation after initial disturbance, which can provide a window of opportunity

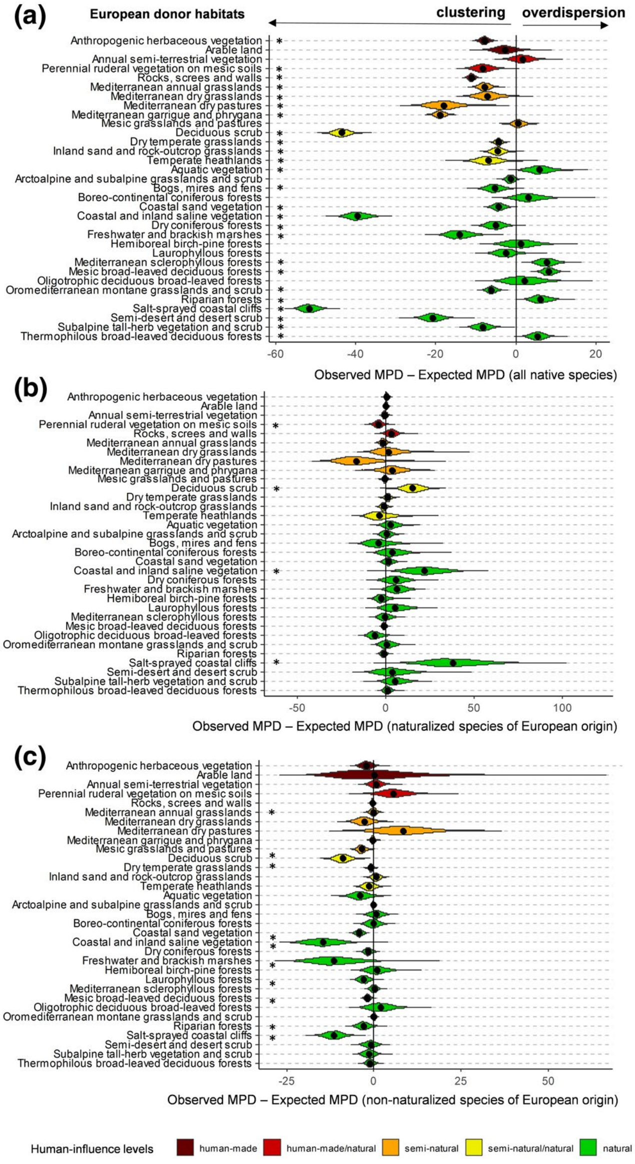


FIGURE 2 Violin plots of observed mean pairwise phylogenetic distance (MPD) minus expected MPD (ΔMPD) for (a) all native species in 33 European habitats, and two subsets of each habitat species pool; (b) species naturalized outside Europe, and (c) species non-naturalized outside Europe. Wider sections in the violin plots indicate a higher probability of occurrence of a particular value. For each violin plot, we show the estimate of the phylogenetic structure (ΔMPD), as well as the uncertainty around it, that is, the length of the violin plot. Habitats are grouped and sorted by a decreasing level of human influence. We considered a species pool to be significantly (*) clustered or overdispersed when the .975 or .025 quantiles of the distribution did not exceed zero, respectively

for incoming aliens until native ruderal species take over (Davis et al., 2000). Such groups of disturbance-adapted alien species thus tend to be from the same lineages and probably have the same life strategies and utilize the same resources as disturbance-adapted natives (Lososová et al., 2015). In the invaded range, they cause even stronger phylogenetic clustering of the invaded disturbed communities (Brunbjerg et al., 2012), decrease their trait-state dispersion (Gerhold et al., 2011) and finally can also contribute to phylogenetic homogenization (Winter et al., 2009).

