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Abundance of introduced species at home predicts abundance away in herbaceous communities

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ABSTRACT

Many ecosystems worldwide are dominated by introduced plant species, leading to loss of biodiversity and ecosystem function. A common but rarely tested assumption is that these plants are more abundant in introduced versus native communities, because ecological or evolutionary-based shifts in populations underlie invasion success. Here data for 26 herbaceous species at 39 sites, within eight countries, revealed that species abundances were similar at native (home) and introduced (away) sites—grass species were generally abundant home and away, while forbs were low in abundance, but more abundant at home. Sites with six or more of these species had similar community abundance hierarchies, suggesting suites of introduced species are assembling similarly on different continents. Overall, we found substantial changes to populations are not necessarily a pre-condition for invasion success and that increases in species abundance are unusual. Instead, abundance at home predicts abundance away, a potentially useful additional criterion for biosecurity programs.

INTRODUCTION

As non-native plants, particularly invasive species, have come to dominate large tracts of land, it is widely assumed that they are more abundant at sites in their introduced (away) versus native (home) range (Hierro *et al.* 2005; Qian & Ricklefs 2006; van Kleunen *et al.* 2010; Williams *et al.* 2010). This ‘abundance assumption’ is based on the potential changes in the ecological or evolutionary dynamics of populations during the invasion process which may confer an advantage to non-native species in their new ranges (Mitchell *et al.* 2006). For example, the enemy release hypothesis posits that higher abundance in the away range occurs due to release from specialist enemies, whereas native species are susceptible to a variety of controlling factors (enemy release hypothesis, Keane & Crawley 2002). The evolution of increased competitive ability (EICA, Blossey & Notzold 1995) and novel weapons hypotheses (Callaway & Aschehoug 2000) also imply high abundance in the away range due to differences in traits between ranges (increased competitive ability) or differences in the ecological context in which those traits are expressed (novel weapons). Such traits are presumed to be less effective in the native range due to coevolved interactions with competitors and natural enemies. Trait advantages may also develop in the introduced range through ploidy increases or hybridization (Gaskin & Schaal 2002). Regardless of the specific mechanisms, non-native species are often predicted to reach higher abundances in their new ranges, despite lacking evolutionary familiarity with local conditions and small founder populations (i.e. the “invasion paradox”, Sax & Brown 2000; Rout & Callaway 2009).

Testing the ‘abundance assumption’ using standardized data at home and away sites has thus far focused on a small number of species known to be highly abundant in their away

range (see Hinz & Schwarzlander 2004 for summary; e.g. *Centaurea solstitialis*, Hierro *et al.* 2005 and; *Cynoglossum officinale*, Williams *et al.* 2010). Given the comparatively large number of naturalized species found globally, however, it is unclear whether these studies capture general abundance patterns for introduced plant species (van Kleunen *et al.* 2010; Williams *et al.* 2010) or rather reflect unusual, but important, exceptions. An alternative but largely untested scenario is that levels of abundance are similar at sites home and away for most species (Qian & Ricklefs 2006; La Sorte *et al.* 2007; La Sorte & Pysek 2009). This could occur because away communities may be regulated by processes closely resembling those at home, particularly because of the strong interaction between invasion success and human disturbance (La Sorte *et al.* 2007; HilleRisLambers *et al.* 2010). Abundances may also be similar home and away because of physiological or morphological traits of a species that conserves its hierarchy within a community (Baker 1964; Rejmanek & Richardson 1996). If disturbances or environmental conditions between distant sites are similar, and characteristically dominant species are introduced, then these species may thrive similarly in their introduced range. Furthermore, if introductions also include large numbers of co-occurring, dominant and subdominant species, as can occur in agronomic systems, it is even conceivable that similar communities may develop home and away.

To test the ‘abundance assumption’, we compared the levels of abundance for 26 species at 39 herbaceous dominated communities located mainly within New Zealand, Switzerland, USA and the United Kingdom, but also within Australia, Canada, China and Germany (Fig. 1). Sites were selected without specific criteria for species presences or abundances, thereby capturing species with a range of local population sizes. We used these data to: 1) test the assumption that plant species are more abundant at sites away than at

home; and 2) determine whether community composition and relative abundance are similar home and away, given that many of the planet's herbaceous communities including grasslands have undergone comparable degrees of human transformation in terms of disturbance and species introductions (Ceballos *et al.* 2010; Henwood 2010).

METHODS

Study sites

All sites are part of the Nutrient Network (<http://nutnet.science.oregonstate.edu>), a cooperative global experiment consisting of 51 sites dominated by herbaceous species, of which 39 are included in this study (Fig. 1 and Table S1 in Supporting Information). In the Nutrient Network study, population, community, and ecosystem-scale vegetation data, including species-specific distribution and abundance data, were collected with standardized protocols. Each site was relatively homogeneous (i.e., no variability in disturbance history), representative of a particular ecosystem (e.g. tallgrass prairie), and at least 0.1 ha in size. Sites occur in both hemispheres, and capture gradients of latitude from 37° N to 54° S, mean annual precipitation from 250 to 2314 mm yr⁻¹ and elevation from 0.5 to 3500 m a.s.l.

