

Patterns of trait convergence and divergence among native and exotic species in herbaceous plant communities are not modified by nitrogen enrichment

Elsa E. Cleland^{1*}, Chris M. Clark², Scott L. Collins³, Joseph E. Fargione⁴, Laura Gough⁵, Katherine L. Gross⁶, Steven C. Pennings⁷ and Katharine N. Suding⁸

¹Ecology, Behavior & Evolution Section, University of California, San Diego, CA 92093, USA; ²School of Life Sciences, Arizona State University, Tempe, AZ 85287, USA; ³Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA; ⁴The Nature Conservancy, North America Region, Minneapolis, MN 55415, USA; ⁵Department of Biology, University of Texas at Arlington, Arlington, TX 76019, USA; ⁶W.K. Kellogg Biological Station and Department of Plant Biology, Michigan State University, Hickory Corners, MI 49060, USA; ⁷Department of Biology and Biochemistry, University of Houston, Houston, TX 77204, USA; and ⁸Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720, USA

Summary

1. Community assembly theories predict that the success of invading species into a new community should be predictable by functional traits. Environmental filters could constrain the number of successful ecological strategies in a habitat, resulting in similar suites of traits between native and successfully invading species (convergence). Conversely, concepts of limiting similarity and competitive exclusion predict native species will prevent invasion by functionally similar exotic species, resulting in trait divergence between the two species pools. Nutrient availability may further alter the strength of convergent or divergent forces in community assembly, by relaxing environmental constraints and/or influencing competitive interactions.

2. To investigate how nutrient availability influences forces of divergence and convergence during the invasion of exotic species into native communities, we conducted multivariate analyses of community composition and functional traits from naturally assembled plant communities in long-term nitrogen (N) addition experiments across North America.

3. Relative abundances of key functional traits differed between the native and exotic plant communities, consistent with limiting similarity or a trait bias in the exotic species pool. Environmental context also played an important role in invasion because sites varied in the identity of the traits that predicted dissimilarity between native and exotic communities. Nitrogen enrichment did not alter these patterns.

4. Nitrogen enrichment tended to increase exotic abundance, but this result was driven by a dramatic increase in exotics in only a few experiments. When similarity between native and exotic communities was included in the statistical model, N enrichment no longer predicted an increase in exotic relative abundance. Instead, sites with the highest abundance of exotic species were the ones where native and exotic communities had the highest trait similarity.

5. Synthesis. Our analysis of natural patterns of invasion across herbaceous communities in North America found evidence of both divergent and convergent forces on community assembly with exotic species. Together, these results suggest that while functionally dissimilar exotic species may be more likely to invade, they are unlikely to become abundant unless they have traits pre-adapting them to environmental conditions in their invaded range. Contrary to prior studies, invasion was not consistently promoted by N enrichment.

*Correspondence author. E-mail: ecleland@ucsd.edu

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Introduction

Invasions by exotic species have fascinated ecologists as natural experiments in community assembly (i.e. Elton 1958), and a renewed interest in the mechanisms that enable invasion has been fuelled by the widespread deleterious ecological and economic impacts of species invasions (Pimentel, Zuniga & Morrison 2005). Competition for limiting resources among co-occurring species has long been thought to be a major factor in determining plant community composition (MacArthur 1970; Tilman 1982, 1988). The theory of competitive exclusion assumes that multiple species will only coexist if they have different niches (Hutchinson 1959), and the concept of limiting similarity logically follows, predicting that species will coexist only if they can utilize different pools of resources (MacArthur & Levins 1967; Abrams 1983). While these theories were originally based on hypothesized differences in resource use, researchers looking for evidence of limiting similarity as a structuring force in communities have often relied instead on differences among species traits (Weiher, Clarke & Keddy 1998; Stubbs & Wilson 2004). Functional traits are the ecological attributes of a species that relate both to strategies of resource capture and to the effect that the species has on the overall pool of resources in the ecosystem (Lavorel & Garnier 2002). This relationship between traits and resource-consumption patterns predicts that an exotic species will be less likely to establish if there is a species present in the resident community with the same suite of functional traits (Elton 1958; Lodge 1993), and evidence from experimentally created communities supports this hypothesis (Fargione, Brown & Tilman 2003; Hooper & Dukes 2010; but see Emery 2007). If limiting similarity is an important factor in preventing invasion, then naturally assembled communities would be predicted to have divergent functional traits between co-existing native and exotic species.