4.2 | Exceptions from the random selection of naturalized species in European human-influenced habitats

In transitional human-made to natural habitats that occur in both human-disturbed and natural areas, such as perennial ruderal vegetation, we found that species that managed to naturalize were phylogenetically clustered. This group of species that are phylogenetically more closely related than expected share the same strategies advantageous for growing in disturbed environments. In contrast, non-naturalized species constitute a smaller fraction of the species pool of perennial ruderal vegetation and represent a phylogenetically random mixture. Many of these non-naturalized species are probably less adapted to disturbance and only survive in less disturbed sites. In contrast, non-naturalized species on rocks, screes and walls, which also belong to human-made to natural habitats, were more closely related than under random expectation and consisted of genera occurring at high elevations (e.g., *Draba*) or on islands (e.g., *Aeonium* and *Monanthes*). Therefore, the species of these lineages may have a low chance of being introduced to a new range compared to species from the human-influenced lowland habitat types. The only overdispersed phylogenetic pattern of naturalized species of European origin in human-influenced habitats was in deciduous scrub, which provided significantly more distantly related species than expected for naturalization. These species are represented by various life-forms such as herbs, grasses and shrubs from various lineages. They coexist especially in early successional stages, and thus tend to share tolerance to disturbance (Prach et al., 2013).

4.3 | The donor role of human-influenced habitats increases towards lineage-rich, yet clustered species pools

Even though we found that across all human-influenced habitats, their donor role slightly increases if they include more distantly related species, we showed that their species pools are generally phylogenetically clustered with respect to the whole European flora (see also Lososová et al., 2021). Among human-influenced habitats, phylogenetic clustering was strongest in semi-natural Mediterranean vegetation types, such as dry grasslands, pastures, garrigue and phrygana, where summer drought is a key environmental filter driving the survival of specialized lineages. However, Mediterranean habitats are not the most important donors of naturalized species in Europe. The most important European donor habitats include anthropogenic herbaceous vegetation and weeds on arable land (Kalusová et al., 2017). In these habitats, the selection pressure

TABLE 2 Results from the median and repeated generalized linear models (GLMs, binomial distribution) testing for the effect of the phylogenetic structure and human-influence level in 33 European habitats on the habitat's donor role, that is, the proportion of plant species donated for naturalization outside Europe

	Median GLM			Repeated GLMs with 999 MPD randomizations				
All species	**Estimate**	***SE***	***p***	**% of positive estimates**	**% of significant ($p < .05$)**	**% of negative estimates**	**% of significant ($p < .05$)**	**Overall significance**
(Intercept)	−0.558	0.048	< .001	0	0	100	100	*
Median of ΔMPD	0.037	0.005	< .001	99.9	98.4	0.1	0	*
Human-influence level	−0.225	0.057	< .001	3.3	0	96.7	81.5	ns
Median of ΔMPD:Human-influence level	−0.018	0.005	< .001	6.4	0.3	90.2	70.7	ns

Note: ns = not significant; *SE* = standard error. The repeated GLMs successively introduced each ΔMPD from the randomizations to obtain the distribution of estimates and their *p*-values across all randomizations. We determined the overall significance of the explanatory variables (indicated with *) when > 97.5% of estimates from the repeated model had the same direction (positive or negative) as the estimates from the simple model and reached $p < .05$. The significance of each GLM was tested with the likelihood-ratio χ^2 test.

Predictor variables in the median GLM include the phylogenetic structure of the habitat species pool, measured as the median of observed mean pairwise phylogenetic distance (MPD) minus expected MPD (ΔMPD), the level of human-influence, and the interaction between the two

by human disturbance is not coupled with water stress as in the Mediterranean habitat types, which results in a weaker phylogenetic clustering in the non-Mediterranean habitats.