The species identified by the principal investigators at each site were classified as native or introduced by the local researchers. Within the 51 Nutrient Network sites, we searched for plant species recorded at sites both home and away and identified 12 grass and 14 forb species from 39 sites (Table 1 and see Table S2 in Supporting Information for a detailed description of the sites where each species using number references shown in Fig.1). To provide a measure of the economic, environmental and social impacts these species have made within introduced countries, we then looked up the official weed status of each of the 26 species. All but three of these 26 species were designated as “weeds” on government and

conservation agency websites relevant to each of the respective countries (Canadian Food Inspection Agency 2008; New Zealand Plant Conservation Network 2010; Thorp 2010; United States Department of Agriculture 2010). Using Weber's reference guide to world environmental weeds, we found that 16 of the 26 species are considered naturalized species with 10 of these also considered invasive (Table 1, Weber 2005). There was uncertainty regarding the pan-global origins of some species (i.e., *Festuca rubra*, *Poa pratensis*, and *Achillea millefolium* are variously classified as native or introduced in North America). Where this uncertainty arose, principal investigators reviewed the origins of these species in their local area to determine whether the local populations were in their native or introduced ranges.

Experimental design

Sites were selected randomly with regards to the abundances of the 26 study species, and sampling followed a standardized protocol. The majority of sites (35 of the 39) established three replicate blocks, which were divided into ten-25 m² plots (see Table S1 Supporting Information as some sites established more than 30 plots). Aerial cover of each species was visually estimated using a modified Daubenmire method (Daubenmire 1959), where cover was estimated to the nearest 1% within one-1 m² sub-plot in each plot. At the nine New Zealand sites, cover estimates (using the method described above) were made for 30-1 m² quadrats chosen from an area of between 90-120 m² using stratified sampling.

Data analyses

To analyze differences in the cover of the 26 study species, we developed a Linear Mixed Effects Model (hereafter LMEM) using R 2.11.1 (R Foundation for Statistical Computing; R package nlme). We first calculated relative cover for each plot, i.e. the cover

of each study species relative to the sum of cover for all species per plot. We arc-sine transformed the relative cover values and then modeled cover of the study species as a function of provenance (introduced or native), and life-form (grass or forb species) with a random effects structure of species/site/plot. To maintain the assumption of within-group homoscedasticity, we used the weights function, `varIdent`, to create a constant variance function structure for grass and forb species (Pinheiro & Bates 2000). The best-fit and simplest model was found by removing explanatory variables one at a time from the complete model and the simpler models were compared to the more complex model using a likelihood ratio test (information-theoretic model selection techniques were also used and gave similar qualitative results, see Table S3 in Supporting Information). Maximum likelihood was used when comparing nested models to simplify the model for fixed effects (Pinheiro & Bates 2000; Ives & Zhu 2006). We used diagnostic plots to check model assumptions (Pinheiro & Bates 2000); there was no evidence of correlation of observations within groups and we assumed that within group errors were normally distributed.

Because species abundance can be described using different measures, we also compared the localized dominance or patchiness (mean maximum cover per plot, also arc-sine transformed and hereafter localized dominance), and the commonness of species (percentage of plots where the species were found, hereafter commonness) between ranges. To distinguish between levels of commonness, we plotted the commonness of each species at home sites versus the commonness at away sites and we separated this plot into four quadrants at 50% (Fig. 2): A. shows species that are more common at away sites; B. shows species that are common at both home and away sites; C. shows species that are not common at either home or away sites; and D. shows species that are more common at home sites. We

counted the number of species within each quadrant and compared expected and observed levels, using an Exact Multinomial Goodness of Fit Test (R package EMT), with a distance measure based on probabilities. An Exact Multinomial Test estimates how likely it is that an observation should occur given expected or hypothetical probabilities. Here we used conservative expected probabilities in accordance with the ‘abundance assumption’ (A. 45%, B. 45%, C. 5% D. 5%). A low p -value suggests the observed probabilities are not accurately represented by the hypothetical probabilities.

We determined how community composition varied with a Permutational MANOVA (PERMANOVA), using number of study species per site as the single predictor variable and the relative abundance of all species at a site as the response. PERMANOVA allows us to use the full suite of species abundance data to evaluate the community response because it uses similarity distances and permutations to calculate p -values (Anderson 2001), thus relaxing the assumptions associated with a traditional MANOVA. We used 9999 permutations and the Bray-Curtis similarity metric; relative cover data were square root transformed to emphasize both the dominant and medium abundant species as suggested by Clarke and Green (1988). To visualize the multivariate patterns, we performed non-metric multidimensional scaling (nMDS) on the Bray-Curtis distances. Analyses were performed in Primer 6 (Plymouth Routines in Multivariate Ecological Research).

