Not a melting pot: Plant species aggregate in their non-native range

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Abstract

Aim: Plant species continue to be moved outside of their native range by human activities. Here, we aim to determine whether, once introduced, plants assimilate into native communities or whether they aggregate, thus forming mosaics of native- and alien-rich communities. Alien species might aggregate in their non-native range owing to shared habitat preferences, such as their tendency to establish in high-biomass, species-poor areas.

Location: Twenty-two herbaceous grasslands in 14 countries, mainly in the temperate zone.

Time period: 2012–2016.

Major taxa studied: Plants.

Methods: We used a globally coordinated survey. Within this survey, we found 46 plant species, predominantly from Eurasia, for which we had co-occurrence data in their native and non-native ranges. We tested for differences in co-occurrence patterns of 46 species between their native (home) and non-native (away) range. We also tested whether species had similar habitat preferences, by testing for differences in total biomass and species richness of the patches that species occupy in their native and non-native ranges.

Results: We found the same species to show different patterns of association depending on whether they were in their native or non-native range. Alien species were negatively associated with native species; instead, they aggregated with other alien species in species-poor, high-biomass communities in their non-native range compared with their native range.

Main conclusions: The strong differences between the native (home) and non-native (away) range in species co-occurrence patterns are evidence that the way in which species associate with resident communities in their non-native range is not species dependent, but is instead a property of being away from their native range. These results thus highlight that species might undergo important ecological changes when introduced away from their native range. Overall, we show origin-dependent associations that result in novel communities, in which alien-rich patches exist within a mosaic of native-dominated communities.

KEYWORDS: alien species, biodiversity threats, biological invasions, grassland ecology, native range, novel, ecosystems

1 INTRODUCTION

More than 13,000 plant species have established outside their native range as a result of human activities (van Kleunen et al., 2015). The result of this breakdown of biogeographical barriers is that species from different biogeographical regions have been brought together, creating novel ecosystems (Hobbs et al., 2006). Novel ecosystems are defined as new species associations that are likely to differ from historical communities in their ecosystem function (Hobbs et al., 2006). However, the assembly of these novel communities is poorly studied. It is unknown whether alien species are being assimilated into native communities or disproportionately aggregating with other alien species. Aggregation of alien species would result in novel ecosystems composed of a mosaic of alien- versus native-dominated communities. Whether alien species merge with the local communities or not could be species dependent (Buckley & Catford, 2016; Firn et al., 2011), with species retaining similar patterns of association in their native and non-native ranges (van Kleunen, Dawson, Schlaepfer, Jeschke, & Fischer, 2010). Alternatively, given that species interactions tend to be context dependent, the new conditions in the non-native range (Atwater, Ervine, & Barney, 2018) could lead to differences in how species associate with the resident community in their native and non-native ranges. Differences could also arise from the interaction with a community they have not previously encountered (Callaway et al., 2011). Determining how alien species interact with the resident community is key if we are to understand whether, and how, communities re-assemble after species introductions, which is a long-standing goal of invasion and conservation biology (Kuebbing & Nuñez, 2015; Wilsey, Teaschner, Daneshgar, Isbell, & Polley, 2009).

The association between alien and native species can determine whether alien species aggregate with each other or merge with the native community. Alien species tend to negatively associate with native species (Vilà et al., 2011), although some evidence suggests that they tend to positively associate with other alien species (Bernard-Verdier & Hulme, 2015). However, the degree of association has not been comprehensively assessed. Alien species might aggregate within their non-native range owing to shared habitat preferences for high-biomass, species-poor areas (Levine, Adler, & Yelenik, 2004); these areas tend to have higher resource availability, which could facilitate invasion (Thomsen & D'Antonio, 2007) by decreasing abiotic resistance (Rejmanek, 1989). Alternatively, the propagule pressure of alien species could be higher in human-dominated, disturbed areas where biomass tends to be high and species richness low (Colautti, Grigorovich, & MacIsaac, 2006; Pyšek et al., 2010). Alien species may also aggregate by facilitating each others' establishment, a process known as invasional meltdown (Simberloff & Von Holle, 1999). Alien plant species may facilitate each other directly, by modifying habitat conditions (e.g., resource availability or disturbance regimens; D'Antonio & Vitousek, 1992; Von Holle, Joseph, Largay, & Lohnes, 2006). However, facilitation may be also indirect, with alien species having a more negative impact on native species than on other alien species (Kuebbing & Nuñez, 2016).