Resource availability, particularly resources that are limiting for growth, may significantly alter species interactions during community assembly. Soil nitrogen (N) is a limiting resource for primary production in ecosystems across the globe (Elser *et al.* 2007), and numerous researchers have found increased invasion with enhanced N availability (e.g. Huenneke *et al.* 1990; Burke & Grime 1996; Maron & Connors 1996; Bobbink, Hornung & Roelofs 1998; Davis & Pelsor 2001; reviewed in Daehler 2003). If enhanced resource availability reduces competition intensity, then the influence of limiting similarity may be relaxed, allowing the establishment of invading species (i.e. the fluctuating resource hypothesis, Davis, Grime & Thompson 2000). The hypothesis that N enrichment could reduce the strength of competition and thus reduce the strength of limiting similarity during community assembly remains to be tested. An alternative hypothesis is that enhanced N availability could intensify competition, leading to dominance by the best N competitor (Grime 1977), or N enrichment could shift competition from one

resource to another (e.g. from N to light) without reducing the overall competition for resources (Wilson & Tilman 1991). This could shift the identity of functional traits that predict competitive dominance or exclusion within a community, leading to convergence towards a common set of traits necessary to compete in a highly productive environment (Grime 2006).

Environmental or habitat filtering could also cause convergence in functional traits among native and invasive species, if environmental conditions that vary among habitats impose strong constraints on the success of all species, requiring natives and invaders to have similar suites of the key traits that allow persistence in a particular environment (Keddy 1992; Weiher & Keddy 1999). In contrast to the prior niche-based hypotheses, neutral theory suggests that stochastic demographic processes could result in a null expectation of no trait differences between native and exotic species (Hubbell 2005; Daleo, Alberti & Iribarne 2009).

The goal of this study was to determine whether natural patterns of invasion are consistent with the concepts of limiting similarity (divergence in traits between native and exotic species) and environmental filtering (convergence in traits between native and exotic species) and to evaluate whether nutrient enrichment influences these patterns. To accomplish this goal, we synthesized multiple data sets from N fertilization experiments in naturally assembled herbaceous communities across North America. In the course of our research, we asked the following five questions: (i) Do exotic species increase in abundance relative to native species under nutrient enrichment, suggesting they possess traits that allow them to thrive in high-resource conditions? (ii) Do native and exotic portions of plant communities differ in suites of functional traits, consistent with patterns driven by limiting similarity and complementary resource capture? (iii) Alternatively, if native and exotic plant communities have similar suites of functional traits, do these traits vary among sites, indicating the importance of environmental filters in determining the potential suite of traits present in certain environments? (iv) Does nutrient enrichment increase trait similarity between the native and exotic portions of the plant community? This pattern could arise either because reduced competition for nutrients allows similar species to coexist or because increased competition for N and/or other resources (such as light) selects for the same traits in both native and exotic species (Grime 2006). Finally, (v) do sites with the greatest trait divergence between native and exotic species have the highest rate of invasion, as measured by exotic relative abundance?

Materials and methods

DATA BASE

Drawing on a data base of N fertilization experiments in predominantly herbaceous ecosystems (Cleland *et al.* 2008), we identified

seven sites with experiments that contained both native and exotic species (Table 1). Among the sites, there were fertilization experiments performed in multiple community types that varied in time since disturbance (CDR and KBS) or performed along with other crossed factors (added water at JRG and SGS, burning and/or mowing at KNZ). Rather than using a reduced data set, we chose to use all of the available data to expand our environmental inference space, and when appropriate defined community type or other experimental treatments as random factors nested within site. All experiments measured species composition in both control and fertilized plots. Methods for measuring species composition varied among experiments, including destructive biomass harvests, visual percentage cover estimation and abundance-based pin counts but were standardized by calculating relative abundance of each species in the experimental plot. Abundance and biomass are often correlated (e.g. Chiarucci *et al.* 1999), and while differing metrics could potentially explain variation in findings across sites, only one metric was used within each site. The data used in this manuscript represent the relative abundance responses to fertilization in 667 experimental plots, for 418 taxa (mostly identified to species, but occasionally genera), in addition to associated species traits.