RESULTS

Differences in relative cover home and away

Differences in mean relative cover of the study species were best explained by the LMEM that included the interaction of life-form and provenance ($LR_8=5.23$, $P<0.02$). These findings suggest that cover differed depending on life-form and provenance (home or away)

and that the effect of life-form and provenance together was not additive (Supporting Information Table S3). Mean relative cover for the grass species did not differ between home and away sites, whereas forb species were higher in relative cover at home sites (Fig. 2 and see Table S4 in Supporting Information for model coefficients and parameter estimates).

Despite the overall trend of a similar mean relative cover home and away for grasses, individual species showed differences. The perennial grasses *Alopecurus pratensis*, *Lolium perenne*, *Festuca rubra*, and *Poa pratensis* had a higher mean relative cover at away sites; while *Agrostis capillaris* had a higher mean relative cover at home sites (Fig. 3 a and see Fig. S2-S3 in Supporting Information for individual maps showing mean relative cover for each species at sites home and away). All other grasses and forbs were low in their mean relative cover with the majority of these species being similar in cover home and away or more abundant at home sites (Fig. 3 a inset and see Fig. S2-S4 in Supporting Information). Overall, we found a significant positive rank (Spearman's $\rho = 0.483$, $P < 0.01$) between mean relative cover home and away. We also conducted a t-test on the distances from the 1 to 1 line of equal cover home and away and found these values did not differ significantly between home and away sites ($t_{50}=0.35$, $P < 0.80$). This result suggests that although mean relative cover values for individual species were found above and below the 1 to 1 line statistically there was no significant difference in the overall relationship across species.

The same grasses with a high mean relative cover also had a high mean maximum cover per plot, a measure of localized dominance or patchiness (Fig. 3 b). The maximum cover of the 14 forbs examined also varied, but only *Plantago lanceolata* and *Bellis perennis* were more common at away sites (Fig. 3 b). We found only a marginally significant positive correlation between the mean maximum cover home and away (Spearman's $\rho = 0.379$,

$P < 0.07$); however, t-test results on residuals from the 1 to 1 line were not significantly different between home and away sites ($t_{50} = 1.33$, $P < 0.20$). Ten of the 26 study species were surveyed at just one home or away site (Table 1). We repeated the correlation analyses described above without including these species and found similar overall trends.

We also calculated the percentage of plots where the species was found at sites home and away, a measure of commonness (Fig. 4). If species were more common at away sites then we would have expected the majority of species to be found in quadrant A of Fig. 4. The quadrants were, however, occupied non-randomly (Exact Multinomial Test, using the counts of species found in each quadrant and conservative expected probabilities based on the ‘abundance’ assumption, $p < 0.002$), but not as predicted. Instead, most grass species (9 of 12) were found in quadrant B, indicating they are common at sites both home and away (Fig. 4). Three forbs were found in quadrant B and three forbs found in quadrant C. *Plantago lanceolata* and *Bellis perennis* were the only forbs found in quadrant A. The remaining five forb species were more common at home sites (quadrant D). Additionally, while there appeared to be a strong linear relationship between native and introduced plot occupancy when occupancy was $< 50\%$ (all forbs), there was high variation when occupancy was $> 50\%$ (Fig. 4), suggesting that commonness in the home range provides little power to predict a species’ commonness in an introduced site. The ten species identified as world invasive species in Weber (2005) (highlighted in Fig. 3 and 4), did not consistently have higher relative cover than others at the plot scale; however, five of ten species (4 grass spp. and 1 forb) were common in both home and away sites (quadrant B, Fig. 4).

Community level similarity

Community similarity increased with the number of study species present (Fig. 4 PERMANOVA: $F_{1,36} = 1.13$ $P < 0.055$, see also Figure S1, Supporting Information for the relationship between average similarity and the number of study species at a site); while sites with < 5 study species varied in their species composition and relative cover, sites with > 5 species, and especially those with > 10 , showed highly similar communities even when sites were geographically distant (Fig. 4).

DISCUSSION

Large increases in the abundance of species in territories where they lack an evolutionary history is a paradox which has long attracted the attention of ecologists (Darwin 1859; Wallace 1881; Elton 1958), and a number of invasive plant species clearly follow this pattern (Siemann & Rogers 2001; Daehler 2003; Hierro *et al.* 2006; Williams *et al.* 2010). However, the generality of this pattern has been largely untested—do species that are more abundant away represent unusual, but important, anomalies? Here, we show that most species that we examined were not more abundant in territories they have invaded. Only a subset of the 26 species we examined conformed to the ‘abundance assumption’, in terms of increased relative cover at away sites (23% of the species we examined), localized dominance (50%) and commonness (12%). These abundance patterns differed between life-forms. Grass species tended to be abundant both at sites home and away, and forb species tended to be low in abundance, or even lower in abundance away than at home, when values were averaged across sites. This finding conforms to predictions in the core-satellite population hypothesis made by Hanski (1982)—that core species are common wherever they occur and satellite species are rare wherever they occur. Collins and Glenn (1990) found this pattern held at multiple spatial scales from small patches to regional scales, but our results

suggest species abundance may be conserved on different continents, at least in herbaceous communities.

