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

Global Ecology and Biogeography *https://doi.org/10.1111/geb.13046*

First published: 17 December 2019

Short running title: Species aggregate in their non-native range

Keywords: Alien species, native range, non-native range, biodiversity threats, grassland ecology, biological invasions, novel ecosystems

Type of article: Research papers

ABSTRACT

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

Location: 22 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 range. We test 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 area species occupy at home and away.

Results: We found the same species to show different patterns of association, depending on whether they were in their native or non-native range. We did not find species to assimilate into native communities in their non-native range. Instead, species were negatively associated with native species, but aggregated with other alien species in species-poor, high-biomass communities, in their non-native, compared to their native range.

Main conclusions: The strong home vs. away differences in species co-occurrence patterns evidence that how species associate with resident communities in their non-native range is not species-dependent, but rather a property of being away from their native range. These results thus highlight that species may undergo important ecological and evolutionary change due to being introduced away from their native range.

INTRODUCTION

Over 13,000 plant species have established outside their native range due to human activities (van Kleunen et al., 2015). This breakdown of biogeographical barriers is bringing species from different biogeographical regions together, creating novel ecosystems (Hobbs et al., 2006). Novel ecosystems are defined as new species associations, with the potential to alter ecosystem function (Hobbs et al., 2006). However, it is unknown whether alien species are being assimilated into native communities or disproportionately aggregating with other alien species. Their aggregation would result in novel ecosystems composed of a mosaic of alien- vs. native-dominated communities. Whether alien species merge or not with the local communities could be species-dependent (Buckley & Catford, 2016; Davis et al., 2011; Firn et al., 2011), thus resulting in similar patterns of association across ranges (native and non-native) (van Kleunen, Dawson, Schlaepfer, Jeschke, & Fischer, 2010). Alternatively, species may undergo important ecological and evolutionary changes due to being introduced away from their native range (Atwater, Ervine, & Barney, 2018; Broennimann et al., 2007) and interacting with a community they have no previous history with (Blossey & Notzold, 1995; Callaway & Ridenour, 2004; Saul & Jeschke, 2015). Ecological and evolutionary changes upon introduction could result in important differences in how species associate with the local community in their native vs. non-native range (Callaway & Ridenour, 2004; Callaway et al., 2011). Determining how alien species interact with the resident community is key to understand if, 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 resident native community. Alien species tend to negatively associate with native species (Vilà et al., 2011), yet some evidence suggests that they tend to positively associate with other alien species (Bernard-Verdier & Hulme, 2015), but this has not been comprehensively assessed. Alien species may aggregate within their non-native range due to shared habitat preferences for high-biomass, species-poor areas (Levine, Adler, & Yelenik, 2004); these areas tend to have higher resource availability, which is known to facilitate invasion (Thomsen & D'Antonio, 2007) by decreasing abiotic resistance (Rejmanek, 1989). Alien species may also aggregate due to 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 regimes) (D'Antonio & Vitousek, 1992; Von Holle, Joseph, Largay, & Lohnes, 2006). However, facilitation may be also indirect, with alien species more strongly suppressing native species, compared to other alien species (Kuebbing & Nuñez, 2016) which could lead to the potential aggregation among alien species.

The association of species with the resident community upon introduction, or lack thereof, can raise important management and conservation concerns (Hobbs, Higgs, & Harris, 2009). Species could be merging with the resident, native community upon introduction, forming new 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 and altered ecosystem functions (Vilà et al., 2011). Thus, species may, once introduced, be excluding native species and increasing biomass in the areas where they establish (Vilà et al., 2011). Evidence suggests that many species have more negative effects on species richness in their non-native ranges, compared to their native ranges (Becerra et al., 2018; Shah et al., 2014). Further, by aggregating in the non-native range, their added or synergistic 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).

To better understand how being introduced away from the native range alters species co-occurrence patterns requires a biogeographical approach that examines species associational patterns within their native and non-native range (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 (Fig. 1, Appendix S1 in Supporting Information). Within this survey, we found 46 species, predominantly from Eurasia, for which we had co-occurrence data in their native and non-native range. Focusing on these 46 species we test (1) whether Eurasian species tend to aggregate in their non-native, compared to their native range, associating with areas of higher alien species richness, (2) whether they tend to associate with high-biomass, species-poor areas in their non-native range, (3) if the accumulation of alien species in an area results in even lower native species richness and even higher biomass, and (4) whether the patterns observed depend upon species biogeographical origin, the region they were introduced to, species characteristics, such as life cycle and growth form, and/or sampling grain.

MATERIALS AND METHODS

Study sites

We used data from 123 sampling grids across 22 herbaceous grasslands (Fig. 1) that were part of the globally distributed Herbaceous Diversity Network (HerbDivNet), which aims to study the relationship between species richness and community productivity (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 at least 3 months after the last mowing, grazing or fire event at each site.

Sampling design

At 22 sites, we sampled 2 to 14 grids (Appendix S1). Grids were 8 × 8 m and contained 64 1-m^2 contiguous quadrats. Within each site, grids were established in areas of low (~1 - 300 g/m^2), mid (~300 - 800 g/m^2) and high (> 800 g/m^2) aboveground biomass, when possible. In each quadrat, all species present were identified and counted at peak vegetation growth (Fraser et al., 2015). All species were then classified as native or alien. Native species were defined as those 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 (Petr Pyšek et al., 2004). Alien species were defined as those whose presence in the area is due to the intentional or accidental introduction as a result of human activity (Petr Pyšek et al., 2004; Richardson et al., 2000). 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 in a quadrat.

Litter and aboveground biomass were harvested, dried and weighed by quadrat (note that alien and native species' biomass were 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 both in their native (home) and non-native (away) range, we extracted the data on total, native and alien species richness, as well as total aboveground biomass of all quadrats 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 × 8 m) were also obtained for the 46 species at home and away. These 46 species were classified according to the continent of origin, the continent into which they were introduced (Appendix S2), life cycle (short-lived: annual, biennial; long-lived: perennial), and growth form (grass, forb). Species were also classified as naturalized or invasive (IUCN, 2017; Richardson et al., 2000) based on databases and published studies available for each of species' non-native range (Appendix S2). These types of classifications are contentious, as 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 or no differences between plant species designated as invasive or naturalized in their co-occurrence patterns at home or away (*data not shown*). This likely suggests that the designations as naturalized or invasive based on local databases and previous studies are unreliable predictors of alien species invasive behaviour.

Statistical analyses

To assess whether Eurasian species tended to aggregate in their non-native, compared to their native range, we focused on the species for which we had data both at home and away. We tested for differences in native and alien species richness of the areas (quadrats) these species occupied in their native vs. non-native range using generalized linear mixed models (GLMM) with a negative binomial distribution. Range (native vs. non-native) was specified as a fixed effect in the model, and species and sampling grids within species, as random effects. We have species in the same genus (e.g. *Bromus, Agrostis*) that could have similar associational patterns. However, adding species within genus as a random factor in the model does not alter results (*results not shown*).

To test whether species were more likely to be present in high-biomass, species-poor areas we tested for differences in community biomass and total species richness between the areas (quadrats) occupied at home vs. away. Differences in community biomass were tested for using a linear mixed model (LMM) with a normal distribution, where 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.

The aggregation of alien species could be associated with greater declines in native species richness and greater changes in total biomass. The possible effect (i.e.

impact) of alien species on the communities they invade were assessed by comparing adjacent invaded and non-invaded areas (invaded and non-invaded areas within grids). Comparing adjacent invaded and non-invaded areas to determine species impact is the most commonly used approach in invasion studies (Petr Pyšek et al., 2012; Vilà et al., 2011). Across the 22 sites, we selected the grids that had both invaded (those with at least one alien species) and non-invaded (those with no alien species) quadrats (total = 71 grids). Within those grids, we then tested for differences in native species richness between invaded and non-invaded quadrats using a negative binomial GLMM, specifying grids within sites as a random factor. Differences in total biomass between invaded and non-invaded quadrats were evaluated using a LMM, specifying grids within sites as a random factor, as above. Further, to evaluate whether not only the presence, but also the number of alien species in an area (i.e. their aggregation) was associated with greater native species loss and changes in biomass, we tested, within the invaded quadrats, for the effect of alien species richness on native species richness and total biomass, using similar models as above.

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

RESULTS

Of the 1757 species identified across all sites, 46 species were recorded in both their native (home) and non-native (away) range (Appendix S2). Of these 46 species, 42 species were from Eurasia. Since including/excluding the non-Eurasian species did not alter the results (Fig. 2, Appendix S3), we retained them in all analyses.

Across the 46 species, we found great differences in species co-occurrence patterns depending on whether they are in their native or non-native range. Alien species co-occurred with fewer native species in their non-native range, compared to their native range (Fig. 2B) yet they co-occurred with a higher number of alien species (Fig. 2A, Appendix S3). Specifically, although native species richness was higher than alien species richness in both ranges, the proportion of alien to native species increased significantly in the non-native range: there were substantially fewer native species

(~60%) in the areas species occupied in their non-native, compared to their native range (Fig. 2B), while alien species richness was almost five times greater (Fig. 2A).

The co-occurrence of alien species could be partly explained by shared-habitat preferences, as the 46 species were found to occupy species-poor, high-biomass areas in their non-native, compared to their native range (Fig. 2C, D, Appendix S3). Specifically, species occupied areas (quadrats) with ~58% higher biomass (Fig. 2C) and ~50% fewer species (Fig. 2D) in their non-native, compared to their native range (Appendix S3).

When comparing adjacent invaded and non-invaded areas (within grids) we found that invaded quadrats had ~15% lower native species richness (*estimate* ± *se* = 0.037 ± 0.02, $P = 0.02$) than non-invaded quadrats. Total aboveground biomass, on the other hand, was not different between invaded and non-invaded quadrats within grids (*estimate* ± *se* = 0.012 ± 0.02, $P = 0.43$), suggesting alien species did not increase the biomass of the areas they established in, but rather tended to establish in high-biomass areas. Although alien species appeared to decrease native species richness (see above), a higher number of alien species in invaded quadrats did not result in even lower native species richness (*estimate* ± *se* = -0.03 ± 0.04, $P = 0.48$). Greater alien species richness was also not associated with greater total biomass (*estimate* ± *se* = 0.001 ± 0.01, $P = 0.92$).