Categorical trait information was assembled for each species in each experiment, including life-form (graminoid, forb or woody), photosynthetic pathway of graminoids (C3 or C4), N-fixing potential of forbs (N-fixing or non-N-fixing), leaf habit of woody species (deciduous or evergreen), canopy height at maturity (upper, middle or bottom of the canopy), clonal strategy (non-clonal, rhizomatous or caespitose), life span (annual or biennial/perennial) and origin (native or exotic). All traits except for height were based on descrip-

tions in published floras or found in peer-reviewed literature; height classifications were based on the observations of the researchers from each site. Recent advances in identifying trait differences in regional and global lists of native vs. exotic species (Hamilton *et al.* 2005; Leishman *et al.* 2007; Ordóñez, Wright & Olff 2010; Van Kleunen *et al.* 2010) have focused on continuous functional traits such as specific leaf area, seed size or leaf nutrient content. These easily measured 'soft traits' can be good predictors of resource capture and are related to 'hard traits' that directly measure resource uptake (Diaz *et al.* 2004). The categorical functional groupings we used here reflect broad differences in rates of resource capture and growth. Our assumption is that these categorical traits reflect differences in resource capture, although many 'hard traits' vary as much within functional groups as among them (Wright *et al.* 2006); we recognize this limits our ability to infer the mechanistic basis of community assembly.

This data base of species relative abundances in response to fertilization, along with species trait information, is a product of the PDT-Net working group (productivity, diversity and trait network), and these data are publicly available (Cleland *et al.* 2008).

THE EFFECT OF FERTILIZATION ON EXOTIC ABUNDANCE

Exotic relative abundance was calculated for each plot, within each experiment, and averaged across all years of observation. Data from all experiments were analysed together using the MIXED procedure in SAS v. 9.2 (SAS-Institute 2008). The influence of N fertilization on exotic relative abundance was tested using a linear mixed model

Table 1. Summary of N fertilization experiments utilized for analyses in this manuscript. Abbreviations used in the 'Experiment' column are consistent with data presented in Fig. 1 and published in Cleland *et al.* (2008)

Experiment	Community description	Plot size (m ²)	No. of plots	Addition rate (g N m ⁻² year ⁻¹)	Years	Method	Methods reference
CAR – 6	High marsh zone	0.25	10	140	1999–2005	% cover	Pennings & Callaway (1992)*
CDR – 1	Old field 'C' abandoned in 1934	0.3	6	9.5	1982–2001	Biomass	Tilman (1987)
CDR – 2	Old field 'B' abandoned in 1957	0.3	6	9.5	1982–2001	Biomass	Tilman (1987)
CDR – 3	Old field 'A' abandoned in 1968	0.3	6	9.5	1982–2001	Biomass	Tilman (1987)
CDR – 4	Native oak savanna, field 'D'	0.3	6	9.5	1982–2001	Biomass	Tilman (1987)
JRG – 1	Annual grassland	0.5	8	7	1999–2002	Pin hits	Zavaleta <i>et al.</i> (2003)
JRG – 2	Annual grassland, added water	0.5	8	7	1999–2002	Pin hits	Zavaleta <i>et al.</i> (2003)
KBS – 1	Old field, annually tilled	1	6	12.3	1992–2002	Biomass	Huberty, Gross & Miller (1998)
KBS – 2	Old field, untilled	1	6	12.3	1992–2002	Biomass	Huberty, Gross & Miller (1998)
KNZ – 5	Tall-grass prairie, unmanipulated	1	6	10	1999	Cover classes	Collins <i>et al.</i> (1998)
KNZ – 6	Tall-grass prairie, mowed	1	6	10	1999	Cover classes	Collins <i>et al.</i> (1998)
KNZ – 7	Tall-grass prairie, burned	1	6	10	1999	Cover classes	Collins <i>et al.</i> (1998)
KNZ – 8	Tall-grass prairie, burned and mowed	1	6	10	1999	Cover classes	Collins <i>et al.</i> (1998)
SEV	Desert grassland	1	10	10	2004	Seasonal cover	Collins, unpublished
SGS – 1	Short-grass steppe	0.1	50	6	2000	Cover classes	Lauenroth & Burke, unpublished
SGS – 2	Short-grass steppe, added water	0.1	50	6	2000	Cover classes	Lauenroth & Burke, unpublished

The first three letters abbreviate the site, many of which are Long Term Ecological Research (LTER) sites: CAR, Carpenteria; CDR, Cedar Creek; JRG, Jasper Ridge Biological Preserve; KBS, Kellogg Biological Station; KNZ, Konza Prairie; SEV, Sevilletta; SGS, Short-grass steppe. 'Plot size' indicates the size of the plot measured for species composition, No. of plots reflects the level of replication for each of control and fertilized plots, and the method for species composition is indicated in the 'Method' column. 'Years' indicate the year(s) the data were collected. *Data are unpublished but citation provides information on site and vegetation.

where fertilization treatment (N) and SITE were factorial fixed factors, and EXPERIMENT was included as a random factor nested within SITE. There were different numbers of replicate plots in each experiment (Table 1); the MIXED procedure accounted for this unbalanced design by using restricted maximum likelihood to estimate generalized least squares and the Kenward–Roger procedure for calculating denominator degrees of freedom (Littell, Stroup & Freund 2002). *Post hoc* comparisons of least-squared means were used to evaluate differences among levels of significant model terms.