We found that the similarity between sites in terms of species composition and abundance increased with the number of study species recorded at a site (Fig. 4). This finding suggests that either invasion is increasing the compositional similarity of these herbaceous communities and/or that human activities are creating novel, but similar environmental conditions that favor the growth of a common pool of species. Of the 39 sites, 21 shared at least six of the study species, at which point they became compositionally similar (including one site in Canada, nine in New Zealand, one in Switzerland, three in the United Kingdom, and six in the USA). Because the sites included in this study were chosen independently of the species they contained, these findings suggest that herbaceous communities are increasing in similarity globally within temperate zones. The majority of studies investigating the homogenization of flora across continental and regional scales have found increasing similarity between urban and rural communities with the main causal mechanism being human-assisted dispersal (Qian & Ricklefs 2006; La Sorte *et al.* 2007; La Sorte & Pysek 2009). Ecosystems dominated by herbaceous species (e.g. grasslands) tend to be strongly human influenced and therefore our findings are consistent with these other studies.

Although we did not test the mechanism explaining these results, the strong similarity in community composition between sites with six or more of the study's 26 species suggests their establishment was either preceded by or co-occurred with human disturbances that favor the persistence of similar sets of species. Less deterministic mechanisms are also possible; for example, species that are abundant at home are likely to be transported at higher frequencies to away sites, either intentionally or accidentally. We found limited evidence that

establishment of species in new territories necessarily leads to higher population abundance, as has been predicted by several hypotheses describing the process of invasion (Mitchell *et al.* 2006). Rather, the apparent abundance of exotic grasses may represent the selective movement of dominants from primarily European grasslands. These results have some resemblance to a meta-analysis comparison of plant sizes between native and introduced populations in the United States and Europe (Thebauld & Simberloff 2001). That study addressed a similarly ubiquitous assumption that plant size (height, biomass) is greater for introduced plants in their away ranges. Although many species did fit this pattern at some sites, the overall analysis did not support the general assumption and many species were actually larger at native sites. In our study, we measured abundance and not size, but the similarity of the general trends in the results suggests that naturalizations need not always involve significant ecological or evolutionary changes to populations.

Because of extensive human influence on herbaceous communities, our results may not reflect patterns in other systems that are less impacted by anthropogenic disturbances. Grass-dominated systems worldwide have undergone various degrees of agricultural use that has displaced or greatly reduced native communities (Seabloom *et al.* 2003; MacDougall & Turkington 2005). These include shifts in grazing regimes and the replacement of native herbivores with domestic ones that can destabilize co-evolved plant-herbivore interactions (Parker *et al.* 2006), and the introduction of non-native seeds, often repeatedly and in large quantities over a range of local habitats (MacDougall *et al.* 2004). The extensive human influences on herbaceous communities may mean that population-based advantages, which are thought to create high abundances in away ranges (e.g. enemy release or novel weapons),

are not a necessary pre-condition for establishment and persistence in many herbaceous systems.

Many of the invasive plant species included in this study were intentionally introduced for social, economic, and environmental needs, such as soil stabilization, pasture improvement, horticulture, and agriculture (Weber 2005), thereby overcoming global dispersal barriers (Lockwood *et al.* 2005; Lambdon & Hulme 2006). These introductions were typically coupled with cultivation and high propagule pressure, where grass seed was collected systematically by agronomists to favor species with high forage production, palatability, and grazer tolerance (Mack 1989; Williams & Baruch 2000). In some cases, introductions were even preceded by intensive common garden trials at agricultural stations, which selected for individuals capable of withstanding local abiotic limitations (Lolicato & Rumball 1994; Huyghe 2010). The end results are herbaceous species with pan-global distributions and high local abundances in all territories, not just away from home.

These findings have potential implications for biosecurity screening procedures. Developing reliable standards for preventing the introduction of plant species with a high potential for invasiveness is imperative for protecting biodiversity and conserving natural environments (Vitousek *et al.* 1996; Mack *et al.* 2000). The most widely used biosecurity screening process is the Australian Weed Risk Assessment system (Pheloung *et al.* 1999; Gordon *et al.* 2008), which is based on species' history, climate, and distribution, weed status elsewhere, undesirable traits, biology, and ecology. Our results highlight one criterion potentially missing from this list: an estimate of the mean abundance of a plant species at sites in its home range. However, we also recognize that a species does not have to be high in abundance to have a high negative impact and that high impact invaders can arise from

species that are indeed relatively low in abundance home and away. For example, the two noxious weeds in this study, *Cirsium arvense* and *Cirsium vulgare*, were relatively low in abundance compared to other herbaceous species, but are considered weed species in both their home and away range. In summary, plant species are not necessarily more abundant in their introduced range, although there are exceptional species that defy this trend. For important theoretical and applied reasons, we should no longer be asking whether species are more abundant away, but concentrate on identifying the reasons for exceptions to the general trend of a similar abundance at home and away sites.