The association of species with the resident community upon introduction, or lack thereof, has implications for management and conservation (Hobbs, Higgs, & Harris, 2009). Species could be merging with the native community upon introduction, forming novel communities that retain both native and alien species components, thus adding to biodiversity (Hobbs et al., 2009; Thomas & Palmer, 2015). Alternatively, if alien species aggregate with each other instead of merging, they could lead to the replacement of native communities, reduced diversity, and more greatly altered ecosystem functions (Vilà et al., 2011). Evidence suggests that many species have more negative effects on species richness in their non-native ranges compared with their native ranges (Becerra et al., 2018; Shah et al., 2014). Furthermore, by aggregating in the non-native range, their combined effects could lead to even lower native species richness and even greater changes in ecosystem processes in those areas (Kuebbing, Nuñez, & Simberloff, 2013; Simberloff & Von Holle, 1999).

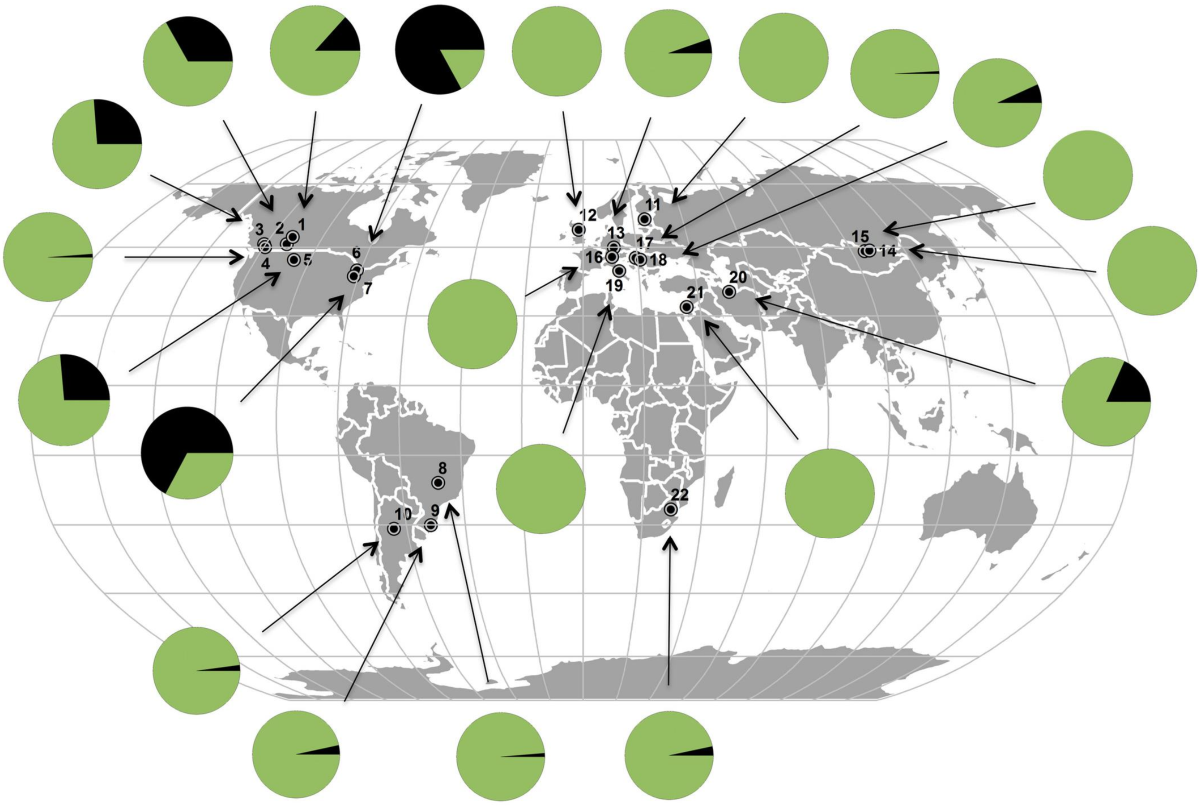

Figure 1. Site locations. Geographical distribution of the 22 study sites. Pie charts indicate the proportion of native (green) versus alien (black) species richness per site. The numbers on the map correspond to the field sites as listed in the Supporting Information (Appendix S1)