MULTI-VARIATE TRAIT ANALYSES

We tested whether the native and exotic communities differed in their suites of functional traits at two scales: first at the neighbourhood scale using plot-level data, and second at the experiment level using data aggregated from all plots in each experiment. The rationale for performing the analyses at these two scales stems from the hypothesis that biotic interactions leading to limiting similarity during community assembly primarily play out at local (neighbourhood) scales (MacArthur 1970; Tilman 1982). Functional trait differences between native and exotic portions of the plant community at larger scales could suggest that (i) limiting similarity in neighbourhoods scales up to influence community-wide composition, (ii) the pool of potential invaders in that location differs because of historical influences of human introduction (Mack & Lonsdale 2001) or (iii) the exotic species pool is limited to species with traits related to long-distance dispersal and colonization (Turnbull, Rees & Crawley 1999; Hamilton *et al.* 2005).

In the data base of naturally assembled communities utilized in our analyses, 85% of the species have a mean relative abundance below 10%, and 32% of the species have a mean relative abundance below 1%. Thus, an analysis focused on traits differing between the list of native vs. exotic species would be overwhelmingly biased towards differences among rare species. Abundant species use the majority of the local resources and are therefore likely to have a greater influence on community assembly processes than are rare species (e.g. Smith & Knapp 2003), often referred to as the biomass ratio hypothesis (Grime 1998). Hence, abundance-weighted trait values may be more appropriate for predicting ecosystem-scale phenomena on the basis of plant traits (Garnier *et al.* 2004; Díaz *et al.* 2007). Here, we employed a novel approach for the analysis of trait differences; we calculated the relative abundance of traits (regardless of species identity) within the native and exotic communities, thereby creating continuous measures of trait abundances and avoiding the potential bias imposed by large numbers of rare species. This is similar to the ‘guild proportionality’ metric (i.e. Wilson & Watkins 1994) but calculates the summed relative abundances of species with given traits, rather than the number of species with a particular trait designation.

These community-aggregated trait abundances were calculated by summing the relative abundances of all native or exotic species with each categorical functional trait and calculating the average relative trait abundance across all years of data collection. For the neighbourhood-scale analysis, these trait abundances were calculated for every plot (see example calculation for the experimental-scale analysis in the following paragraph that used the identical calculation, just aggregated at a larger scale). All analyses were repeated using only the latest year of data available for each site, the results of which did not qualitatively differ from those using averages over the entire temporal period (results not shown). Further, a prior analysis of temporal responses using the longest term data sets from this data base found that these herbaceous plant communities respond quickly to nutrient enrichment (Collins *et al.* 2008), and together, these findings suggest

that our analyses are biased neither by differences in duration among the experiments nor inclusion of multiple years of data when available.

For the analysis at the level of experimental area, trait relative abundances for native vs. exotic communities were calculated as averages across all plots and years. As with the neighbourhood-scale analysis, these were calculated separately for control and fertilized treatments. For instance, in experiment CDR-3 (Field A at the Cedar Creek Natural History Area), graminoids with C3 photosynthesis comprised 7% of native species biomass in control plots, 87% of exotic species biomass in control plots, 11% of native species biomass in fertilized plots and 96% of exotic species biomass in fertilized plots. These relative abundance values were calculated for each of the 14 categorical functional traits (see previous data base description). This method effectively normalized trait abundances between native and exotic communities, ensuring that the multivariate analysis tested for trait overlap via similarities in the relative abundances of traits, and was not confounded by absolute differences in abundance of native vs. exotic species (tested separately, as described previously).

The following analyses were performed at both the neighbourhood and experiment levels using the program PRIMER-e v.6. We first calculated the Bray–Curtis dissimilarity between every pair of samples (Bray & Curtis 1957). Bray–Curtis dissimilarity is an appropriate distance measure for proportional data (e.g. relative abundance data) and performs well in multivariate analyses (Clarke & Warwick 2001). This resulting distance matrix was analysed using the PERMANOVA procedure, which analyses distance measures in any linear model with categorical factors, and tests for significance by permutation of the distance matrix (Anderson 2001; McArdle & Anderson 2001; Anderson & Ter Braak 2003). This analytical procedure has seldom been applied to terrestrial plant community data (but see Reynolds *et al.* 2007; Houseman *et al.* 2008), yet has significant advantages over other techniques in that it allows the use of any distance measure and can test for interaction terms in factorial analyses.