The aggregation of species in species-poor, high-biomass areas in their non-native, compared to their native range, appears to be highly consistent. While most Eurasian species were introduced to North America, they showed the same patterns of association when introduced elsewhere (Appendix S4), suggesting these results were not dependent upon the biogeographic region into which species are introduced. Results were also consistent with respect to species' life cycles (annual vs. perennial, Appendix S5) and growth forms (grasses vs. forbs, Appendix S6). Further, the patterns observed were not driven by the higher representation of European species (Appendix S7),, nor by particular species. In fact, we found that most of the 46 studied species co-occurred with a higher number of alien species (half of the species) (Appendix S8: Fig. S8.6), occupied areas of lower native species richness (72% of the species) (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) (Appendix S8: Fig. S8.9) in their non-native vs. native range (Appendix S8); very few species showed the opposite trends. Lastly, the same patterns of species aggregation in species-poor, high-biomass areas in their non-native, compared to their native range, were observed at the grid scale (Appendix S9).

DISCUSSION

Overall, our results show that Eurasian species tend to aggregate in species-poor, high-biomass areas in their non-native range (Fig. 2). This is the first multi-species, worldwide field study to test for differences in species association patterns at home vs. away, 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 widespread new species association (Hobbs et al., 2006), as 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 (Fig. 2A), forming novel communities with spatially segregated alien-rich patches within a native-dominated community. This type of novel communities is formed due to origin-dependent associations with alien species showing a positive association with other alien species, but a negative association with native species. These species associations and overall habitat use were an emerging property of 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 (Fig. 2). This supports the idea that species undergo important ecological and evolutionary changes following introduction (Atwater et al., 2018; Blossey & Notzold, 1995; Callaway & Ridenour, 2004).

The association of alien species to areas of low native species richness (Fig. 2B) could be due to pre-existing conditions or to a negative impact on native species richness. Species occupied areas of ~60% lower native species richness in their non-native range, yet we also found invaded quadrats had ~15% lower native species richness than adjacent non-invaded quadrats. Comparing adjacent invaded and non-invaded quadrats is a commonly used method to estimate species impact (Vilà et al., 2011). Hence, these results suggest a combination of preferential establishment in species-poor areas, that may pose lower biotic resistance (Levine et al., 2004) and negative impacts on native species richness (Becerra et al., 2018; Shah et al., 2014). A more negative impact on native species, over other alien species, could lead to indirect facilitation (Kuebbing & Nuñez, 2016) which could explain the co-occurrence among alien species (Fig. 2A), and suggest a potential invasional meltdown (Simberloff & Von Holle, 1999)

Different factors may explain why alien species tended to co-occur with each other (Fig. 2A). Although propagule pressure could explain alien species co-occurrence patterns (Colautti, Grigorovich, & MacIsaac, 2006), the aggregation of alien species in certain quadrats within grids (64 m^2) makes this an unlikely explanation (propagule pressure is unlikely to be different at that scale). Disturbance could also explain the aggregation of alien species in species-poor, high-biomass areas (Hobbs & Huenneke, 1992; P. Pyšek et al., 2010). However, species are unlikely to associate with disturbed areas only in their non-native range. Further, the sites sampled were chosen to have close-to-natural disturbance regimes (Fraser et al., 2014, 2015). This is evidenced by the generally low average number/proportion of alien species per site and the accumulation of litter biomass: litter biomass represents 26% of the total biomass across sites, which is within the range observed for natural grasslands (Coupland, 1979) (Appendix S1). Alien species also showed similar habitat preferences (Chytrý et al., 2008) for high-biomass areas where competition is likely to be strong (Grime, 1973) and nutrient availability is likely higher (Thomsen & D'Antonio, 2007). Determining why species tend to associate with these habitats in their non-native range is beyond the scope of this study. Yet, evidence generally suggests that escaping from natural enemies (herbivores, pathogens, 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 areas in their non-native range was a highly consistent result across the species examined in this study. Although nutrient availability tends to favour the growth of grasses over forbs (You et al., 2017), both were associated with high biomass areas in their non-native range (Appendix S6). Further, short-lived species are generally thought to be more successful invaders over long-lived species (Petr Pyšek & Richardson, 2007). However, no advantages of short- over long-lived species have been found in sites with close-to-natural disturbances (Catford et al., 2019), such as our. Consistent with global trends (van Kleunen et al., 2015), our sampling was not balanced by region, but rather species were mainly from Eurasia, and most were introduced to North America. Yet, co-occurrence patterns were consistent, independent upon where species were introduced to (Appendix S4) or from (Appendix S7). Eurasian and/or European species have a long history of association with human activities (MacDougall et al., 2018) which likely enabled their introduction and their potential arrival into similar general areas within the non-native range (Hodkinson & Thompson, 1997). However, since species co-occurrence patterns (Fig. 2A, B) and overall habitat-use at local scales (Fig. 2C, D) were not inherent properties of the species, but rather emerge following introduction, species from other biogeographical regions could also respond similarly to being introduced.

The differences found in how alien species associate with the resident community at home vs. away can have important implications for management and conservation. We found alien species to aggregate, thus not causing changes throughout the community, but rather to potentially cause greater changes in particular areas. 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 is consistent with other studies (Rauschert & Shea, 2012). Since the co-occurrence of alien species appears to be widespread (see also (Kuebbing et al., 2013), communities should be managed talking this into consideration. Single species management strategies may result in the increased abundance of other alien species (Bush, Seastedt, & Buckner, 2007) and to a greater replacement of native communities. Understanding what determines alien species co-occurrence patterns may also help in managing these systems. Future studies should aim at understanding the mechanisms behind these origin-dependent associations.

ACKNOWLEDGMENT

SJ.F.C. was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant and Discovery Grant Supplement. A.F. was supported by Fundação Grupo Boticário, Brazil (0153_2011_PR) and grants from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, 306170/2015-9, 303988/2018-5 and 310022/2015-0). B.B., B.E. and S.U. were supported by the PIRE Mongolia project (U.S. National Science Foundation OISE 0729786) and by the Taylor Family-Asia Foundation Endowed Chair in Ecology and Conservation Biology. G.E.O. was supported by a grant from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, 310022/2015-0). K.K., M.M. and M.Z. were supported by the Estonian Research Council (IUT 20-28) and the European Regional Development Fund (Centre of Excellence EcolChange). S.B. was supported by the GINOP-2.3.2-15-2016-00019 project. L.E. was supported by grants from CONICET, UNC and IAI. L.H.F. was supported by an NSERC Discovery Grant and an NSERC Industrial Research Chair.

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 ini-tial draft of the manuscript. All authors contributed to editing of sub-sequent drafts.

DATA ACCESSIBILITY

The data that support the findings of this study are openly avail-able in the Dryad repository at https ://doi.org/10.5061/dryad.3ffbg 79dh.

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Data accessibility statement: Data will be made available in the Dryad data repository, upon acceptance.

Figures

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

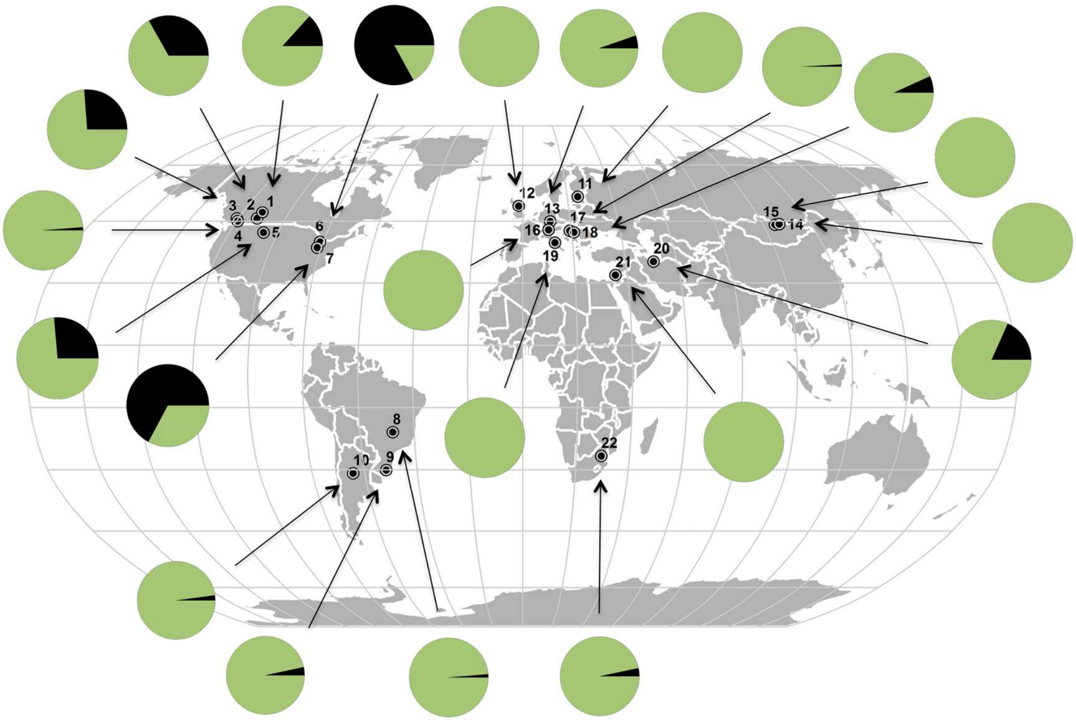
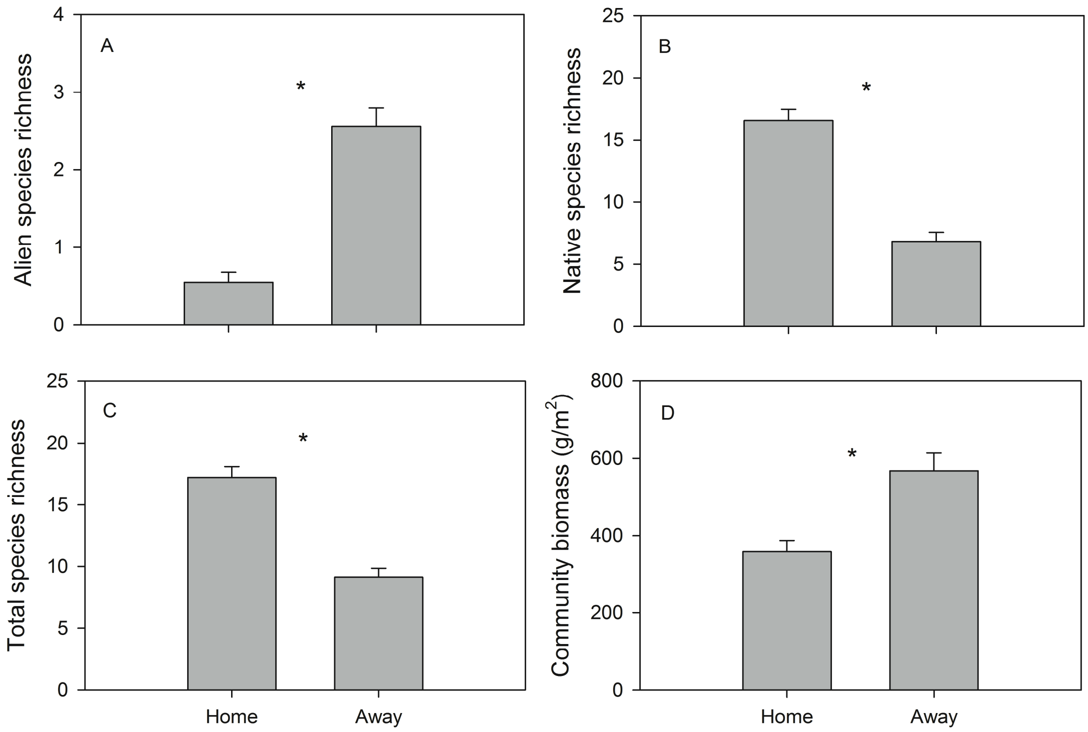