To gain a better understanding of how introduction away from the native range could alter the way in which species associate with the resident community, we took a biogeographical approach. We examined species associational patterns within their native and non-native ranges (Hierro, Maron, & Callaway, 2005; van Kleunen et al., 2010). We used a globally coordinated survey (Fraser, Jentsch, & Sternberg, 2014; Fraser et al., 2015) that spanned 123 sampling grids in 22 herbaceous grasslands in 14 countries (Figure 1; Supporting Information Appendix S1). Within this survey, we found 46 plant species, predominantly from Eurasia, for which we had co-occurrence data in their native and non-native ranges. Focusing mainly on these 46 species we tested: (a) whether species tend to aggregate more in their non-native range compared with their native range, associating with patches of higher alien species richness; (b) whether species tend to associate with high-biomass, species-poor patches in their non-native range; (c) whether the accumulation of alien species in a patch is related to even lower native species richness and even higher biomass compared with patches containing fewer alien species; and (d) whether the patterns observed depend upon the biogeographical origin of the species, the region to which they were introduced, species characteristics, such as life cycle and growth form, and/or sampling grain.

2 MATERIALS AND METHODS

2.1 Study sites

We used data from 123 sampling grids across 22 herbaceous grasslands (Figure 1) that were part of a globally coordinated survey, the Herbaceous Diversity Network (HerbDivNet; Fraser et al., 2013). The HerbDivNet was designed to study the relationship between species richness and community productivity and to identify generality beyond individual, local patterns (Fraser et al., 2014, 2015). The HerbDivNet sites are semi-natural grasslands. Most of them are under some form of management (e.g., mowing, grazing, fire), yet sampling was performed ≥ 3 months after the last mowing, grazing or fire event at each site.

2.2 Sampling design

At 22 sites, we sampled between two and 14 grids (Supporting Information Appendix S1). Grids were 8 m × 8 m and contained 64 contiguous plots, each of 1 m^2. Within each site, grids were established in areas of low (*c*. 1–300 g/m^2), mid (*c*. 300–800 g/m^2) and high (>800 g/m^2) aboveground biomass, when possible. In each plot, all species present were identified and counted at peak vegetation growth (Fraser et al., 2015). All species were then classified as native or alien based on available scientific databases. Native species are species that evolved in a given area or that arrived there by natural means (without intentional or unintentional human intervention) from an area in which they are native (Pyšek et al., 2004). Alien species are those species whose presence in the area is attributable to the intentional or accidental introduction as a result of human activity (Pyšek et al., 2004; Richardson et al., 2000). These are widely agreed-upon definitions of native and alien species, adopted by most scientific databases to classify species (e.g., USDA, FloraWeb). Species for which alien genotypes have been introduced within their native range were designated as both native and alien and were thus excluded from the analyses, except when examining the total number of species per plot and grid.

Litter and aboveground biomass were harvested, dried and weighed by plot (note that the biomass of alien and native species was not separated). Total aboveground biomass (live + litter biomass) was used as a proxy of productivity, given that litter is a function of annual net productivity and can be an important driver of plant communities. See Fraser et al. (2014, 2015) for more details on sampling design.

For the 46 species found in both their native (home) and non-native (away) ranges, we extracted the data on total, native and alien species richness, in addition to total aboveground biomass of all plots in which they were present in their native and non-native range. Total biomass and total, native and alien species richness at the grid level (8 m × 8 m) were also obtained for the 46 species in their native and non-native ranges. These 46 species were classified according to the continent of origin, the continent into which they were introduced, life cycle (short-lived: annual, biennial; or long-lived: perennial) and growth form (grass or forb) (Supporting Information Appendix S2). Species were also classified as naturalized or invasive (IUCN, 2017; Richardson et al., 2000) based on databases and published studies available for the non-native range for each of the species (Supporting Information Appendix S2). These types of classifications are contentious, because they are considered to be largely arbitrary and inconsistent across sources (Blackburn et al., 2014; Hulme et al., 2013; Simberloff et al., 2013). Accordingly, when we explored whether species co-occurrence patterns were associated with species status (naturalized/invasive), we found only small differences or no difference between plant species designated as invasive or naturalized in their co-occurrence patterns in their native and non-native ranges (data not shown). This likely suggests that the designation of species as naturalized or invasive based on local databases and previous studies is an unreliable predictor of alien species local invasive behaviour, rather than no difference between naturalized and invasive species co-occurrence patterns in their native and non-native ranges.