ORIGIN (native or exotic) and N (fertilized or control) were fixed factors in the linear model, in addition to an interaction term (ORIGIN \times N) to test whether trait dissimilarity was altered by N enrichment. To account for our expectation that there would be different suites of traits present in different environments, SITE was included as a fixed factor and EXPERIMENT was included as a random factor nested within SITE. The final linear model was fully factorial and included all higher-order interaction terms.

The distance matrix was permuted 999 times, and type III sums of squares were used to test for significance of the factors. Previous analyses that used randomization procedures to test for non-neutral patterns in species traits have been criticized because they randomized across environmental gradients or disrupted the observed correlation structure among traits (discussed in Stubbs & Wilson 2004). These issues are overcome in this analysis because the distance metric is calculated for the full suite of traits, and the distance matrix is subsequently permuted, where the SITE and EXPERIMENT factors encompass the variance in distance because of environmental heterogeneity. It is important to note that the random EXPERIMENT factor accounted for variation associated with any additional manipulations (e.g. burning or mowing in the KNZ experiments), by restricting the permutation procedure, to test for the likelihood of significance as compared to data randomized within experiments, and does not inflate the degrees of freedom or trait variation associated with the SITE factor.

Significant interactions between SITE and other factors were evaluated with a series of post hoc analyses. First, a PERMANOVA analysis was run separately for each site using plot-level data to identify the

sites where each effect was significant. Univariate analyses were conducted for each trait as post hoc tests to determine which traits contributed most to a significant $\text{SITE} \times \text{ORIGIN}$ interaction in the multivariate analysis, because the ORIGIN effect was significant at every site. These univariate *post hoc* analyses were conducted using linear mixed models in SAS as described in the previous section, where ORIGIN , N and SITE were fixed factors, and EXPERIMENT was included as a random factor nested within SITE when multiple experiments were present at a given location. While the univariate analyses do not take trait correlations into account, they are useful for identifying patterns of significant differences. A separate *post hoc* SIMPER analysis was used to identify the traits that contributed towards a higher-order $\text{SITE} \times \text{ORIGIN} \times \text{N}$ interaction. A SIMPER analysis identifies the percentage dissimilarity contributed by each trait in a multivariate analysis (Clarke & Warwick 2001); this method for *post hoc* analysis was only performed on the data from CDR because individual PERMANOVA analysis performed for each site identified CDR as the only site in which there was a significant $\text{ORIGIN} \times \text{N}$ interaction.

Principle components analysis (PCA) was employed to visualize the relationships among traits and their variation across experiments (McCune & Grace 2002). This ordination was performed using PRIMER-e v.6, based on Euclidean distances among mean trait abundances calculated for each experiment, within the native and exotic communities and within control and fertilized plots. Pearson correlations were calculated between PCA axis scores and trait abundances for each site, in order to define the PCA axes according to the composite traits they represented. All data were ordinated in the same PCA, so the axis scores are the same for native and exotic origin, and fertilized and control plots, but the data are displayed in separate panels to facilitate a comparison of the patterns.

Finally, to test the hypothesis that trait overlap between native and exotic communities should influence the overall levels of invasion, we performed a linear mixed-model analysis in SAS v 9.2 to predict exotic relative abundance by N treatment (categorical factor) and similarity (SIM) between the native and exotic communities (similarity = $1 - \text{Bray-Curtis}$ dissimilarity). These analyses were performed at the plot (neighbourhood) and experimental scales. EXPERIMENT was included as a random factor nested within SITE for the plot-level analysis. Each experiment was a replicate for the experiment-level

analysis, so in this case, SITE was included in the analysis as a random factor, so that degrees of freedom were not inflated.

Results

THE EFFECT OF FERTILIZATION ON EXOTIC ABUNDANCE

Exotic relative abundance varied strongly among SITES ($F_{6,8.9} = 5.98$, $P = 0.02$, Table S1), as did the response of exotic relative abundance to N enrichment ($\text{SITE} \times \text{N}$, $F_{6,644} = 31.8$, $P < 0.001$, Fig. 1). Averaged across all experiments, N enrichment increased exotic relative abundance ($F_{1,644} = 17$, $P < 0.001$) but this was driven by a significant response of exotic relative abundance in only a few experiments (CDR Old Fields A, B and C and the tall-grass prairie sites at KNZ that were mowed).