Figure 2: Characteristics of the communities (quadrats) in which species are found in their native (home) and non-native (away) range. (A) Alien species richness, (B) native species richness, (C), total species richness and (D) community biomass of the quadrats occupied by species at home vs. away. Bars indicate mean ± se. Means per treatment were calculated by averaging species' means. See Appendix S2 for details on sample size for each of the 46 species included and Appendix S3 for statistical outputs. * indicates significant differences among treatments ($P < 0.05$).



Supporting Information

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

Appendix S1 – Study sites

Table S1.1: Subset of Herbaceous Diversity Network sites used in this study. Grids are 8x8 m areas, each with 64 1-m2 quadrats. Number of native species, number of alien species, percent of alien species , total aboveground biomass and litter biomass per quadrat were calculated per site.

Site ID	Country	N° of grids	Number of native species per quadrat (mean ± se)	Number of alien species per quadrat (mean ± se)	Percent of alien species per quadrat (mean ± se)	Total aboveground biomass per quadrat (g/m^2) (mean ± se)	Litter biomass per quadrat (g/m^2) (mean ± se)
1	Canada	6	10.1 ± 0.23	0.9 ± 0.06	13.3 ± 1.12	293.8 ± 8.1	82.4 ± 4.10
2	Canada	6	5.2 ± 0.20	1.7 ± 0.12	33.2 ± 2.32	473.7 ± 16.2	183.0 ± 7.51
3	Canada	14	4.8 ± 0.07	1.6 ± 0.04	26.2 ± 0.82	489.3 ± 15.4	176.8 ± 7.21
4	Canada	4	13 ± 0.19	0.2 ± 0.03	1.2 ± 0.17	280.7 ± 10.0	51.9 ± 2.42
5	USA	6	4.5 ± 0.09	2 ± 0.10	26.4 ± 1.18	337.1 ± 12.4	94.3 ± 4.67
6	Canada	2	1.1 ± 0.08	4.4 ± 0.08	83.0 ± 1.21	390.8 ± 7.5	150.8 ± 4.61
7	USA	6	1.7 ± 0.13	0.9 ± 0.03	67.2 ± 2.16	1592.7 ± 59.9	855.9 ± 35.66
8	Brazil	4	5.2 ± 0.22	0.04 ± 0.01	1.3 ± 0.46	472.1 ± 13.0	118.7 ± 5.25
9	Brazil	2	26.7 ± 0.53	0.9 ± 0.05	3.4 ± 0.21	215.8 ± 4.7	39.1 ± 1.36
10	Argentina	4	19.6 ± 0.49	0.3 ± 0.03	2.1 ± 0.25	959.3 ± 48.7	322.5 ± 18.83
11	Estonia	10	18.7 ± 0.32	0	0	479.0 ± 13.6	120.7 ± 6.08
12	UK	4	10.9 ± 0.13	0	0	568.4 ± 22.2	0
13	Germany	6	12.6 ± 0.42	0.8 ± 0.04	5.3 ± 0.29	416.7 ± 15.5	94.0 ± 7.49
14*	Mongolia	4	15.9 ± 0.24	0	0	NA	NA
15	Mongolia	6	14.1 ± 0.21	0	0	317.8 ± 5.7	87.5 ± 2.78
16	Austria	6	22.6 ± 0.37	0	0	324.9 ± 5.8	11.6 ± 0.64
17	Hungary	2	5.7 ± 0.16	0.1 ± 0.02	0.9 ± 0.33	112.4 ± 4.2	77.2 ± 3.93
18	Hungary	2	16.3 ± 0.26	1.2 ± 0.06	6.8 ± 0.36	605.2 ± 12.1	242.9 ± 8.44
19	Italy	6	19.9 ± 0.25	0	0	365.3 ± 6.2	33.5 ± 1.49
20	Iran	11	9.6 ± 0.12	2.4 ± 0.06	18.3 ± 0.42	431.0 ± 11.0	17.9 ± 0.50
21	Israel	6	16.4 ± 0.43	0	0	288.2 ± 8.6	14.9 ± 1.15
22	South Africa	6	7.8 ± 0.17	0.1 ± 0.02	3.3 ± 0.49	533.4 ± 16.7	71.2 ± 2.82

* Litter biomass was not harvested at this site, and therefore a measure of total biomass was unavailable.

Appendix S2 – Study species

Table S2.2: List of the 46 species for which we have data at home (native range) and away (non-native range). Only the portion of the native and non-native range where species was encountered is indicated. 26 species were considered invasive in the non-native range, while 23 species considered naturalized (non-invasive) in the non-native range. Note that some species may be considered invasive in some non-native range, while not in others.

References (Ref.) are provided for the classification of species as native or alien, and of alien species into naturalized or invasive. Sample size (n, number of quadrats) is provided for the native range, followed by the non-native range.

Species	Native range	Non-native range	Invasive status	Ref.	n	Family	Growth Form	Life cycle
Agropyron cristatum	Mongolia	AB Canada BC, Canada	Naturalized	1, 2	83, 28	Poaceae	Grass	Perennial
Agrostis capillaris	Germany Austria UK Estonia	OH, USA	Naturalized	3-6	319, 3	Poaceae	Grass	Perennial
Agrostis gigantea	Mongolia	BC, Canada	Naturalized	2, 7	3, 34	Poaceae	Grass	Perennial
Agrostis stolonifera	Austria Estonia	BC, Canada	Naturalized	2-5, 7	80, 26	Poaceae	Grass	Perennial
Alyssum simplex	Italy	Iran	Invasive	8-11	45, 1	Brassicaceae	Forb	Annual
Anagallis arvensis	Israel	Iran	Invasive	8, 9, 12	82, 124	Primulaceae	Forb	Annual/ biennial

Arrhenatherum elatius	Hungary Germany Austria Italy Estonia	ON, Canada	Naturalized	2, 3, 5, 10, 11, 13, 14	330, 88	Poaceae	Grass	Perennial
Astragalus cicer	Hungary	AB, Canada	Naturalized	2, 14, 15	47, 5	Fabaceae	Forb	Perennial
Axyris amaranthoides	Mongolia	AB, Canada	Naturalized	2	15, 62	Amaranthaceae	Forb	Annual
Bromus inermis	Mongolia	AB, Canada ON, Canada MT, USA	Invasive	1, 2, 7, 16, 17	172, 408	Poaceae	Grass	Perennial
Bromus squarrosus	Hungary	BC, Canada	Naturalized	2, 14	23, 78	Poaceae	Grass	Annual
Bromus tectorum	Iran	BC, Canada OH, USA MT, USA	Invasive	2, 6, 8, 9, 17	65, 164	Poaceae	Grass	Annual
Buglossoides arvensis	Hungary Italy	Iran	Invasive	8-11, 14	43, 58	Boraginaceae	Forb	Annual
Capsella bursapastoris	Germany Israel	Iran	Invasive	3, 4, 8, 9, 12	25, 125	Brassicaceae	Forb	Annual
Carex stenophylla	AB, Canada	Iran	Invasive	2, 8, 9	289, 176	Cyperaceae	Sedge	Perennial
Cirsium arvense	Italy	AB, Canada Iran OH, USA	Invasive	2, 8-11, 18-20	59, 58	Asteraceae	Forb	Perennial
Convolvulus arvensis	Hungary Germany Italy	MT, USA	Invasive	2-4, 10, 11, 14, 17	178, 21	Convolvulaceae	Forb	Perennial
Cynodon dactylon	Israel South Africa	Hungary Argentina Brazil	Invasive	21-23	58, 95	Poaceae	Grass	Perennial

Daucus carota	Germany Israel	ON, Canada	Naturalized	2-4, 12, 13	65, 36	Apiaceae	Forb	Biennial
Elymus repens	Germany Italy Estonia	AB, Canada BC, Canada	Invasive	2-5, 10, 11, 14, 24, 25	288, 286	Poaceae	Grass	Perennial
Erigeron canadensis	MT, USA	South Africa	Naturalized	2, 26	7, 39	Asteraceae	Forb	Annual/ biennial
Erigeron primulifolium	Brazil	South Africa	Naturalized	26, 27	5, 2	Asteraceae	Forb	Annual/ perennial
Festuca pratensis	Germany Austria UK Estonia	ON, Canada	Naturalized	2-5	204, 6	Poaceae	Grass	Perennial
Galium album	Germany Estonia	ON, Canada	Naturalized	2-5, 13	278, 6	Rubiaceae	Forb	Perennial
Lepidium ruderale	Mongolia	Iran	Invasive	7-9	1, 5	Brassicaceae	Forb	Annual/ biennial
Linaria genistifolia	Hungary	BC, Canada	Invasive	2, 14	3, 49	Plantaginaceae	Forb	Perennial
Lolium perenne	Germany UK Italy	ON, Canada Iran	Invasive	2-4, 8-11	307, 188	Poaceae	Grass	Perennial
Lotus corniculatus	Hungary Germany Austria UK Italy Estonia	OH, USA	Invasive	3-5, 10, 11, 13, 14, 28	299, 4	Fabaceae	Forb	Perennial
Lysimachia nummularia	Estonia	OH, USA	Invasive	5, 28, 29	13, 14	Primulaceae	Forb	Perennial