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Table1: List of the 26 study species sampled at sites both home and away. The species in bold are identified as naturalized, with a * indicating the species is also listed as invasive by Weber (2005); ✓ indicates a declared weed species; and † indicates not a listed weed species in the respective country. The sources used to determine weed status in each country are listed next to each of the following country acronyms: AU= Australia (Thorp 2010), CA= Canada (Canadian Food Inspection Agency 2008), CN= China, DE= Germany, NZ= New Zealand (New Zealand Plant Conservation Network 2010), SW= Switzerland, UK= United Kingdom and US = United States (United States Department of Agriculture 2010).

Species	Family	Life-form	Life-history	# of Sites (away)	# of Sites (home)
<i>Achillea millefolium</i>	Asteraceae	Forb	Perennial	6 (NZ✓)	10 (US✓, SW)
*<i>Agrostis capillaris</i>	Poaceae	Graminoid	Perennial	8 (NZ✓, US †)	5 (DE, SW, UK)
*<i>Agrostis stolonifera</i>	Poaceae	Graminoid	Perennial	4 (NZ✓, US✓)	1 (CN)
<i>Alopecurus pratensis</i>	Poaceae	Graminoid	Perennial	2 (CA †, US †)	2 (SW, UK)
*<i>Anthoxanthum odoratum</i>	Poaceae	Graminoid	Perennial	11 (CA ✓, NZ✓, US †)	4 (SW, UK)
*<i>Arrhenatherum elatius</i>	Poaceae	Graminoid	Perennial	1 (US✓)	2 (UK)
<i>Bellis perennis</i>	Asteraceae	Forb	Perennial	4 (CA✓, NZ †)	1 (SW)
<i>Cerastium fontanum</i>	Caryophyllaceae	Forb	Perennial	7 (NZ ✓)	4 (SW, UK)
*<i>Cirsium arvense</i>	Asteraceae	Forb	Perennial	8 (NZ✓, US✓)	3 (UK✓)
*<i>Cirsium vulgare</i>	Asteraceae	Forb	Annual/Biennial	11 (CA✓, NZ✓, US✓)	3 (UK✓)
*<i>Dactylis glomerata</i>	Poaceae	Graminoid	Perennial	11 (NZ✓, US✓)	3 (SW, UK)
<i>Festuca rubra</i>	Poaceae	Graminoid	Perennial	7 (CA †, NZ✓, US †)	3 (SW, UK)
*<i>Hieracium pilosella</i>	Asteraceae	Forb	Perennial	5 (NZ✓)	1 (SW)
<i>Holcus lanatus</i>	Poaceae	Graminoid	Perennial	12 (NZ✓, US✓)	4 (DE, UK, SW)
<i>Lolium perenne</i>	Poaceae	Graminoid	Perennial	8 (NZ✓)	1 (SW)
<i>Myosotis discolor</i>	Boraginaceae	Forb	Annual	5 (CA †, US †)	1 (UK)
<i>Phleum pratense</i>	Poaceae	Graminoid	Perennial	7 (NZ †, US✓)	1 (SW)
<i>Plantago lanceolata</i>	Plantaginaceae	Forb	Perennial	15 (CA✓, NZ †, US✓)	1 (SW)
*<i>Poa pratensis</i>	Poaceae	Graminoid	Perennial	17 (CA✓, NZ✓, US✓)	6 (CN, SW, UK)
<i>Poa trivialis</i>	Poaceae	Graminoid	Perennial	2 (NZ †)	1 (SW)
<i>Prunella vulgaris</i>	Lamiaceae	Forb	Perennial	8 (NZ †, US✓)	2 (SW, UK)
<i>Ranunculus repens</i>	Ranunculaceae	Forb	Perennial	3 (NZ✓)	2 (UK)
*<i>Rumex acetosella</i>	Polygonaceae	Forb	Perennial	13 (AU✓, NZ †, US✓)	2 (UK)
<i>Taraxacum officinale</i>	Asteraceae	Forb	Perennial	14 (CA✓, NZ✓, US✓)	1 (SW)
<i>Trifolium pratense</i>	Fabaceae	Forb	Perennial	3 (NZ †, US †)	3 (SW, UK)
<i>Trifolium repens</i>	Fabaceae	Forb	Perennial	7 (NZ✓, US✓)	4 (SW, UK)

Figure 1. Map showing the locations of the 39 Nutrient Network sites included in this study. The reference numbers included in the map correspond to detailed descriptions of the sites shown in Table S1 in Supporting Information including habitat type, rainfall, and mean summer and winter temperatures and the reference numbers shown in Table 1.

Figure 2. Mean relative cover for grass and forb species at sites home and away (± 1 SE). Data have been arc-sine transformed. Black circles show data values and white circles show parameter estimates from the LMEM.