NATIVE AND EXOTIC SPECIES POSSESS DIFFERENT SUITES OF TRAITS

Native and exotic communities differed significantly in their suites of traits at both the neighbourhood (ORIGIN pseudo $F_{1,9} = 15.2$, $P = 0.001$, Table S2) and experiment (ORIGIN pseudo $F_{1,9} = 16.1$, $P = 0.001$) scales. Analyses at both spatial scales found that the distribution of functional traits varied among sites (SITE , neighbourhood pseudo $F_{6,9} = 7.0$, $P = 0.001$, experiment pseudo $F_{6,9} = 6.9$, $P = 0.001$, Table S3), as did the extent and identity of trait differences between native and exotic plant communities ($\text{SITE} \times \text{ORIGIN}$ neighbourhood pseudo $F_{6,9} = 6.2$, $P = 0.001$, experiment pseudo $F_{6,9} = 5.9$, $P = 0.001$, Table 2). In two sites, there was only one exotic species present; as a result, the relative abundance of each functional trait for exotic origin was either 100% or 0% (CAR-6 & SEV). These sites were also unusual because of the high input of N necessary to overcome tidal flushing at the marsh site (CAR-6) and because these two sites had the smallest plot sizes (Table 1). A signal of limiting similarity could be stronger in smaller neighbourhoods where interspecific interactions are most apparent, such that variation in plot size might influence the multivariate analysis of trait similarity. To address these issues, the PERMANOVA analyses were run again with these two sites excluded, but the results did not differ from the analysis with the full suite of sites (results not shown).

In univariate analyses conducted separately for each trait, all traits except the abundances of N-fixing forbs and species in the bottom of the canopy were significantly different between the native and exotic communities (ORIGIN terms less than $P < 0.05$, Table S4), but the level of difference varied among sites, as evidenced by a significant $\text{SITE} \times \text{ORIGIN}$ interaction for every trait ($P < 0.05$) except for N-fixing forbs. Annuals were more abundant within the exotic communities, while perennial and woody species were more abundant within the native communities (*post hoc* comparisons, Table 2). Generally, the native communities had higher abundance of bottom- or mid-canopy clonal

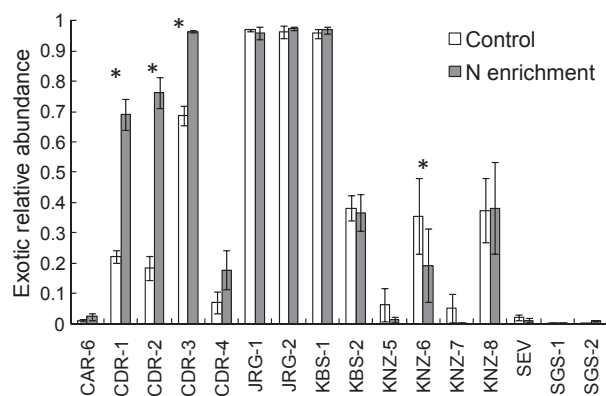


Fig. 1. Means of exotic relative abundance for control and N-fertilized plots in each experiment, averaged across all years. Abbreviations for experiments are as listed in Table 1. Error bars indicate 1 SE of the mean. The asterisk indicates a significant difference between least-squared means of control and fertilized plots at individual experiments ($P < 0.05$).

Table 2. In order to understand the significant SITE × ORIGIN interactions in the univariate analyses of trait abundance differences between the native and exotic communities (full statistical output in Table S4), differences in least-squared means and standard errors were evaluated for each trait, in every SITE × ORIGIN combination. If a trait was significantly more common within the native or exotic community at a given site, then the origin (native vs. exotic) is listed below, along with the statistical significance of the *post hoc* test

Site	Clonality			Life span			Life-form			Height				
	Caespitose	Rhizomatous	Non-clonal	Annual	Perennial	C3	C4	N-fixing forb	Non-N-fixing forb	Deciduous woody	Evergreen woody	Bottom canopy	Middle canopy	Upper canopy
CAR	***Native	**Native	***Exotic	***Exotic	***Native	***Exotic	**Native	NS	NS	NS	***Native	**Native	NS	***Exotic
CDR	***Native	***Exotic	**Native	NS	NS	***Exotic	***Native	***Native	***Native	***Native	***Native	***Exotic	***Native	***Native
JRG	***Native	NS	***Exotic	***Exotic	***Native	***Exotic	NS	NS	NS	NS	NS	*Exotic	***Exotic	***Native
KBS	NS	**Native	*Exotic	NS	NS	***Exotic	NS	***Native	NS	NS	NS	NS	NS	NS
KNZ	*Exotic	***Native	***Exotic	***Exotic	***Native	*Exotic	NS	***Native	NS	NS	NS	NS	NS	NS
SEV	NS	NS	NS	***Exotic	***Native	***Native	***Exotic	***Native	NS	NS	NS	**Native	***Native	***Exotic
SGS	***Native	***Native	***Exotic	***Exotic	***Native	*Native	***Native	***Exotic	**Native	*Native	*Native	***Native	**Native	***Exotic