Malva parviflora	Israel	Iran	Invasive	8, 9, 12	5, 9	Malvaceae	Forb	Annual/ biennial/ perennial
Medicago lupulina	Iran Italy Estonia	BC, Canada MT, USA	Invasive (Canada) Naturalized (US)	2, 5, 8-11, 17	259, 129	Fabaceae	Forb	Annual/ perennial
Medicago minima	Hungary	Iran	Invasive	8, 9, 14	11, 17	Fabaceae	Forb	Annual
Medicago polymorpha	Israel	Iran	Invasive	8, 9, 12	40, 5	Fabaceae	Forb	Annual/ biennial
Phleum pratense	Germany Italy Estonia	BC, Canada	Naturalized	2-5, 10, 11	223, 58	Poaceae	Grass	Perennial
Plantago lanceolata	Hungary UK Italy Estonia	Germany ON, Canada Iran	Naturalized (Germany, Canada) Invasive (Iran)	2-5, 8-11, 14	452, 454	Plantaginaceae	Forb	Perennial
Plantago ovata	Israel	Iran	Invasive	8, 9, 12	4, 3	Plantaginaceae	Forb	Annual
Poa bulbosa	Hungary Israel Italy	Iran	Invasive	8-12, 14	103, 171	Poaceae	Grass	Perennial
Polygonum aviculare	Mongolia	MT, USA	Invasive	2, 7, 17, 24	2, 1	Polygonaceae	Forb	Annual/ perennial
Rhamnus cathartica	Estonia	ON, Canada OH, USA	Invasive	2, 5, 28, 30	25, 3	Rhamnaceae	Shrub	Perennial
Rumex acetosella	Germany	BC, Canada	Naturalized	2-4, 13, 31	32, 2	Polygonaceae	Forb	Perennial
Securigera varia	Hungary	ON, Canada	Naturalized	2, 14	30, 127	Fabaceae	Forb	Perennial
Tagetes minuta	Argentina	South Africa	Naturalized	21, 26	84, 5	Asteraceae	Forb	Annual

Taraxacum campylodes	Germany Mongolia Austria Italy Estonia	AB, Canada BC, Canada MT, USA Argentina	Naturalized (Canada) Invasive (Argentina, USA)	2-5, 10, 11, 21, 24, 31, 32	293, 675	Asteraceae	Forb	Perennial
Trifolium pratense	Germany Austria Iran UK Italy Estonia	BC, Canada	Naturalized	2-5, 8-11	637, 50	Fabaceae	Forb	Biennial/ perennial
Veronica officinalis	Estonia	ON, Canada	Naturalized	2, 5	22, 1	Plantaginaceae	Forb	Perennial
Vicia sativa	Italy	Hungary	Naturalized	3, 4, 10, 11, 14	11, 6	Fabaceae	Forb	Annual

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Appendix S3 – All species vs. Eurasian species

Table S3.3: Differences at home vs. away for the 42 Eurasian species and for all 46 species. General and generalized linear mixed model results of the effect of species range (home vs. away) on community biomass, total species richness, native species richness and alien species richness of the areas occupied. SE = standard error

Biogeogr. Origin	Resp. variable	Coefficient ± SE	p-value
Eurasian	Total biomass	-0.11 ± 0.03	< 0.001
(42 spp)	Total species richness	0.63 ± 0.05	< 0.001
	Native species richness	1.03 ± 0.07	< 0.001
	Alien species richness	-3.73 ± 0.29	< 0.001
All 46 species	Total biomass	-0.11 ± 0.03	< 0.001
	Total species richness	0.61 ± 0.05	< 0.001
	Native species richness	0.98 ± 0.07	< 0.001
	Exotic species richness	-3.34 ± 0.27	< 0.001

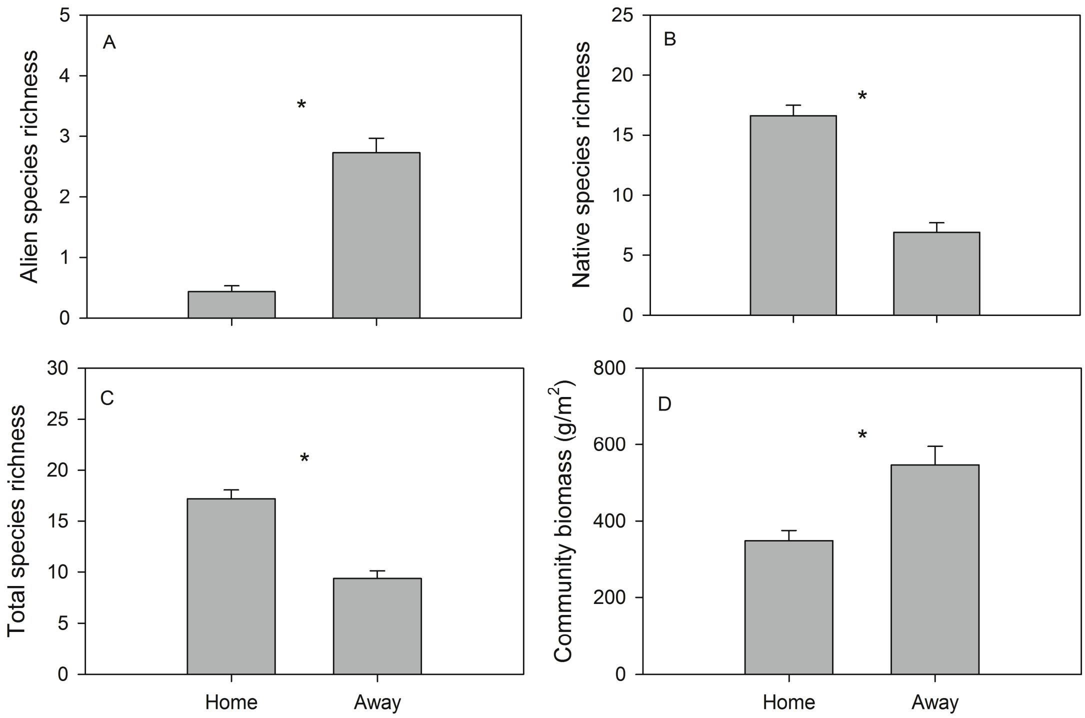

Figure S3.1: Characteristics of the communities (quadrats) in which the 42 Eurasian species are found in their native (home) and non-native (away) range. (A) Community biomass, (B) total species richness, (C) native species richness and (D) alien species richness of the quadrats occupied by species at home vs. away. Bars indicate mean ± se. Means per treatment were calculated by averaging species' means. See Appendix S2 for details on sample size for each of the 46 species included and Table S3.3 for statistical outputs. * indicates significant differences among treatments ($P < 0.05$).

Appendix S4 – Species introduced to North America vs. elsewhere

Table S4.4: Differences at home vs. away for species introduced to North America and elsewhere. General and generalized linear mixed model results of the effect of species range (home vs. away) on community biomass, total species richness, native species richness and alien species richness of the areas occupied. SE = standard error.

Introd. biogeogr range	**Resp. variable**	**Coefficient ± SE**	**p-value**
North America	Total biomass	-0.09 ± 0.03	0.0085
(30 spp)	Total species richness	0.91 ± 0.05	< 0.001
	Native species richness	1.41 ± 0.07	< 0.001
	Alien species richness	-3.802 ± 0.34	< 0.001
Other	Total biomass	-0.16 ± 0.05	0.001
(20 spp)	Total species richness	0.26 ± 0.08	< 0.001
	Native species richness	0.37 ± 0.08	< 0.001
	Alien species richness	-3.57 ± 0.49	< 0.001

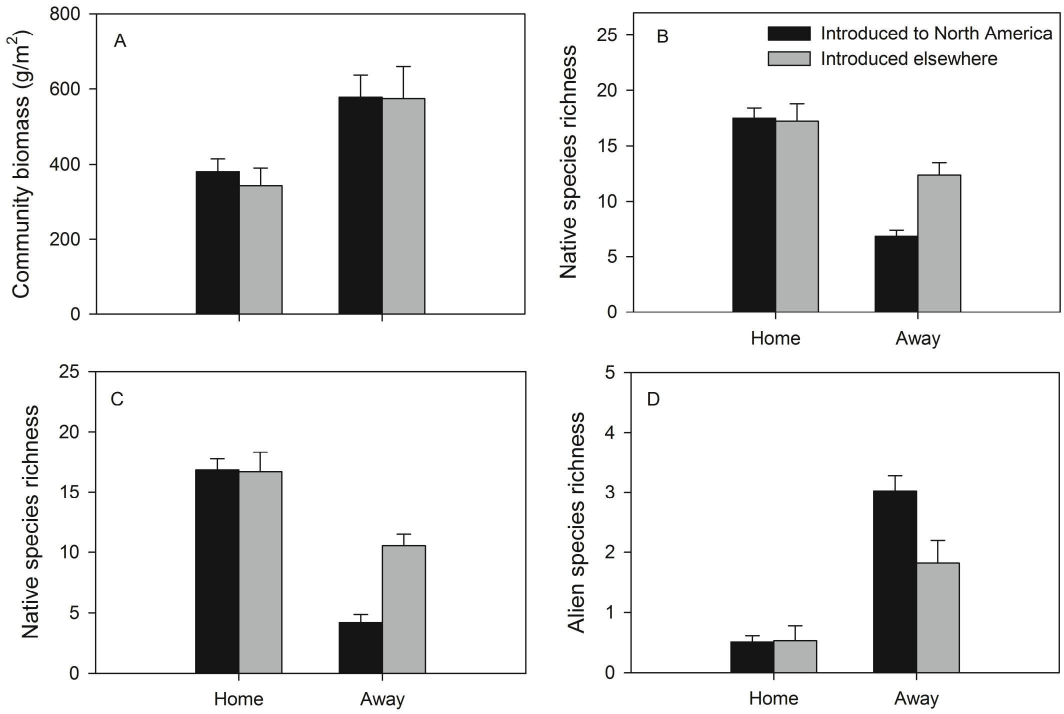

Figure S4.2: Characteristics of the communities in which species are found in their native (home) and non-native (away) range, for species introduced to North America and elsewhere. Means per treatment were calculated by averaging species' means. Bars indicate mean ± se. See Table S4.4 for details in sample size and statistical outputs.

