LETTER

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

Jennifer Firn,[1]* Joslin L. Moore,[2] Andrew S. MacDougall,[3] Elizabeth T. Borer,[4] Eric W. Seabloom,[4] Janneke HilleRisLambers,[5] W. Stanley Harpole,[6] Elsa E. Cleland,[7] Cynthia S. Brown,[8] Johannes M. H. Knops,[9] Suzanne M. Prober,[10] David A. Pyke,[11] Kelly A. Farrell,[12] John D. Bakker,[13] Lydia R. O`Halloran,[4] Peter B. Adler,[14] Scott L. Collins,[15] Carla M. D`Antonio,[16] Michael J. Crawley,[17] Elizabeth M. Wolkovich,[18] Kimberly J. La Pierre,[19] Brett A. Melbourne,[20] Yann Hautier,[21] John W. Morgan,[22] Andrew D. B. Leakey,[23] Adam Kay,[24] Rebecca McCulley,[25] Kendi F. Davies,[20] Carly J. Stevens,[26] Cheng-Jin Chu,[27] Karen D. Holl,[28] Julia A. Klein,[29] Philip A. Fay,[30] Nicole Hagenah,[19,31] Kevin P. Kirkman[31] and Yvonne M. Buckley[1,32]

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 vs. 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 that suites of introduced species are assembling similarly on different continents. Overall, we found that 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 programmes.

Keywords

Biogeography, biosecurity, disturbance, global meta-study, homogenization of communities, invasion paradox, mechanisms of invasion, Nutrient Network, plant invasion, propagule pressure.

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[1]CSIRO Ecosystem Sciences, St. Lucia, Qld 4067, Australia

[2]AEDA, School of Botany, University of Melbourne, Parkville, Vic. 3010, Australia

[3]Department of Integrative Biology, University of Guelph, Guelph, ON N1G 2W1, Canada

[4]Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN 55108, USA

[5]Biology Department, University of Washington, Seattle, WA 98195-1800, USA

[6]Ecology, Evolution and Organismal Biology, Iowa State University, Ames, IA 50011, USA

[7]Ecology, Behavior, Evolution Section, University of California San Diego, La Jolla, CA 92093, USA

[8]Department of Bioagricultural Sciences and Pest Management, Colorado State University, Fort Collins, CO 80523, USA

[9]School of Biological Sciences, University of Nebraska, 348 Manter Hall, Lincoln, NE 68588-0118, USA

[10]CSIRO Ecosystem Sciences, Private Mail Bag 5, PO Wembley, WA 6913, Australia

[11]U.S. Geological Survey, Forest, Rangeland Ecosystem Science Center, 3200 SW Jefferson Way, Corvallis, OR 97331, USA

[12]Department of Zoology, Oregon State University, Corvallis, OR 97331, USA

[13]School of Forest Resources, University of Washington, Box 354115, Seattle, WA 98195-4115, USA

[14]Department of Wildland Resources and Ecology Center, Utah State University, Logan, UT 84322, USA

[15]Department of Biology, MSC03-2020, University of New Mexico, Albuquerque, NM 87131, USA

[16]Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106, USA

[17]Department of Biology, Imperial College London, Silwood Park, Ascot SL5 7PY, UK

[18]National Centre for Ecological Analysis and Synthesis, Santa Barbara, CA 93101, USA

[19]Department of Ecology, Evolutionary Biology, Yale University, New Haven, CT 06520, USA

[20]Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309, USA

[21]Institute of Evolutionary Biology, Environmental Studies, University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland

[22]Department of Botany, La Trobe University, Bundoora, Vic. 3086, Australia

[23]Department of Plant Biology, Institute for Genomic Biology, University of Illinois at Urbana-Champaign, Urbana, IL 61821, USA

[24]Department of Biology, University of St. Thomas, St. Paul, MN 55105, USA

[25]Department of Plant, Soil Sciences, University of Kentucky, Lexington, KY 40546-0091, USA

[26]Department of Life Sciences, The Open University, Walton Hall, Milton Keynes MK7 6AA, UK

[27]MOE Key Laboratory of Arid, Grassland Ecology, Lanzhou University, Lanzhou 730000, China

[28]Environmental Studies Department, University of California, Santa Cruz, CA 95064, USA

[29]Natural Resource Ecology Laboratory, Colorado State University, Campus Delivery 1472, Fort Collins, CO 80523-1472, USA

[30]USDA ARS Grassland Soil and Water Research Laboratory, Temple, TX 76502, USA

[31]School of Biological, Conservation Sciences, University of KwaZulu-Natal, Scottsville, Pietermaritzburg 3209, South Africa

[32]School of Biological Sciences, The University of Queensland, St. Lucia, Qld 4072, Australia

*Correspondence and present address: Queensland University of Technology, School of Biogeosciences, Brisbane, Qld 4001, Australia.