Figure 3. a) Mean relative cover of species per plot (± 1 SE). Data are for the 26 study species (from a potential pool of 39 sites). Black circles show forb species and white circles show grass species; black triangles show forb species and white triangles show grass species labeled as world invasive species by Weber (2005). The line shows the 1:1 relationship. Inset shows the mean relative cover for grass and forb species not distinguishable in the larger figure because of their low cover with the same 1:1 relationship. b) Mean relative maximum cover of species per plot (± 1 SE). Black circles show forb species and white circles show grass species; black triangles show forb species and white triangles show grass species labeled as world invasive species by Weber (2005). The line shows a 1:1 relationship.

Figure 4. The percentage of plots (%) occupied by each species (26 species) at introduced and native sites (from a potential pool of 39 sites) or commonness of species at a site. Black circles show forb species and white circles show grass species; black triangles show forb species and white triangles show grass species labeled as world invasive species by Weber (2005). Quadrant A. shows species that are more common at away sites; B. shows species that are common at both home and away sites; C. shows species that are not common at both home and away sites; and D. shows species that are common at home sites.

Figure 5. nMDS plots for each of the 39 sites using species relative cover as the basis and Bray-Curtis similarity index. The data were square root transformed to remove the bias towards rare species and the axes are equally scaled. The symbols represent the countries in which each site was located. The labels next to the symbols indicate whether the site contains study species in their native (home) and/or introduced (away) range: H&A = site contains both home and away study species, A = site contains away study species, and H = site contains home study species. Symbol colors represent the number of study species found at each site. 2D stress level: 0.17

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SUPPORTING INFORMATION:

Table S1. Description of the 39 sites including habitat, elevation (m), mean annual precipitation per year (MAP), winter low temperatures (°C), summer high temperatures (°C), and the number of plots surveyed.

Map Ref.	SITE	HABITAT	COUNTRY	LATITUDE	LONGITUDE	ELEVATION (M)	MAP (MM/YR)	Winter LOW TEMP (°C)	Summer HIGH TEMP (°C)	PLOTS
1	bogong.au	SUB-ALPINE GRASSLAND	Australia	-36.87	147.25	1760	1217.0	-3.0	17.4	30
2	cowi.ca	OLD FIELD; SAVANNA	Canada	48.46	-123.38	50	1038.6	-1.1	23.3	30
3	azi.cn	ALPINE MEADOW	China	33.58	101.53	3500	620.0	-13.0	32.0	30
4	pape.de	OLD FIELD	Germany	53.09	7.47	1	850.1	0.6	22.3	30
5	cs.nz	GRASSLAND	New Zealand	-43.18	171.75	800	1362.9	-3.3	20.1	30
6	dn.nz	GRASSLAND	New Zealand	-44.92	170.68	800	479.3	-0.4	18.8	30
7	fh.nz	GRASSLAND	New Zealand	-46.08	168.33	110	1048.9	-1.9	18.7	30
8	ka.nz	GRASSLAND	New Zealand	-43.15	171.10	300	623.4	-0.7	19.9	30
9	kk.nz	GRASSLAND	New Zealand	-42.42	173.70	80	703.8	5.9	21.7	30
10	rc.nz	GRASSLAND	New Zealand	-44.17	170.98	510	623.4	-0.7	23.7	30
11	tc.nz	GRASSLAND	New Zealand	-46.18	168.43	600	1048.9	1.9	18.7	30
12	wd.nz	GRASSLAND	New Zealand	-44.80	170.08	140	479.3	-0.4	18.8	30
13	wk.nz	GRASSLAND	New Zealand	-46.05	168.33	100	1048.9	1.9	18.7	30
14	frue.sw	PASTURE	Switzerland	47.37	8.55	995	1102.0	-1.0	21.0	30
15	valm.sw	ALPINE GRASSLAND	Switzerland	46.63	10.37	2320	950.0	-15.7	17.0	30
16	hero.uk	MESIC GRASSLAND	United Kingdom	51.41	-0.64	60	678.0	2.0	22.0	30
17	lancaster.uk	MESIC GRASSLAND	United Kingdom	53.99	-2.63	180	1222.5	-2.7	25.0	30
18	rook.uk	MESIC GRASSLAND	United Kingdom	51.41	-0.64	60	678.0	2.0	22.0	30
19	amcamp.us	GRASSLAND	USA	48.47	-123.01	41	672.4	2.0	21.5	30
20	barta.us	SANDHILLS GRASSLAND	USA	42.24	-99.65	767	568.0	-13.1	29.9	30
21	bnch.us	MONTANE MEADOW	USA	44.21	-122.26	1500	2160.0	-1.3	30.2	30
22	bttr.us	MONTANE MEADOW	USA	44.21	-122.26	1500	2160.0	-1.3	30.2	30
23	cdcr.us	TALLGRASS PRAIRIE	USA	45.40	-93.20	270	800.0	-16.8	26.9	50
24	elkh.us	COASTAL PRAIRIE	USA	36.98	-122.05	50	445.9	5.2	19.9	30
25	fnly.us	MESIC GRASSLAND	USA	44.41	-123.28	68	1200.0	0.9	27.3	30