Appendix S5 – Species' life cycles

Table S5.5: Differences at home vs. away across life cycles. General and generalized linear mixed model results of the effect of species range (home vs. away) on community biomass, total species richness, native species richness and alien species richness of the areas occupied. SE = standard error.

Life cycle	Resp. variable	Coefficient ± SE	p-value
Short lived	Total biomass	-0.19 ± 0.07	0.007
(15 spp)	Total species richness	0.38 ± 0.12	0.001
	Native species richness	0.60 ± 0.15	< 0.001
	Alien species richness	-2.52 ± 0.07	< 0.001
Longed lived	Total biomass	-0.09 ± 0.03	0.009
(26 spp)	Total species richness	0.67 ± 0.05	< 0.001
	Native species richness	1.07 ± 0.08	< 0.001
	Alien species richness	-3.57 ± 0.03	< 0.001

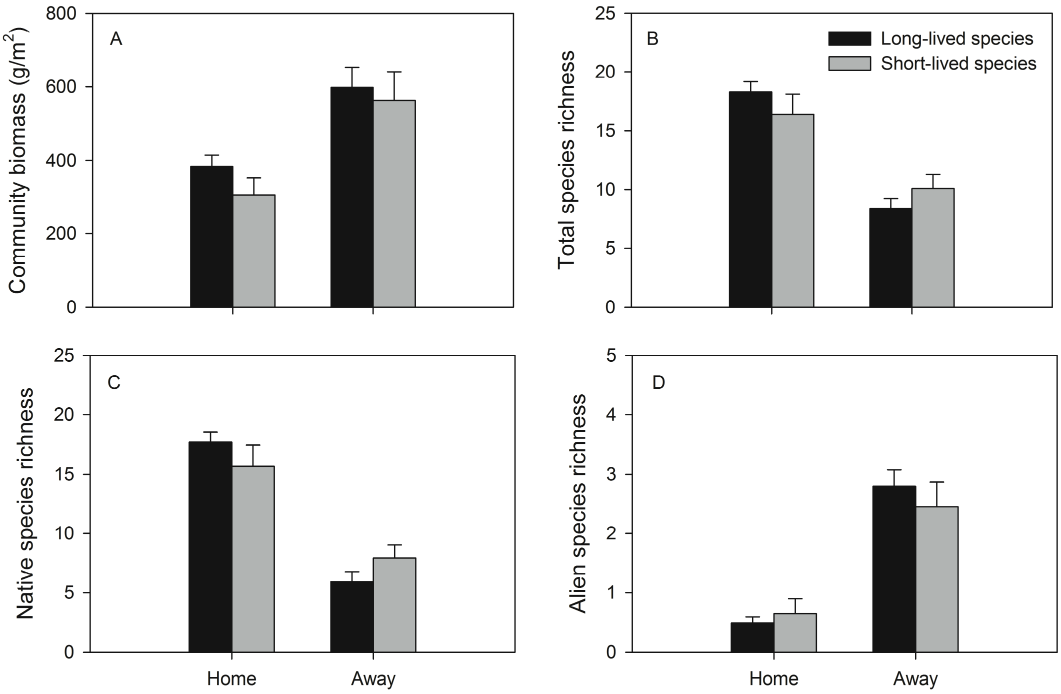

Figure S5.3: Characteristics of the communities in which species are found in their native (home) and non-native (away) range, depending on life cycle. Means per treatment were calculated by averaging species' means. Bars indicate mean ± se. See Table S5.5 for details in sample size and statistical outputs.

Appendix S6 – Species' growth forms

Table S6.6: Differences at home vs. away across growth forms. General and generalized linear mixed model results of the effect of species range (home vs. away) on community biomass, total species richness, native species richness and alien species richness of the areas occupied. SE = standard error.

Growth forms	**Resp. variable**	**Coefficient ± SE**	**p-value**
Grasses	Total biomass	-0.12 ± 0.05	0.02
(14 spp)	Total species richness	0.61 ± 0.08	< 0.001
	Native species richness	1.06 ± 0.12	< 0.001
	Alien species richness	-3.21 ± 0.43	< 0.001
Forbs	Total biomass	-0.11 ± 0.04	0.005
(30 spp)	Total species richness	0.72 ± 0.06	< 0.001
	Native species richness	1.02 ± 0.08	< 0.001
	Alien species richness	-3.49 ± 0.35	< 0.001

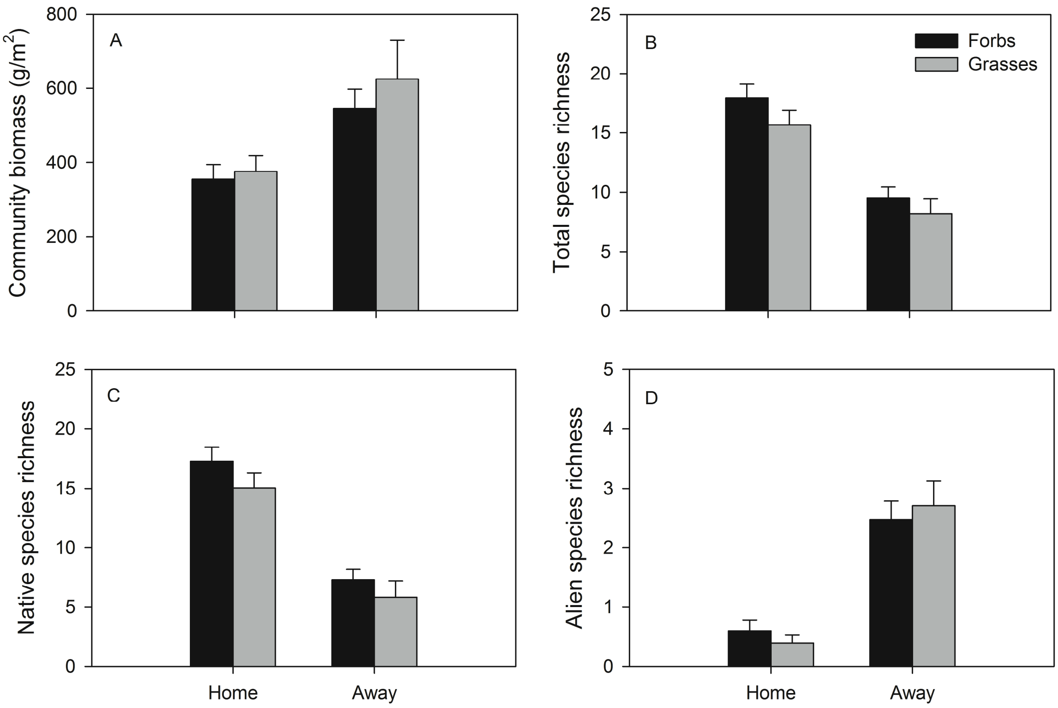

Figure S6.4: Characteristics of the communities in which species are found in their native (home) and non-native (away) range, depending on growth form (forbs, grasses). Means per treatment were calculated by averaging species' means. Bars indicate mean ± se. See Table S6.6 for details in sample size and statistical outputs.

Appendix S7 – European vs. non-European species

Table S7.7: Differences at home vs. away for European and non-European species. General and generalized linear mixed model results of the effect of species range (home vs. away) on community biomass, total species richness, native species richness and alien species richness of the areas occupied. SE = standard error

Biogeogr. Origin	**Resp. variable**	**Coefficient ± SE**	**p-value**
European	Total biomass	-0.09 ± 0.04	0.02
(29 spp)	Total species richness	0.71 ± 0.05	< 0.001
	Native species richness	1.08 ± 0.07	< 0.001
	Alien species richness	-3.51 ± 0.31	< 0.001
Non-European	Total biomass	-0.17 ± 0.05	0.002
(23 spp)	Total species richness	0.53 ± 0.07	< 0.001
	Native species richness	0.53 ± 0.07	< 0.001
	Alien species richness	-2.61 ± 0.33	< 0.001

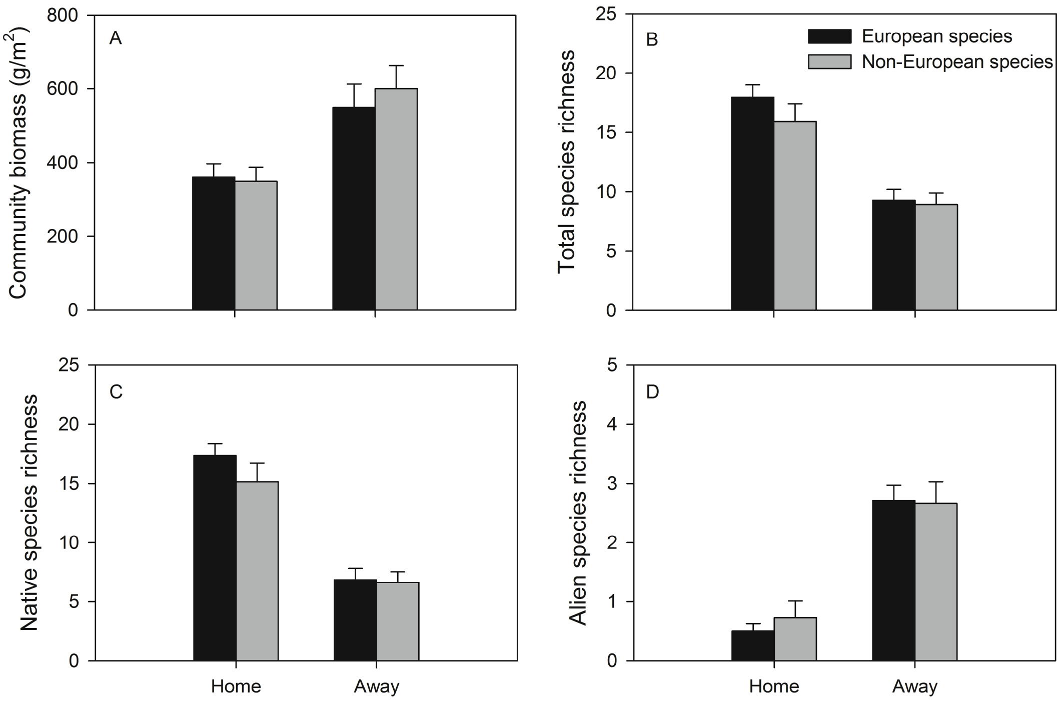

Figure S7.5: Characteristics of the communities in which species are found in their native (home) and non-native (away) range, for European and non-European species. Means per treatment were calculated by averaging species' means. Bars indicate mean ± se. See Table S7.7 for details in sample size and statistical outputs.