E-mail: jennifer.firn@qut.edu.au

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) vs. 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 (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 solstistialis*, 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.umn.edu/), a cooperative global experiment consisting of 51 sites dominated by herbaceous species, of which 39 are included in this study (Fig. 1; Table S1). In the Nutrient Network study, population, community and ecosystem-scale vegetation data, including species-specific distribution and abundance data, were collected with standardized

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 including habitat type, rainfall and mean summer and winter temperatures and the reference numbers.

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 year^{-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 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 regard 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 m^2 plots (see Table S1 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 m^2 sub-plot in each plot. At the nine New Zealand sites, cover estimates (using the method described above) were made for 30-1 m^2 quadrats chosen from an area of between 90 and 120 m^2 using stratified sampling.

Data analyses

To analyse differences in the cover of the 26 study species, we developed a Linear Mixed Effects Model (LMEM) using R 2.11.1 (R Foundation for Statistical Computing; R package nlme, Vienna, Austria). 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 modelled cover of the study species as a function of provenance (introduced or native), and life-form (grass or forb species) with a

Table 1 List of the 26 study species sampled at sites both home and away

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

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; US, United States (United States Department of Agriculture 2010).

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 with 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). 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 vs. 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 EMT 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 that 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
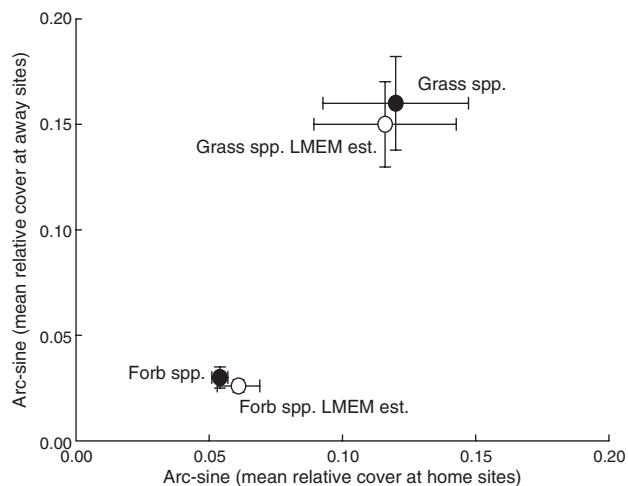
all species at a site as the response. PERMANOVA allows us to use the full suite of species abundance data to evaluate the community response because it uses similarity distances and permutations to calculate P-values (Anderson 2001), thus relaxing the assumptions associated with a traditional MANOVA. 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 & 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, Plymouth, UK).
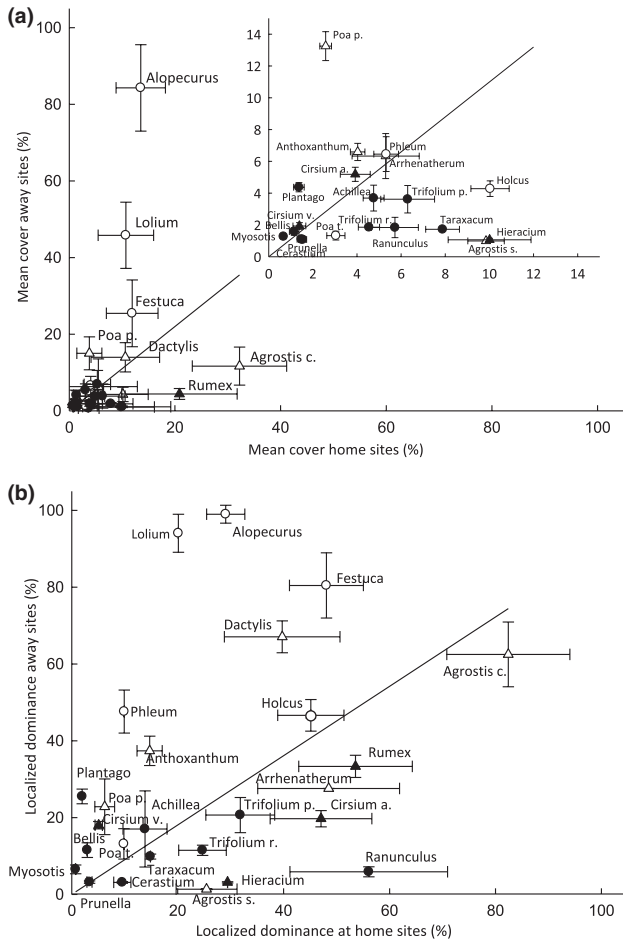
RESULTS