****P* < 0.0001, ***P* < 0.001, **P* < 0.05. The relative abundance of each trait within the native and exotic communities is listed by experiment in Table S3.

species (either caespitose or rhizomatous) and non-N-fixing forbs, while the exotic communities had higher abundances of upper-canopy, non-clonal and C3-graminoid species. For other traits in the data base, some were more abundant in one community (native vs. exotic) in some sites, but the reverse was true at other sites. *Post hoc* tests helped to identify these exceptions. For example, while the native community is more likely to have rhizomatous species at most sites, at CDR, the exotic community has significantly higher abundance of rhizomatous species (Table 2). Hence, while the multivariate analyses are powerful for detecting the amount of community variation attributable to different factors, care should be taken to evaluate the patterns of individual traits as they vary across sites.

These univariate *post hoc* analyses demonstrated specific differences in trait abundances, but did not account for correlations among traits. Principle components analysis (PCA) was used to visualize the patterns of trait correlations present in the data set used for the overall multivariate analyses (Fig. 2). The first two principle component axes captured 70% of variation in trait composition among the experiments. The ordination shows that there are strong correlations among native origin, perenniality, caespitose clonality and the C4 graminoid life-form, as shown by negative scores on both PCA axes (Pearson correlation coefficients for each trait are shown in Table S5). Exotic species were more likely to be annual, non-clonal, occur in the lower-canopy and be a C3-graminoid than native species, but the SITE × ORIGIN interaction is also apparent in Fig. 2. For instance, in contrast to the overall trends, at SEV (an arid grassland site), exotic invaders are more often C4 than C3 graminoids.

FEW EFFECTS OF N ENRICHMENT ON TRAIT DISTRIBUTIONS

Fertilization generally did not influence the distribution of traits within native or exotic communities (N and ORIGIN × N were non-significant at both neighbourhood and experimental levels, and PERMANOVA analysis results are given in Table S2). There was a significant SITE × ORIGIN × N interaction at the neighbourhood scale (pseudo $F_{6,9} = 2.48$ *P* = 0.04); *post hoc* PERMANOVA analyses run separately for each SITE revealed that there was a significant ORIGIN × N interaction only at CDR. This interaction arose at CDR because different traits contributed most to the dissimilarity between native and exotic communities in the control vs. fertilized treatments (SIMPER *post hoc* analysis, Table 3). C4-graminoids, species with caespitose clonal strategies and upper-canopy dominants (i.e. bunchgrasses) declined sharply with N fertilization in the native community at CDR. However, in the exotic community, species in the upper-canopy increased in abundance when fertilized and those in the bottom canopy declined sharply. The general lack of a fertilization effect on trait abundances is illustrated by the PCA of trait composition (Fig. 2); comparisons of the control and fertilized panels reveal few differences (with the exception of the experiments at CDR discussed previously).