26	glac.us	GRASSLAND RESTORED TALLGRASS	USA	46.87	-123.03	33	1299.8	0.6	25.3	30
27	hall.us	PRAIRIE	USA	36.96	-86.73	194	1282.0	-4.1	31.6	30
28	hnvr.us	OLD FIELD	USA	43.42	-72.14	271	919.5	-13.5	27.4	30
29	hopl.us	ANNUAL GRASSLAND	USA	39.00	-123.07	417	939.8	2.8	32.6	30
30	konz2c.us	TALLGRASS PRAIRIE	USA	39.08	-96.58	440	835.0	-9.0	33.0	30
31	look.us	MONTANE MEADOW	USA	44.21	-122.26	1500	2314.0	-1.3	30.2	30
32	sage.us	MONTANE MEADOW	USA	39.43	-120.24	1920	850.0	-9.8	26.2	30
33	shps.us	SAGEBRUSH STEPPE	USA	44.00	-112.00	910	325.0	-12.0	29.5	40
34	sier.us	ANNUAL GRASSLAND	USA	39.29	-121.34	333	711.2	3.2	35.7	50
35	smith.us	GRASSLAND	USA	48.21	-122.62	62	549.9	1.3	21.7	30
36	spin.us	PASTURE	USA	38.14	-84.50	272	1166.0	-4.4	29.9	30
37	tyso.us	OLD FIELD	USA	38.52	-90.56	169	1090.0	-7.6	31.3	40
38	ucsc.us	COASTAL PRAIRIE	USA	36.87	-121.74	140	844.4	5.0	22.5	30
39	unc.us	OLD FIELD	USA	35.91	-79.06	141	1210.0	-2.6	31.7	30

83 Table S2. Map reference numbers indicating the sites where the abundances of each of the 26 species were recorded.

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Species	Map References #s (away)	Map References #s (home)
<i>Achillea millefolium</i>	6,8,9,10,11,12	15,21,22,23,25,30,31,32,34,37
* <i>Agrostis capillaris</i>	5,7,8,9,10,11,25,26	4,15,16,17,18
* <i>Agrostis stolonifera</i>	23,7,8,10	3
<i>Alopecurus pratensis</i>	2,25	14,16
* <i>Anthoxanthum odoratum</i>	2, 5, 7, 8, 9, 10, 11, 13, 26, 35, 39	14, 16, 17, 18
* <i>Arrhenatherum elatius</i>	26	16,18
<i>Bellis perennis</i>	2,7,11,13	14
<i>Cerastium fontanum</i>	5, 7, 8, 9, 11, 13	14, 16, 17, 18
* <i>Cirsium arvense</i>	7, 8, 9, 11, 13, 19, 27, 35	16,17,18
* <i>Cirsium vulgare</i>	2, 7, 8, 9, 10, 11, 13, 19, 25, 29, 35	16,17,18
* <i>Dactylis glomerata</i>	6, 7, 8, 9, 10, 11, 12, 13, 28, 35, 36	14, 16, 18
<i>Festuca rubra</i>	2, 6, 7, 8, 9, 10, 12,	15, 16, 18, 28
* <i>Hieracium pilosella</i>	5, 7, 8, 11, 13	15
<i>Holcus lanatus</i>	7, 8, 9, 10, 11, 13, 19, 24, 25, 26, 35, 39	4, 14, 16, 18
<i>Lolium perenne</i>	6, 7, 8, 9, 10, 11, 12, 13	14
<i>Myosotis discolor</i>	2, 19, 25, 26, 35	16
<i>Phleum pratense</i>	7, 8, 11, 22, 25, 28, 37	14
<i>Plantago lanceolata</i>	2, 6, 7, 8, 9, 10, 11, 12, 13, 25, 26, 35 36, 38, 39	14
* <i>Poa pratensis</i>	2, 6, 8, 9, 10, 12, 19, 20, 21, 22, 23, 25, 28, 30, 31, 35, 36	3, 14, 16, 17, 18, 39
<i>Poa trivialis</i>	7, 11	14
<i>Prunella vulgaris</i>	10, 11, 13, 22, 25, 36, 39	14, 16
<i>Ranunculus repens</i>	7, 8, 11	16, 17
* <i>Rumex acetosella</i>	1, 5, 19, 22, 23, 24, 25, 26, 28, 31, 35, 38, 39	17, 18
<i>Taraxacum officinale</i>	2, 6, 8, 9, 10, 11, 13, 19, 26, 27, 28, 33, 35, 36	14
<i>Trifolium pratense</i>	12, 27, 36	14, 15, 16
<i>Trifolium repens</i>	5, 6, 8, 9, 10, 13, 28	14, 15, 16, 17

85 Table S3. Comparison of models for mean relative cover (arc-sine transformed) for each of
 86 the 26 study species with different fixed effects and a nested random effects structure of
 87 species/site/plot, using information-theoretic model selection procedures and maximum
 88 likelihood.