2.3 Statistical analyses

To assess whether species tended to aggregate more in their non-native compared with their native range, we focused on the species for which we had data in both their native and non-native ranges. We tested for differences in native and alien species richness of the patches these species occupied (1 m^2 plots) in their native versus non-native range using generalized linear mixed models (GLMMs) with a negative binomial distribution. Range (native versus non-native) was specified as a fixed effect in the model, and species and sampling grids within species were specified as random effects. The dataset included species from the same genus (e.g., *Bromus*, *Agrostis*) that could potentially have similar associational patterns. However, adding species within genus as a random factor in the model did not alter the results (data not shown).

To evaluate whether species were more likely to be present in high-biomass, species-poor patches, we tested for differences in community biomass and total species richness between the plots occupied by the 46 species in their native and non-native ranges. Differences in community biomass were tested using a linear mixed model (LMM) with a normal distribution, in which range was specified as a fixed effect and species and sampling grids within species as random effects. Differences in total species richness were assessed with a negative binomial GLMM, with range specified as a fixed effect and species and sampling grid within species as random effects.

We assessed the possible effects (i.e., impacts) of alien species on the communities in which they establish by comparing adjacent invaded and non-invaded patches (invaded and non-invaded 1 m^2 plots within 64 m^2 grids) across the 22 sites (focusing beyond the 46 focal species). Comparison between adjacent invaded and non-invaded patches to determine species impact is the most commonly used approach in invasion studies (Pyšek et al., 2012; Vilà et al., 2011). Across the 22 sites, we selected those grids that had both invaded (those with at least one alien species) and non-invaded (those with no alien species) plots (total = 71 grids). Within those grids, we then tested for differences in native species richness between invaded and non-invaded plots using a negative binomial GLMM, specifying grids within sites as a random factor. Differences in the total biomass between invaded and non-invaded plots were evaluated using an LMM, specifying grids within sites as a random factor, as above. Furthermore, to evaluate whether not only the presence, but also the number of alien species in a patch (i.e., their aggregation) was associated with greater native species loss and changes in biomass, we tested, within the invaded plots, for the effect of alien species richness on native species richness and total biomass, using similar models to those described above.

To assess whether our results were robust, we evaluated whether differences across species ranges (native versus non-native range) were consistent or dependent upon where species were introduced to (North America versus elsewhere), or where they were introduced from (European versus non-European species), and upon the life cycle (short-lived versus long-lived) and growth form (grasses versus forbs) of the species. We ran the same models as above for each species group separately. We also performed species-specific analyses to test for the generality of our results. For each of the 46 species, we tested for differences in characteristics of the communities occupied in their native and non-native ranges. We evaluated differences in total community biomass using linear models. Differences in total, native and alien species richness were tested using general linear models (GLMs) with a Poisson or, when over-dispersed, a quasi-Poisson distribution, for each species separately. Lastly, we tested whether similar patterns of species association in the native and non-native range are observed at a larger sampling grain (i.e., at the grid scale, 8 m × 8 m). Differences in total, native and alien species richness between the native and non-native range were assessed using GLMMs, with range as a fixed effect and species as a random effect. We tested for differences in community biomass using an LMM, with range as a fixed effect and species as a random effect. All statistical analyses were performed using the R statistical environment (R Core Team, 2019).

3 RESULTS

Of the 1,757 plant species identified across all sites, 46 species were recorded in both their native (home) and non-native (away) ranges (Supporting Information Appendix S2). Of these 46 species, 42 species were from Eurasia. Given that inclusion/exclusion of the non-Eurasian species did not alter the results (Figure 2; Supporting Information Appendix S3), we retained them in all analyses.