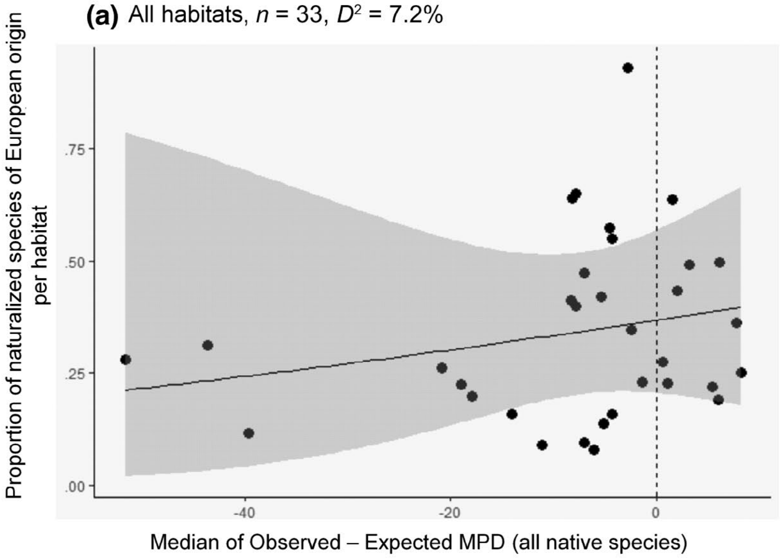
4.4 | The donor role of natural habitats increases towards phylogenetically overdispersed species pools

We found that in natural European habitats with a low degree of human influence, the donor role for naturalization increases from habitats with clustered species pools to those with overdispersed species pools. Aquatic vegetation, Mediterranean sclerophyllous, mesic, thermophilous and riparian broad-leaved deciduous forests are among the habitats with more phylogenetically overdispersed species pools, and most of them provide a relatively high proportion of naturalized species with a random phylogenetic pattern. This relatively high proportion of naturalized species originating from phylogenetically overdispersed natural habitats may be attributed to the fact that in their native range, species have to interact with many members of different lineages with various strategies. Thus, in the invaded range, these same species are able to compete with a broad spectrum of species while coping with various environmental conditions. This is in accordance with the evolutionary imbalance hypothesis (Fridley & Sax, 2014), suggesting that phylogenetically diverse regions are a source of species with a high invasion potential. Strategies gained in phylogenetically overdispersed donor habitats can be advantageous when strong filtering by disturbance is absent in invaded habitats, resulting in higher phylogenetic diversity of the residents (Webb et al., 2002). Indeed, it has been shown that communities with less clustered native species pools are invaded by fewer aliens that form a phylogenetically diverse group and decrease community clustering (Lososová et al., 2015).

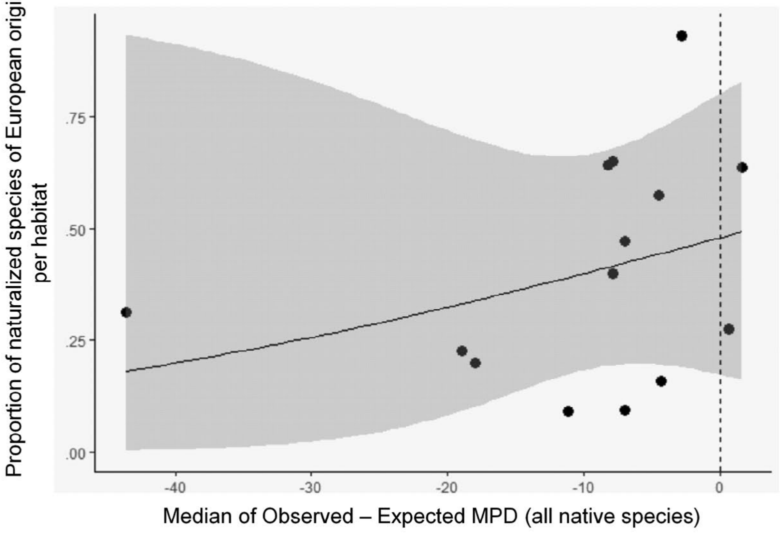
4.5 | Naturalized plants from European natural habitats show no distinct phylogenetic structure

For the naturalized species originating from European natural habitats, there is generally no shared strategy. Therefore, species with various strategies would have a chance to become naturalized outside Europe in less disturbed habitats. Species naturalized from natural habitats that are mostly phylogenetically overdispersed are a random selection from non-randomly phylogenetically structured species pools. The highest proportions of donated naturalized species among natural habitats are in freshwater marshes and riparian forests. This can be caused by adaptations of riparian plants to natural disturbances such as periodic floods (Richardson et al., 2007). While the species pool of freshwater marshes mainly consists of closely related wetland species, the species pool of riparian forests mainly consists of distantly related species adapted to fluvial disturbances. However, for both habitats, the phylogenetic structure of that group of species that have naturalized outside Europe does not deviate from random expectations.