Model	Δ AIC
Life-form $\times$ provenance	0
Life-form	2.79
Life-form + provenance	7.19
Provenance	12.37
Intercept only	12.35

89 Table S4. Parameter estimates for the best-fitting LMEM of relative cover (data were arc-
 90 sine transformed) for all 26 study species with random intercepts due to species ($\sigma^2_{\text{species}}$),
 91 site within species (σ^2_{site}), and plot within site within species (σ^2_{plot}).

Parameter	Effects (differences)	SE
Away grass spp.	0.15	0.02
Home grass spp.	0.11 (-0.04)	0.03
Away forb spp.	0.03 (-0.12)	0.0003
Home forb spp.	0.06 (-0.09)	0.0008
$\sigma^2_{\text{species}}$ (intercept)	0.007	
σ^2_{site} (intercept)	0.007	
σ^2_{plot} (intercept)	0.0004	

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107 Table S5: Details of the contributions by each author to the design, analyses and writing of the manuscript.

Authors	Research Institutions	Nutrient Network coordinators	Developed and framed research questions	Collected Data	Analyzed data	Contributed substantial revisions to data analyses	Wrote the paper	Contributed substantially to paper writing
Jennifer Firn	CSIRO Ecosystem Sciences		✓	✓	✓		✓	
Joslin Moore	University of Melbourne		✓	✓	✓			✓
Andrew MacDougall	University of Guelph			✓			✓	✓
Elizabeth Borer	University of Minnesota	✓	✓	✓		✓		✓
Eric Seabloom	University of Minnesota	✓		✓		✓		✓
Janneke HilleRisLambers	University of Washington		✓	✓	✓			✓
Stan W. Harpole	Iowa State University	✓	✓	✓		✓		✓
Elsa Cleland	University of California			✓		✓		✓
Cynthia Brown	University of Colorado		✓	✓				✓
Johannes M.H. Knops	University of Nebraska		✓	✓				✓
Suzanne Prober	CSIRO Ecosystem Sciences			✓		✓		✓
David Pyke	USGS		✓	✓		✓		✓
Kelly A. Farrell	Oregon State University		✓	✓				✓
Jonathan Bakker	University of Washington			✓		✓		✓
Lydia Ries O'Halloran	University of Minnesota	✓		✓		✓		✓
Peter B. Adler	Utah State University			✓	✓	✓		
Scott Collins	University of New Mexico			✓			✓	✓
Carla D'Antonio	University of California			✓			✓	✓
Mick J. Crawley	Imperial College			✓	✓			✓
Elizabeth Wolkovich	NCEAS			✓		✓	✓	
Kimberly J. La Pierre	Yale University			✓			✓	✓
Brett Melbourne	University of Colorado			✓		✓		✓
Yann Hautier	University of Zurich			✓		✓		✓

John Morgan	La Trobe University			√				√
Andrew DB Leakey	University of Illinois			√				√
Adam Kay	University of St.Thomas			√				√
Rebecca McCulley	University of Kentucky			√				√
Kendi F. Davies	University of Colorado			√				√
Carly Stevens	Open University			√				√
Cheng-Jin Chu	Lanzhou University, China			√				√
Karen D. Holl	University of California			√				√
Julia Klein	Colorado State University			√				√
Philip Fay	USDA-ARS			√				√
Nicole Hagenah	University of Kwazulu-Natal			√				√
Kevin P Kirkman	University of Kwazulu-Natal			√				√
	University of Queensland and CSIRO Ecosystem Sciences							
Yvonne Buckley				√	√	√		√

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109 Figure S1: Average similarity between sites depending on the number of study species

110 present. Average similarity values are based on mean relative cover data for all species found

111 at the 39 sites and calculated using the Bray-Curtis similarity index. The species composition

112 data were square root transformed to remove bias towards rare species.

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114 Figure S2: Map showing the mean relative cover for 6 grass species at all recorded home and
 115 away sites. Blue circles represent home sites and red circles represent away sites. The size of
 116 the circles is proportional to the relative cover of the species at each site.

Figure S3: Map showing the mean relative cover for 6 grass species at all recorded home and away sites. Blue circles represent home sites and red circles represent away sites. The size of the circles is proportional to the relative cover of each species at each site.

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122 Figure S4: Map showing the mean relative cover for 7 forb species at all recorded home and

123 away sites. Blue circles represent home sites and red circles represent away sites. The size of

124 the circles is proportional to the relative cover of the species at each site.

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126 Figure S5: Map showing the mean relative cover for 7 forb species at all recorded home and

127 away sites. Blue circles represent home sites and red circles represent away sites. The size of

128 the circles is proportional to the relative cover of the species at each site.

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