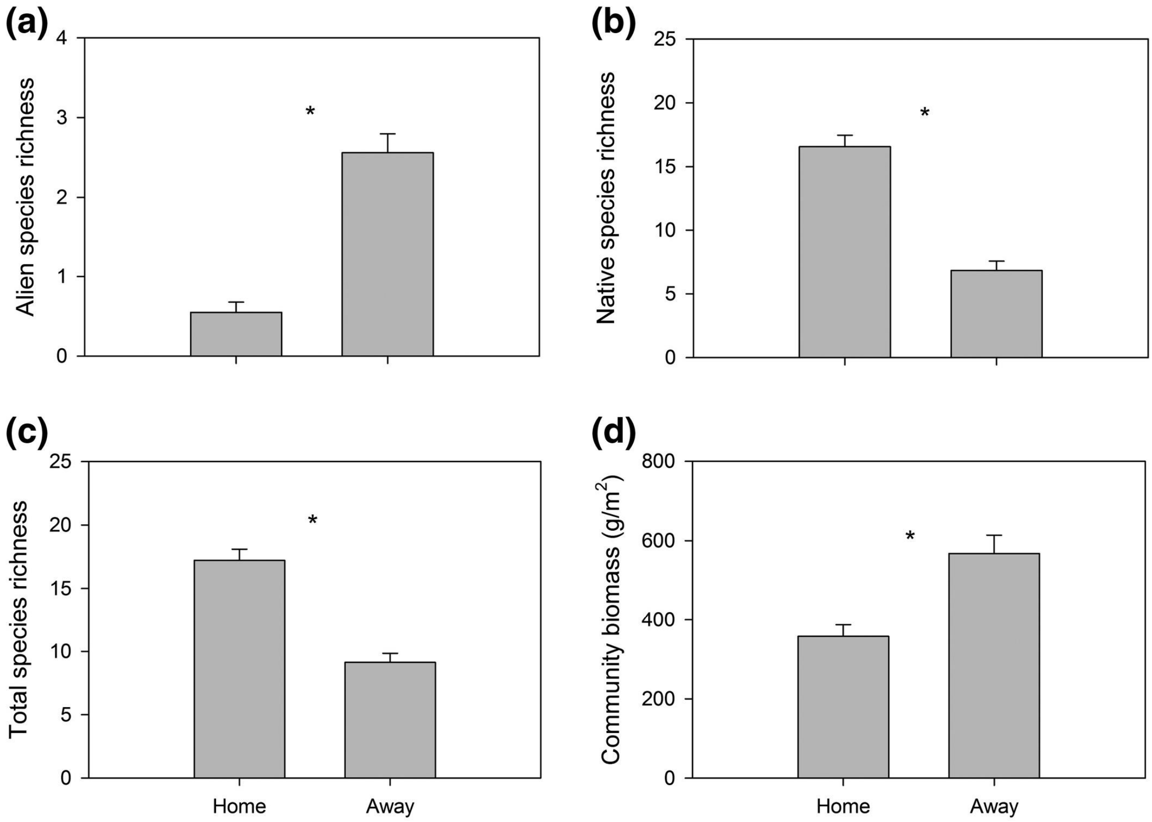

Figure 2. Characteristics of the communities (1 m^2 plots) in which species are found in their native (home) and non-native (away) range. (a) Alien species richness, (b) native species richness, (c) total species richness and (d) community biomass of the plots occupied by species in their native (home) versus non-native (away) range. Note that alien species richness (a) in the home range refers to the number of species that are alien in the site(s) where the focal species is considered native. Bars indicate the mean + *SE*. Means per treatment were calculated by averaging the means for species. See the Supporting Information (Appendix S2) for details on sample size for each of the 46 species included and the Supporting Information (Appendix S3) for statistical outputs. *Significant differences among treatments ($p < .05$)

Across the 46 focal species, we found strong differences in species co-occurrence patterns depending on whether they were in their native or non-native range. Focal species co-occurred with fewer native species in their non-native range compared with their native range (Figure 2b), but they co-occurred with a higher number of alien species (Figure 2a; Supporting Information Appendix S3). Specifically, although native species richness was higher than alien species richness in both ranges, the proportion of alien species in the patches that the focal species occupied in their non-native range increased. The patches that the 46 focal species occupied in their non-native range contained *c*. 60% fewer native species (Figure 2b) and almost five times more alien species than the patches they occupied in their native range (Figure 2a).