(a) All habitats, n = 33, D^2 = 7.2%



(b) Human-influenced habitats, n = 14, D^2 = 4.4%



(c) Natural habitats, n = 19, D^2 = 16.7%

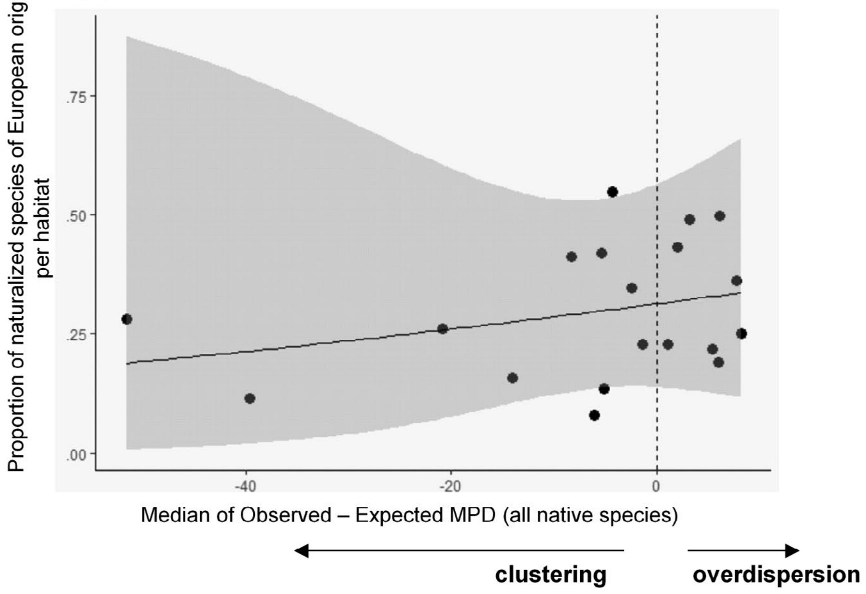


FIGURE 3 Generalized linear models (GLMs, binomial) showing the response of the proportion of European species that have naturalized outside Europe (i.e., habitat's donor role) to the median of observed mean pairwise phylogenetic distance (MPD) minus expected MPD (ΔMPD) from 999 randomizations for all native species in (a) all habitats, (b) human-influenced habitats (including human-made to semi-natural and transitional types), and (c) natural habitats. The dashed line indicates zero median and the grey area indicates the 95% confidence interval

Phylogenetic clustering of species pools of natural European habitats is more intense in those habitats in which environmental stress acts as the main filter (Kelly, 1999). Stressful natural habitats are generally poor donors of naturalized species, because their stress-tolerant species may be adapted neither to disturbance nor to competition (Grime, 2006). Therefore, they lack the characteristics needed to invade. These habitats include bogs, saline and sand coastal vegetation, salt-sprayed cliffs, semi-deserts, and subalpine tall-herb vegetation. In two of these habitats, saline vegetation and salt-sprayed cliffs, the donated naturalized species are a phylogenetically overdispersed selection, in contrast to the random selections from the rest of natural habitats. This indicates that a few species from distant lineages may be able to naturalize outside their native range, whereas very few or no representatives of species-rich halophytic genera such as *Limonium*, *Salicornia* or *Suaeda* are able to naturalize.