Appendix S8 – Species-specific differences at home vs. away

Table S8.8: Species-specific differences in characteristics of the communities occupied at home vs. away. Linear model results of the effect of species range (home vs. away) on community biomass, total species richness, native species richness and alien species richness of the areas occupied. SE = standard error.

Species	Response variables	Coefficient ± SE	P-value
Agropyron cristatum	Total biomass	-0.45 ± 0.04	< 0.001
	Total species richness	1.03 ± 0.08	< 0.001
	Native species richness	2.17 ± 0.14	< 0.001
	Alien species richness	-2.09 ± 0.16	< 0.001
Agrostis capillaris	Total biomass	-0.47 ± 0.13	< 0.001
	Total species richness	3.06 ± 0.95	0.001
	Native species richness	17.3 ± 728	0.981
	Alien species richness	-2.44 ± 0.58	0.675
Agrostis gigantea	Total biomass		
	Total species richness	0.49 ± 0.17	0.004
	Native species richness	0.87 ± 0.18	< 0.001
	Alien species richness	-18.18 ± 2002	0.993
Agrostis stolonifera	Total biomass	-0.05 ± 0.03	0.126
	Total species richness	-0.43 ± 0.87	0.619
	Native species richness	0.1 ± 0.05	0.060
	Alien species richness	0.05 ± 0.06	0.384
Alyssum simplex	Total biomass	-0.64 ± 0.10	< 0.001
	Total species richness	0.20 ± 0.24	0.42
	Native species richness	0.32 ± 0.26	0.215
	Alien species richness	-26.99 ± 46535	1.00
Anagallis arvensis	Total biomass	-0.79 ± 0.03	< 0.001
	Total species richness	0.70 ± 0.03	< 0.001
	Native species richness	0.85 ± 0.04	< 0.001
	Alien species richness	-.20.94 ± 1716	0.99
Arrhenatherum elatius	Total biomass	-0.04 ± 0.02	0.05
	Total species richness	1.55 ± 0.07	< 0.001
	Native species richness	3.03 ± 1.65	< 0.001
	Alien species richness	-1.11 ± 0.08	< 0.001
Astragalus cicer	Total biomass	0.08 ± 0.05	0.111
	Total species richness	0.87 ± 0.17	< 0.001

	Native species richness	0.87 ± 0.18	< 0.001
	Alien species richness	0.56 ± 0.51	0.275
Axyris amaranthoides	Total biomass	-0.20 ± 0.07	0.004
	Total species richness	0.79 ± 0.09	< 0.001
	Native species richness	1.57 ± 0.19	< 0.001
	Alien species richness	-3.03 ± 0.58	< 0.001
Bromus inermis	Total biomass	-0.12 ± 0.02	< 0.001
	Total species richness	0.67 ± 0.04	< 0.001
	Native species richness	1.16 ± 0.06	< 0.001
	Alien species richness	-5.70 ± 0.71	<0.001
Bromus squarrosus	Total biomass	-0.12 ± 0.04	0.003
	Total species richness	-0.07 ± 0.09	0.386
	Native species richness	-0.04 ± 0.09	0.642
	Alien species richness	-3.44 ± 1.00	<0.001
Bromus tectorum	Total biomass	0.16 ± 0.03	< 0.001
	Total species richness	0.04 ± 0.06	0.452
	Native species richness	0.22 ± 0.06	< 0.001
	Alien species richness	-0.44 ± 0.11	< 0.001
Buglossoides arvensis	Total biomass	-0.42 ± 0.05	< 0.001
	Total species richness	-0.41 ± 0.10	< 0.001
	Native species richness	-0.14 ± 0.11	0.185
	Alien species richness	-3.84 ± 0.50	< 0.001
Capsella bursapastoris	Total biomass	-0.06 ± 0.06	0.316
	Total species richness	0.26 ± 0.05	< 0.001
	Native species richness	0.43 ± 0.05	< 0.001
	Alien species richness	-0.23 ± 0.13	0.06
Carex stenophylla	Total biomass	-0.13 ± 0.02	< 0.001
	Total species richness	-0.33 ± 0.03	< 0.001
	Native species richness	-0.16 ± 0.03	< 0.001
	Alien species richness	-0.39 ± 0.06	< 0.001
Cirsium arvense	Total biomass	0.15 ± 0.03	< 0.001
	Total species richness	1.12 ± 0.05	< 0.001
	Native species richness	1.38 ± 0.06	< 0.001
	Alien species richness	-21.2 ± 2023	0.992
Convolvulus arvensis	Total biomass	-0.12 ± 0.04	0.006
	Total species richness	1.40 ± 0.10	< 0.001
	Native species richness	1.84 ± 0.14	< 0.001
	Alien species richness	-1.02 ± 0.16	< 0.001
Cynodon dactylon	Total biomass	-0.13 ± 0.03	< 0.001
	Total species richness	-0.29 ± 0.05	< 0.001
	Native species richness	-0.31 ± 0.05	< 0.001
	Alien species richness	-2.39 ± 0.59	< 0.001
Daucus carota	Total biomass	-0.74 ± 0.07	< 0.001
	Total species richness	1.52 ± 0.07	< 0.001
	Native species richness	2.75 ± 0.13	< 0.001

	Alien species richness	-1.70 ± 0.16	< 0.001
Elymus repens	Total biomass	-0.36 ± 0.02	< 0.001
	Total species richness	0.90 ± 0.04	< 0.001
	Native species richness	1.51 ± 0.05	< 0.001
	Alien species richness	-1.93 ± 0.1	< 0.001
Erigeron canadensis	Total biomass	-0.57 ± 0.03	< 0.001
	Total species richness	0.93 ± 0.15	< 0.001
	Native species richness	0.36 ± 0.18	0.045
	Alien species richness	4.02 ± 0.61	< 0.001
Erigeron primulifolium	Total biomass	-0.59 ± 0.08	< 0.001
	Total species richness	1.96 ± 0.34	< 0.001
	Native species richness	2.06 ± 0.36	< 0.001
	Alien species richness	0.18 ± 1.15	0.875
Festuca pratensis	Total biomass	0.07 ± 0.10	0.487
	Total species richness	1.17 ± 0.30	< 0.001
	Native species richness	2.31 ± 0.58	< 0.001
	Alien species richness	-2.43 ± 0.28	< 0.001
Galium album	Total biomass	-0.05 ± 0.08	0.524
	Total species richness	1.16 ± 0.22	< 0.001
	Native species richness	2.72 ± 0.47	< 0.001
	Alien species richness	-4.09 ± 0.27	< 0.001
Lepidium ruderale	Total biomass	0.04 ± 0.16	0.835
	Total species richness	-0.83 ± 0.52	0.11
	Native species richness	-0.81 ± 0.52	0.12
	Alien species richness	-17.69 ± 9426	0.999
Linaria genistifolia	Total biomass	-0.50 ± 0.06	< 0.001
	Total species richness	-0.05 ± 0.19	0.781
	Native species richness	0.25 ± 0.20	0.219
	Alien species richness	-20.34 ± 5442	0.997
Lolium perenne	Total biomass	0.20 ± 0.02	< 0.001
	Total species richness	0.61 ± 0.05	< 0.001
	Native species richness	0.91 ± 0.06	< 0.001
	Alien species richness	-4.56 ± 0.38	< 0.001
Lotus corniculatus	Total biomass	-0.47 ± 0.17	0.006
	Total species richness	1.15 ± 0.34	< 0.001
	Native species richness	1.24 ± 0.34	< 0.001
	Alien species richness	-0.68 ± 0.51	0.177
Lysimanchia nummularia	Total biomass	0.15 ± 0.03	< 0.001
	Total species richness	0.52 ± 0.13	< 0.001
	Native species richness	0.59 ± 0.14	< 0.001
	Alien species richness	-21.55 ± 7106	0.998
Malva parviflora	Total biomass	-0.10 ± 0.09	0.315
	Total species richness	-0.05 ± 0.13	0.701
	Native species richness	0.34 ± 0.14	0.016
	Alien species richness	-24.15 ± 18893	0.999

Medicago lupulina	Total biomass	-0.16 ± 0.02	< 0.001
	Total species richness	1.11 ± 0.05	< 0.001
	Native species richness	1.39 ± 0.06	< 0.001
	Alien species richness	-0.68 ± 0.10	< 0.001
Medicago minima	Total biomass	-0.23 ± 0.06	< 0.001
	Total species richness	-0.53 ± 0.13	< 0.001
	Native species richness	-0.41 ± 0.15	0.005
	Alien species richness	-3.52 ± 1.01	< 0.001
Medicago polymorpha	Total biomass	0.01 ± 0.08	0.92
	Total species richness	0.27 ± 0.16	0.08
	Native species richness	0.26 ± 0.16	0.10
	Alien species richness	0.00 ± 0.48	1
Phleum pratense	Total biomass	-0.43 ± 0.03	< 0.001
	Total species richness	1.04 ± 0.08	< 0.001
	Native species richness	1.74 ± 0.11	< 0.001
	Alien species richness	-3.51 ± 0.24	< 0.001
Plantago lanceolata	Total biomass	0.03 ± 0.01	0.008
	Total species richness	0.27 ± 0.02	< 0.001
	Native species richness	0.35 ± 0.02	< 0.001
	Alien species richness	-4.65 ± 0.31	< 0.001
Plantago ovata	Total biomass	-0.32 ± 0.20	0.159
	Total species richness	0.30 ± 0.21	0.155
	Native species richness	0.56 ± 0.23	0.015
	Alien species richness	-22.51 ± 12812	0.999
Poa bulbosa	Total biomass	-0.43 ± 0.03	< 0.001
	Total species richness	0.51 ± 0.06	< 0.001
	Native species richness	0.77 ± 0.06	< 0.001
	Alien species richness	-5.72 ± 1.00	< 0.001
Polygonum aviculare	Total biomass		
	Total species richness	0.91 ± 0.49	0.061
	Native species richness	1.39 ± 0.61	0.024
	Alien species richness	-24.40 ± 49252	0.999
Rhamnus cathartica	Total biomass	-0.29 ± 0.04	< 0.001
	Total species richness	1.68 ± 0.28	< 0.001
	Native species richness	2.63 ± 0.45	< 0.001
	Alien species richness	-24.40 ± 13939	0.998
Rumex acetosella	Total biomass	-0.26 ± 0.16	0.124
	Total species richness	0.11 ± 0.18	0.54
	Native species richness	0.17 ± 0.19	0.377
	Alien species richness	0.82 ± 0.72	0.25
Securigera varia	Total biomass	0.11 ± 0.02	< 0.001
	Total species richness	1.42 ± 0.06	< 0.001
	Native species richness	2.78 ± 0.10	< 0.001
	Alien species richness	-1.22 ± 0.19	< 0.001
Tagetes minuta	Total biomass	-0.12 ± 0.15	0.422