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 (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 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*, *F. rubra* and *P. pratensis* had a higher mean relative cover at away sites; while *Agrostis capillaris* had a higher mean relative cover at home sites (Fig. 3a and see Figures S2 and S3 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. 3a inset and see Figures S2–S5). 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.
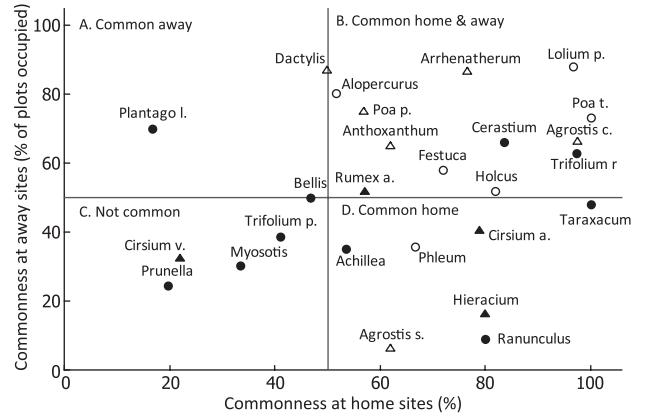
The same grasses with a high mean relative cover also had a high mean maximum cover per plot, a measure of localized dominance or patchiness (Fig. 3b). The maximum cover of the 14 forbs examined also varied, but only *Plantago lanceolata* and *Bellis perennis* were more common at away sites (Fig. 3b). 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

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 Linear Mixed Effects Model (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 labelled as 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 labelled 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 labelled as invasive species by Weber (2005). Quadrant A shows species that are more common at away sites; quadrant B shows species that are common at both home and away sites; quadrant C shows species that are not common at both home and away sites; and quadrant D shows species that are common at home sites.

Figure 5 Non-metric multidimensional scaling 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 colours represent the number of study species found at each site. 2D stress level: 0.17.

expected the majority of species to be found in quadrant A of Fig. 4. The quadrants were, however, occupied non-randomly (EMT, 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 *B. 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 10 species identified as world invasive species in Weber (2005) (highlighted in

Figs 3 and 4), did not consistently have higher relative cover than others at the plot scale; however, five of ten species (four grass spp. and one 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. 5 PERMANOVA: $F_{1,36} = 1.13$, $P < 0.055$, see also

Figure S1 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. 5).

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 & Glenn (1990) found this pattern held at multiple spatial scales from small patches to regional scales, but our results suggest that 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 favour 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 favour 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 coevolved 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 favour 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 intro-duction of plant species with a high potential for invasiveness is imperative for protecting biodiversity and conserving natural envi-ronments (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 with 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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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Average similarity between sites depending on the number of study species present.

Figure S2 Map showing the mean relative cover for six grass species at all recorded home and away sites.

Figure S3 Map showing the mean relative cover for six grass species at all recorded home and away sites.

Figure S4 Map showing the mean relative cover for seven forb species at all recorded home and away sites.

Figure S5 Map showing the mean relative cover for seven forb species at all recorded home and away sites.

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.

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

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

Table S4 Parameter estimates for the best-fitting LMEM of relative cover (data were arc-sine transformed) for all 26 study species with random intercepts due to species (σ^2 species), site within species (σ^2 site), and plot within site within species (σ^2 plot).

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

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