4.6 | Applications and limitations

Successful alien species possess functional traits that contribute to their success in the invaded range (e.g., Hamilton et al., 2005; Kolar & Lodge, 2001; van Kleunen, Dawson, & Maurel, 2015; van Kleunen et al., 2010). Thus, invoking the niche-conservatism principle and assuming that there is one set of traits promoting successful invasion, aliens should generally be phylogenetically clustered (Cadotte et al., 2009). In our study, however, we found that the phylogenetic structure of the species pools of naturalized alien plants is often random with respect to the species pool of the habitat from which they originate. Closely related species of human-made habitats that probably share adaptations to disturbance can naturalize more or less randomly from the phylogeny. In contrast, the phylogenetically more heterogeneous group of species of natural habitats collectively possess a broader range of various strategies, some of which may contribute to invasion success in different ways. Thus, there is no general trend in the relatedness of the species naturalized elsewhere compared to non-naturalized species across European donor habitats. Because traits promoting invasion success are supposed to be shared among close relatives, phylogenetic relatedness is also used as a predictor of invasion success of introduced species (Ackerly, 2003; Wiens, 2004) and can offer valuable information for management decisions (Caley & Kuhnert, 2006; Miller et al., 2011; Pyšek et al., 2004). However, our results show that the use of evolutionary relatedness should be supplemented with information on the donor habitats the introduced species are originally from.

The main limitation of our study is that it is based on the assumption that the phylogenetic distance between species can serve as a proxy for evolved ecological differences between them (Cadotte et al., 2013; de Bello et al., 2017; Kraft & Ackerly, 2010). Thus, closely related species naturalized from the same European habitats should share the same or very similar life strategies. Although we did not consider functional traits of species, the comparison at the habitat scale provides a direct insight into the effects of environmental factors shaping phylogenetic patterns at larger spatial scales (de Bello et al., 2013). Strong environmental filtering, involving both disturbance and stress, increases functional similarity among the species within a species pool (Kembel & Hubbell, 2006). Another confounding factor that can shape functional traits of alien species is human preferences in gardening or crop-planting, both important sources of successful alien species (van Kleunen et al., 2018, 2020). These preferences can be phylogenetically non-random (Cadotte et al., 2009; van Kleunen et al., 2020). Still, for successful establishment outside cultivation and naturalization, alien species need to possess the traits necessary to pass environmental filters of the habitat where they are introduced.

5 | CONCLUSIONS

Based on one of the largest data sets of European vegetated habitats with information for nearly 10,000 plant species, we revealed that the general assumption that alien plants constitute a phylogenetically clustered subset of plant species (Cadotte et al., 2009) is habitat-dependent. Phylogenetically clustered human-influenced European habitats donate groups of closely related species, whereas natural habitats generally donate species with no distinct phylogenetic patterns. However, the selection of naturalized species from European habitat species pools is, in most cases, phylogenetically random. Our results imply that information about the interconnection of the alien species' donor habitats and their evolutionary relatedness can contribute to the faster detection of potentially risky introductions of alien species. Since many alien plant species in the world originated from Europe (van Kleunen, Dawson, Essl, et al., 2015), this study can contribute to improved risk assessment of the introduction of alien species.

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AUTHOR CONTRIBUTIONS

V.K., J.P.C., T.F., M.C. and Z.L. conceived and designed research; M.vK., W.D., F.E., H.K., L.M., P.P., J.P., P.W. and M.W. provided background databases; V.K. analysed data together with T.F. and J.P.C., with inputs from M.vK., and Z.L.; V.K. wrote the text and all authors commented on the manuscript.

DATA AVAILABILITY STATEMENT

All the data sets used are publicly available. Species lists for European vegetation classes are published in Mucina et al. (2016), their appendix S6: list of diagnostic species of classes of the plant communities dominated by vascular plants (EVC1). The Global Naturalized Alien

Flora (GloNAF) database used for identification of naturalized plant species is available on the iDiv data portal at https://idata.idiv.de/DDM/Data/ShowData/257. The final matrix used for calculations, including plant species with naturalization status and their presences in European habitats, is available at https://doi.org/10.5061/dryad.cfxpnvx5q.

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The project was led by **Zdeňka Lososová**, an associate professor of Botany at Masaryk University. She studies factors shaping biodiversity of plant communities, habitat invasibility by alien plants and plant trait patterns including phylogenetic approaches.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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