	Total species richness	1.73 ± 0.37	< 0.001
	Native species richness	1.69 ± 0.40	< 0.001
	Alien species richness	16.2 ± 1551	0.992
Taraxacum campylodes	Total biomass	-0.06 ± 0.02	< 0.001
	Total species richness	0.88 ± 0.02	< 0.001
	Native species richness	1.24 ± 0.03	< 0.001
	Alien species richness	-1.93 ± 0.07	< 0.001
Trifolium pratense	Total biomass	-0.65 ± 0.03	< 0.001
	Total species richness	1.12 ± 0.09	< 0.001
	Native species richness	1.81 ± 0.13	< 0.001
	Alien species richness	-2.10 ± 0.10	< 0.001
Veronica officinalis	Total biomass	-0.07 ± 0.08	0.338
	Total species richness	1.48 ± 0.41	< 0.001
	Native species richness	2.57 ± 0.71	< 0.001
	Alien species richness	-26.69 ± 40367	0.999
Vicia sativa	Total biomass	0.04 ± 0.04	0.426
	Total species richness	0.14 ± 0.11	0.194
	Native species richness	0.18 ± 0.11	0.10
	Alien species richness	-20.61 ± 7725	0.998

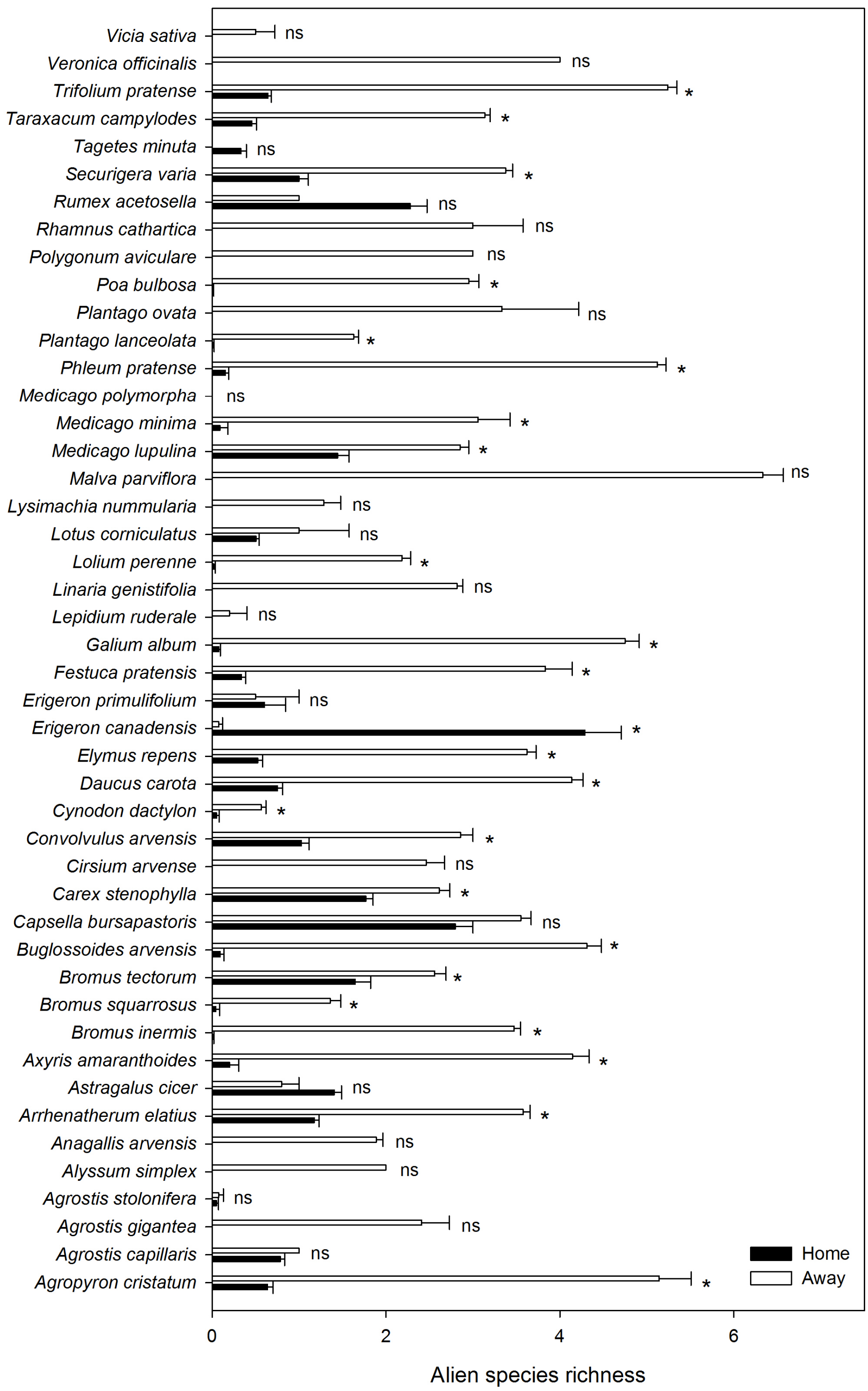

Figure S8.6: Species-specific differences in alien species richness at home vs. away. Bars indicate mean ± se. * indicates significant differences ($P < 0.05$).

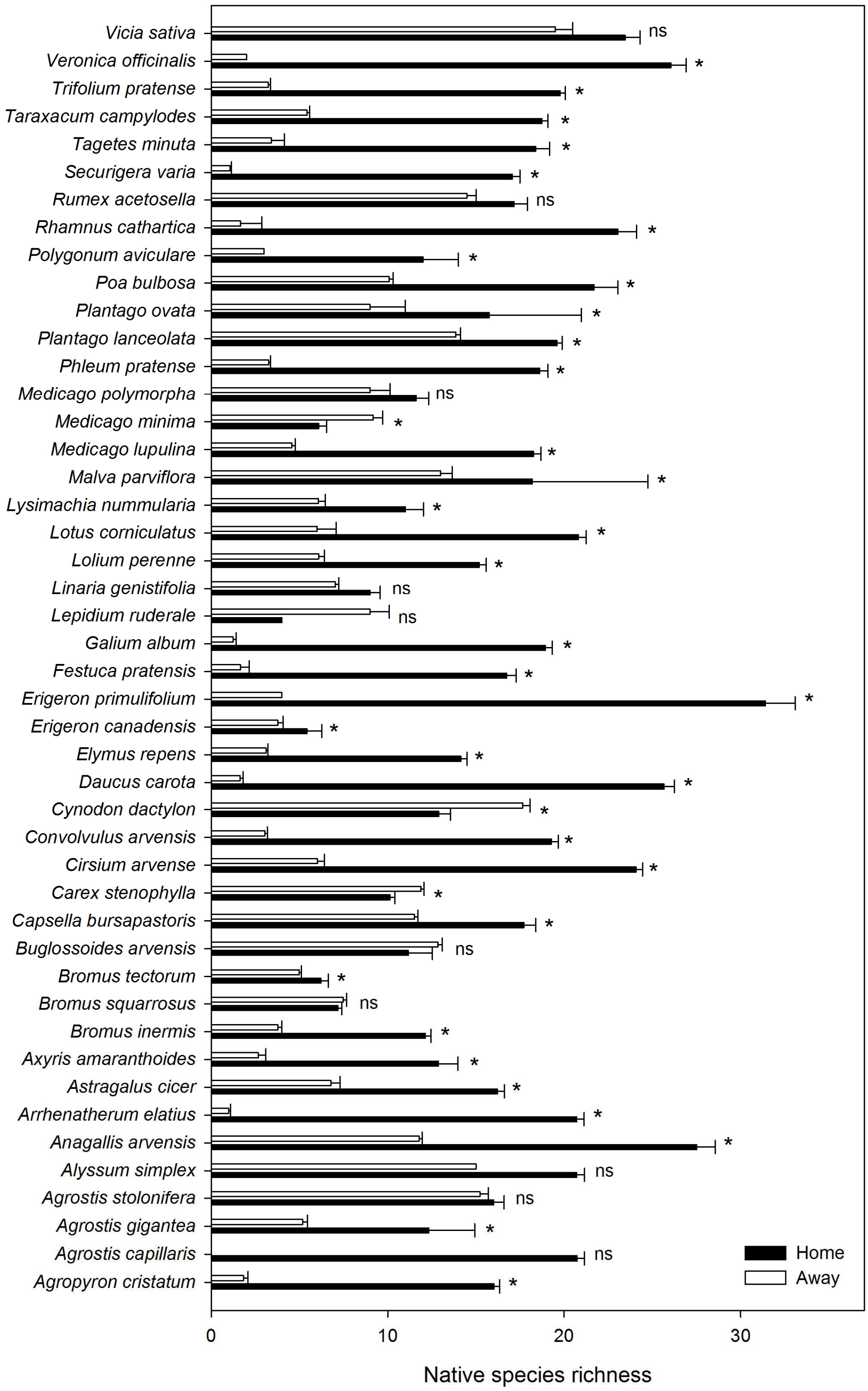

Figure S8.7: Species-specific differences in native species richness at home vs. away. Bars indicate mean ± se. * indicates significant differences ($P < 0.05$).