The co-occurrence of alien species could be explained, in part, by shared habitat preferences, because the 46 focal species were found to occupy species-poor, high-biomass patches in their non-native compared with their native range (Figure 2c,d; Supporting Information Appendix S3). Specifically, species occupied patches (plots) with *c*. 58% higher biomass (Figure 2c) and *c*. 50% fewer species (Figure 2d) in their non-native compared with their native range (Supporting Information Appendix S3).

When comparing adjacent invaded and non-invaded patches (invaded and non-invaded plots within grids), we found that invaded plots had *c*. 15% lower native species richness than non-invaded plots (estimate ± *SE* = 0.037 ± 0.02, *p* = .02). Total aboveground biomass, in contrast, was not different between adjacent invaded and non-invaded plots within grids (estimate ± *SE* = 0.012 ± 0.02, *p* = .43), suggesting that alien species did not increase the biomass of the patches in which they established. Although the presence of alien species was associated with lower native species richness (see above), a higher number of alien species in invaded plots did not result in even lower native species richness (estimate ± *SE* = −0.03 ± 0.04, *p* = .48). Greater alien species richness was also not associated with greater total biomass (estimate ± *SE* = 0.001 ± 0.01, *p* = .92).

The aggregation of species in species-poor, high-biomass patches in their non-native compared with their native range appears to be highly consistent. Most Eurasian species were introduced to North America, but they showed the same patterns of association when introduced elsewhere (Supporting Information Appendix S4). Results were also consistent with respect to life cycles (annual versus perennial; Supporting Information Appendix S5) and growth forms of species (grasses versus forbs; Supporting Information Appendix S6). Furthermore, the patterns observed were not driven by the higher representation of European species (Supporting Information Appendix S7) or by particular species. We found that most of the 46 studied species co-occurred with a higher number of alien species (half of the species; Supporting Information Appendix S8, Fig. S8.6), occupied patches of lower native species richness (72% of the species; Supporting Information Appendix S9, Fig. S8.7), lower total species richness (65% of the species; Appendix S8, Fig. S8.8) and higher biomass (59% of the species; Supporting Information Appendix S8, Fig. S8.9) in their non-native compared with their native range (Supporting Information Appendix S8); very few species showed the opposite trends. Lastly, the same patterns of species aggregation in species-poor, high-biomass patches in their non-native compared with their native range were observed at the grid scale (Supporting Information Appendix S9).

4 DISCUSSION

Overall, our results show that alien plant species tend to aggregate in species-poor, high-biomass patches in their non-native range (Figure 2). This is the first multispecies, worldwide field study to test for differences in species association patterns in their native (home) versus non-native (away) range and the first to document the co-occurrence of species in their non-native range. We show that the breakdown of biogeographical barriers is not resulting in the random association of species, because alien species do not tend to merge with the native community upon introduction. Instead, species are aggregating with other alien species in their non-native range (Figure 2a), forming novel communities, in which alien-rich patches exist within a mosaic of native-dominated communities. This type of novel community is formed as a result of origin-dependent associations, because alien species show a positive association with other alien species, but a negative association with native species. Importantly, these patterns of species association and overall habitat use were attributable to species being introduced away from the native range, not species dependent; the same species showed different patterns of association depending on whether they were in their native or non-native range (Figure 2). This supports the idea that species undergo important ecological and evolutionary changes after introduction (Atwater et al., 2018; Blossey & Notzold, 1995; Callaway & Ridenour, 2004).

The association of alien species with patches of low native species richness (Figure 2b) could be attributable to the preferential establishment of alien species in species-poor patches or to a negative impact on native species richness. Across sites, invaded plots had *c*. 15% lower native species richness than their adjacent non-invaded plots; a difference smaller than the *c*. 60% lower native species richness observed when comparing the plots occupied by the 46 focal species in their non-native range with those occupied in their native range (Figure 2b). Together, these results suggest a combination of alien species preferentially establishing in species-poor patches, which might pose lower biotic resistance (Levine et al., 2004), but also a negative impact of alien species on native species richness (Becerra et al., 2018; Shah et al., 2014). A negative impact on native species, especially if higher than that on other alien species, could lead to indirect facilitation (Kuebbing & Nuñez, 2016), which might explain the co-occurrence among alien species (Figure 2a), and suggest that an invasional meltdown might be occurring (Simberloff & Von Holle, 1999).