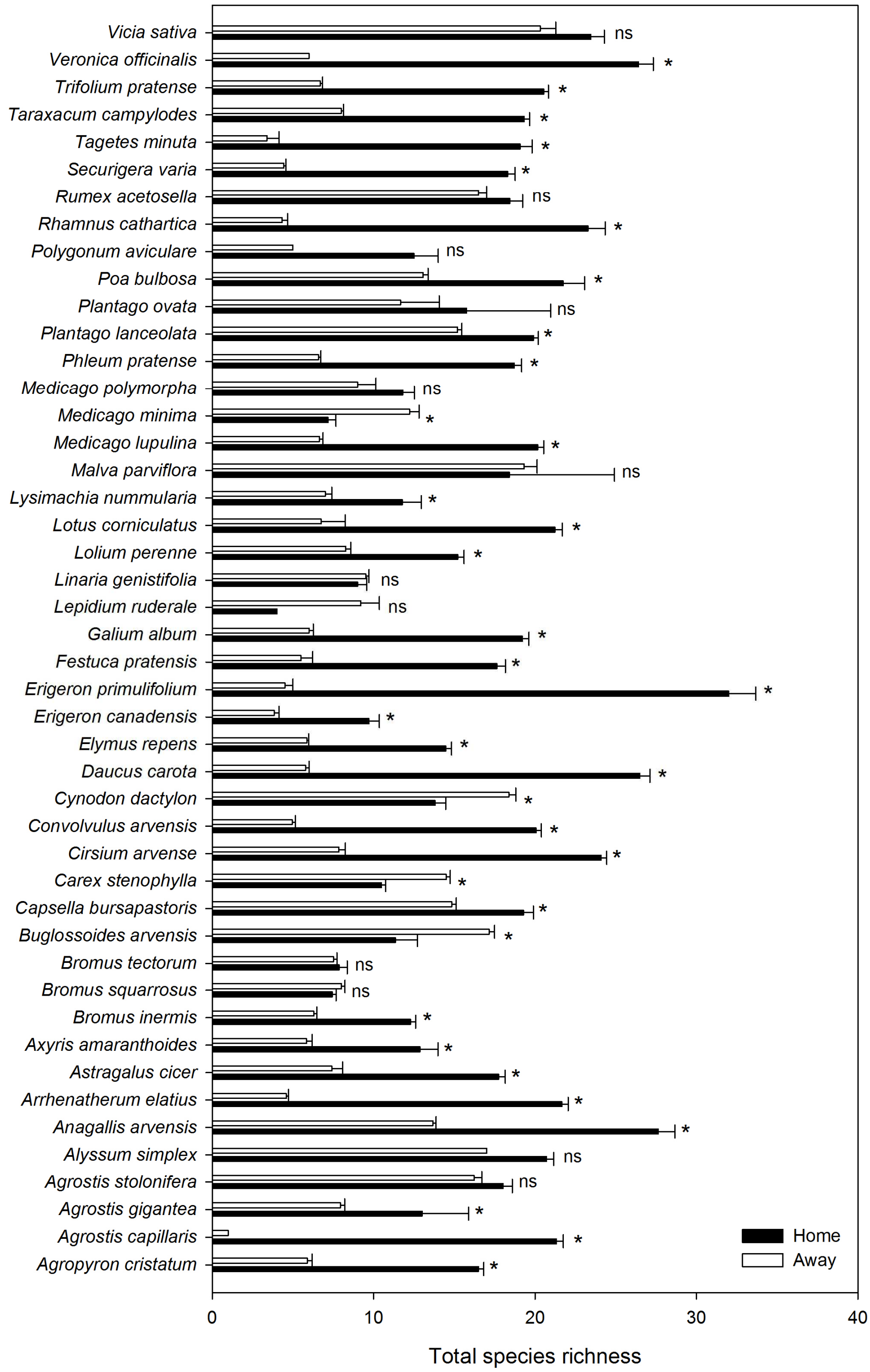

Figure S8.8: Species-specific differences in total species richness at home vs. away. Bars indicate mean ± se. * indicates significant differences ($P < 0.05$).

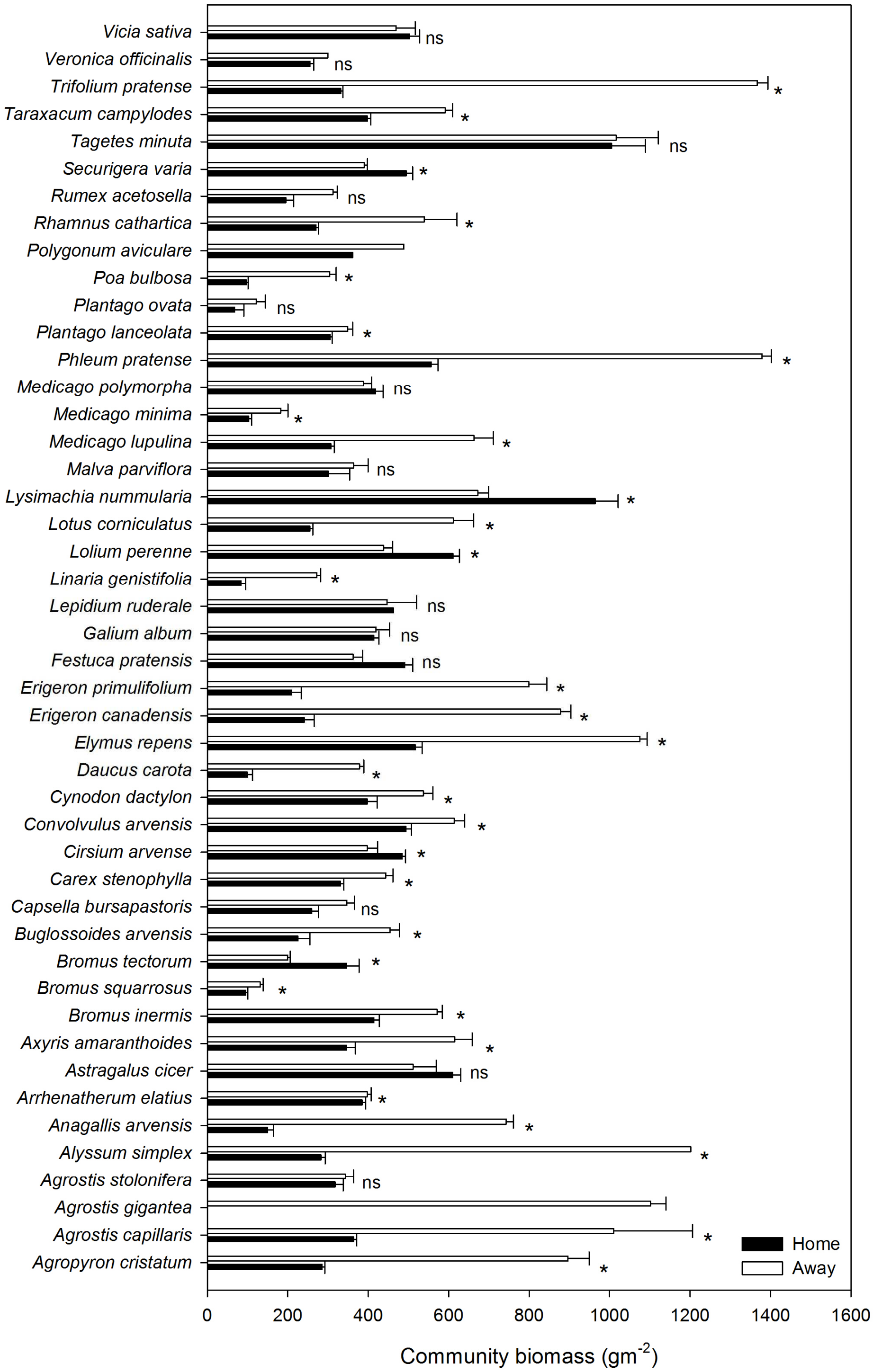

Figure S8.9: Species-specific differences in community biomass at home vs. away. Bars indicate mean ± se. * indicates significant differences ($P < 0.05$).

Appendix S9 – Grid scale results

Table S9.9: Differences at home vs. away for the 46 species at the grid (8 x 8 m) scale. General and generalized linear mixed model results of the effect of species range (home vs. away) on community biomass, total species richness, native species richness and alien species richness of the grids occupied. SE = standard error

Resp. variable	Coefficient ± SE	p-value
Total biomass	-0.12 ± 0.03	< 0.001
Total species richness	1.05 ± 0.09	< 0.001
Native species richness	0.94 ± 0.06	< 0.001
Alien species richness	-1.86 ± 0.01	< 0.001

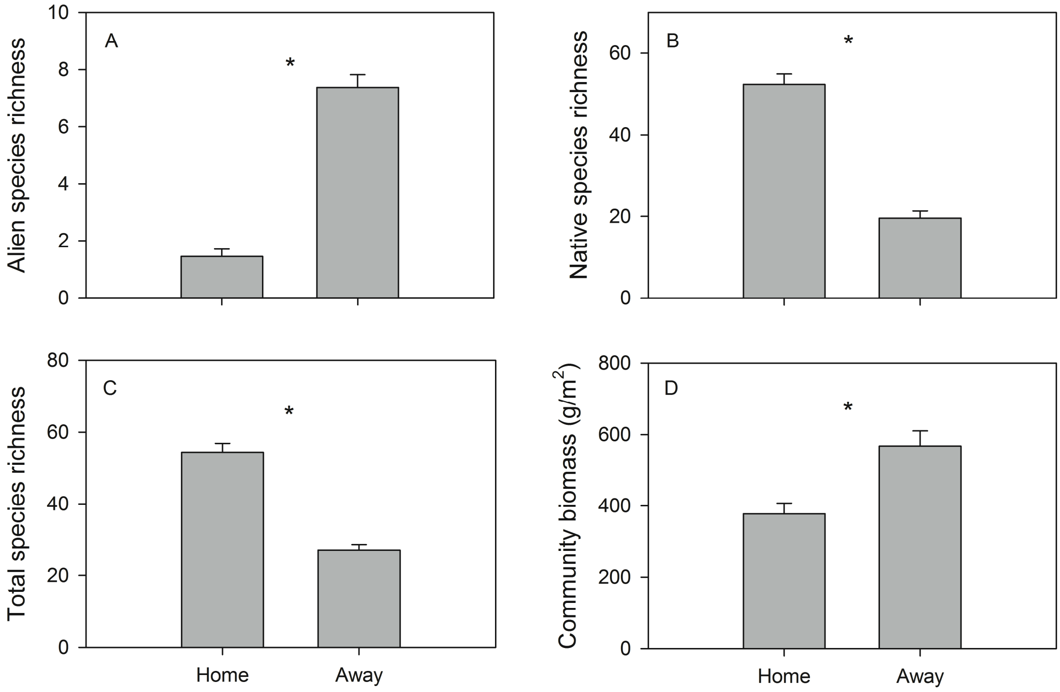

Figure S9.10: Characteristics of the grids (8 x 8 m) in which the 46 species are found in their native (home) and non-native (away) range. (A) Community biomass, (B) total species richness, (C) native species richness and (D) alien species richness of the grids occupied by species at home vs. away. Bars indicate mean ± se. Means per treatment were calculated by averaging species' means. See Table S9.9 for statistical outputs. * indicates significant differences among treatments ($P < 0.05$).