Different factors might explain why alien species tended to co-occur with each other (Figure 2a). Higher propagule pressure into more fertile, high-biomass, species-poor sites could explain alien species occurrence patterns (Colautti et al., 2006). However, the aggregation of alien species in certain plots within grids (64 m^2), across which propagule pressure is likely to be fairly even, indicates that other factors might be involved. Disturbance could explain the aggregation of alien species in species-poor, high-biomass patches (Hobbs & Huenneke, 1992; Pyšek et al., 2010). However, species are unlikely to associate with disturbed patches only in their non-native range. Furthermore, the sites sampled were chosen to have close-to-natural disturbance regimens (Fraser et al., 2014, 2015). Low disturbance levels are also suggested by the generally low average number/proportion of alien species per site and the accumulation of litter biomass. Litter biomass represents an average of 26% of the total biomass across sites, which is within the range observed for natural and semi-natural grasslands (Coupland, 1979; Supporting Information Appendix S1). Alien species also showed similar habitat preferences (Chytrý et al., 2008) for high-biomass patches, where competition is likely to be strong (Grime, 1973) and nutrient availability high (Thomsen & D'Antonio, 2007). Determining why species tend to associate with these habitats in their non-native range is beyond the scope of the present study. Nonetheless, evidence generally suggests that escaping from natural enemies (herbivores, pathogens and competitors; Agrawal et al., 2005; Keane & Crawley, 2002) gives species an advantage in their non-native range (Blossey & Notzold, 1995).

The aggregation of species in high-biomass, species-poor patches in their non-native range was a highly consistent result across the species examined. Although nutrient availability tends to favour the growth of grasses over forbs (You et al., 2017), both growth forms were associated with high-biomass patches in their non-native range (Supporting Information Appendix S6). Short-lived species are also generally thought to be more successful invaders than long-lived species (Pyšek & Richardson, 2007). However, short-lived alien species do not tend to be more dominant than long-lived alien species in sites with close-to-natural disturbances (Catford et al., 2019), such as ours. Our sampling was not balanced by region; instead, species were mainly from Eurasia, and most were introduced to North America, which is consistent with global trends (van Kleunen et al., 2015). Nonetheless, the co-occurrence patterns were consistent, independent of where species were introduced to (Supporting Information Appendix S4) or from (Supporting Information Appendix S7). Eurasian and/or European species have a long history of association with human activities (MacDougall et al., 2018), which is likely to have enabled their introduction and their potential arrival into similar general areas within the non-native range (Hodkinson & Thompson, 1997). However, given that species co-occurrence patterns (Figure 2a,b) and overall habitat use at local scales (Figure 2c,d) were not intrinsic properties of the species, but emerged after introduction, species from other biogeographical regions could also respond in a similar way to being introduced.

The differences found in how alien species associate with the resident community in their native versus non-native range might have important implications for management and conservation. We found that alien species aggregate, thus potentially causing greater changes in particular patches within a site. However, although alien species were associated with low native species richness, we found no evidence of an even lower native species richness as alien species richness increased; this finding is consistent with other studies (Rauschert & Shea, 2012). Communities should be managed considering the fact that the co-occurrence of alien species appears to be widespread (see also Kuebbing et al., 2013). Reducing the dominance of one alien species can lead to the release of secondary invaders, instead of increased abundance of native species (Bush, Seastedt, & Buckner, 2007; Ortega & Pearson, 2010). Future studies should aim at understanding the mechanisms behind these origin-dependent associations to prevent secondary invasions, the possibility of an invasional meltdown and greater biodiversity losses.

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AUTHOR CONTRIBUTIONS

L.H.F., A.J., M.S. and M.Z. are the coordinators of the Herbaceous Diversity Network (HerbDivNet). G.C.S., J.F.C., J.A.B., C.N.C. and E.W.B. conceived the research questions in this manuscript. G.C.S., J.F.C. and J.A.B. decided on the analytical approach and interpreted results. G.C.S. performed the statistical analyses and wrote the initial draft of the manuscript. All authors contributed to editing of subsequent drafts.

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HerbDivNet, the Herbaceous Diversity Network, is a partnership of >60 scientists from 20 countries worldwide, united in using collaborative dispersed experiments to study global patterns and processes of plant diversity.