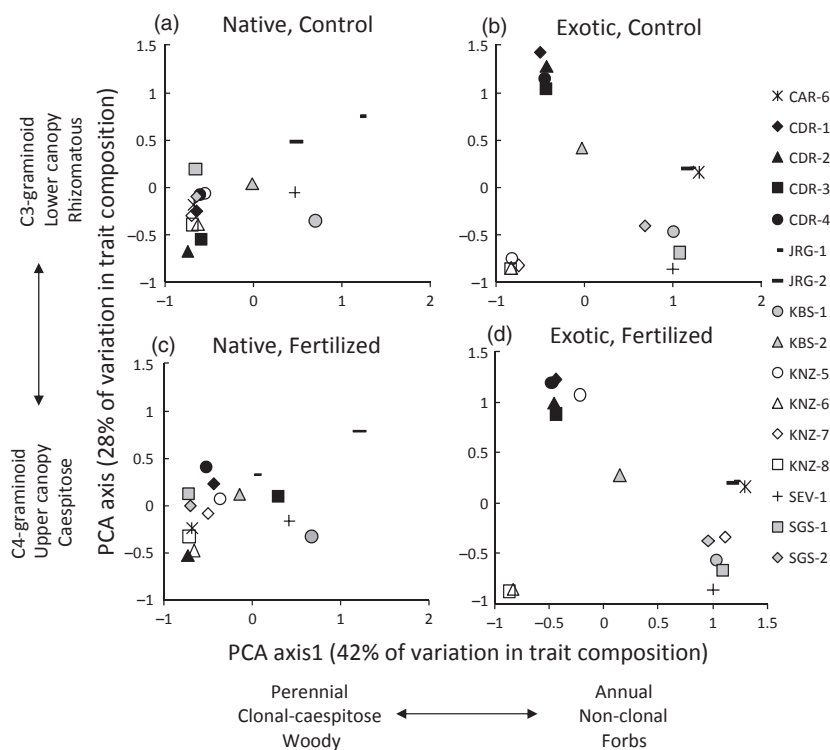


Fig. 2. Principle components analysis (PCA) of trait relative abundances across experiments. Abbreviations for experiments are as listed in Table 1. Values for ORIGIN and N treatments are displayed separately but are based on the same ordination, and thus, the axes are the same for all panels. The correspondence between trait abundances and PCA axis scores was established using Pearson correlations. This figure demonstrates that native communities are often dominated by perennial species with caespitose clonality (a) and shows that while traits dominating exotic communities are frequently different from traits dominating native communities (b & d vs. a & c), the traits that predict these differences vary among sites. This figure also shows that there is very little difference in trait compositions of control and N-fertilized treatments within the experimental communities (a & b vs. c & d), with the exception of the CDR experiments where there was a significant ORIGIN \times N interaction in the multivariate analysis. N addition at CDR led to a significant decline in native C-4 graminoids with caespitose clonality (i.e. bunch grasses).

Table 3. SIMPER analysis showing the traits contributing to the dissimilarity in traits among native and exotic communities in control and N-fertilized treatments in the Cedar Creek LTER. The multivariate PERMANOVA analysis found a significant SITE \times ORIGIN \times N interaction, and subsequent PERMANOVA analyses performed separately for each site showed that there was a significant ORIGIN \times N interaction only at one site: CDR. The SIMPER analysis shows that different traits are responsible for dissimilarity between control and fertilized treatments in the native vs. exotic communities. Traits are listed in order of descending contribution to percentage dissimilarity, up to 90% of the cumulative dissimilarity

Trait	Control abundance	N-Fertilized abundance	Bray-Curtis dissimilarity	Contributed% dissimilarity	Cumulative% dissimilarity
Native community					
C4-graminoid	0.62	0.26	5.77	14.51	14.51
Caespitose	0.68	0.33	5.48	13.79	28.31
Upper canopy	0.73	0.44	4.59	11.54	39.85
Rhizomatous	0.2	0.36	3.88	9.76	49.61
Middle canopy	0.2	0.4	3.86	9.72	59.33
Non-N-fixing forb	0.19	0.39	3.74	9.41	68.74
Non-clonal	0.11	0.28	2.9	7.29	76.03
Deciduous woody	0.04	0.15	1.92	4.83	80.86
Annual	0.02	0.12	1.54	3.86	84.73
Perennial	0.98	0.88	1.54	3.86	88.59
Exotic community					
Upper canopy	0.14	0.52	5.79	33.32	33.32
Bottom canopy	0.75	0.47	5.47	31.47	64.79
Rhizomatous	0.9	0.97	1.18	6.79	71.59
C3-graminoid	0.9	0.97	1.18	6.79	78.38
Non-N-fixing forb	0.09	0.03	1.01	5.79	84.17
Non-clonal	0.07	0.03	0.81	4.68	88.86

HIGH EXOTIC RELATIVE ABUNDANCE PREDICTED BY TRAIT SIMILARITY AT THE EXPERIMENT SCALE

When comparing trait similarity between native and exotic communities at the experiment level, we found a significant positive relationship between exotic relative abundance and trait similarity (SIM $F_{1,22.5} = 6.5$, $P = 0.02$, Fig. 3). At the plot scale, trait similarity was not a significant predictor of exotic relative abundance (Table S6). In these statistical models, N did not have a significant effect on exotic relative abundance at either scale, in contrast to the model that did not include native/exotic community (Fig. 1).

Discussion

Nitrogen addition did not consistently increase the relative abundance of exotic species in the naturally assembled plant communities represented in our data base (Question 1); instead, there was considerable variation among experiments. Exotic abundance increased with fertilization in three experiments, was unchanged in 12 experiments and actually declined with fertilization in the tall-grass prairie site (KNZ), where biomass was removed through mowing (Fig. 1). This finding questions the generality of the long-standing assumption that exotic species establishment is consistently favoured under nutrient enrichment (e.g. Daehler 2003). Maron & Marler (2007) hypothesize that communities will resist invasion under resource enhancement if native species are initially present that can quickly utilize extra resources and hence compete with potential invaders. The mixed responses of exotic species to fertilization across the sites and experiments in this data set heighten the importance of considering the role of environmental and community context in the success of invasions.

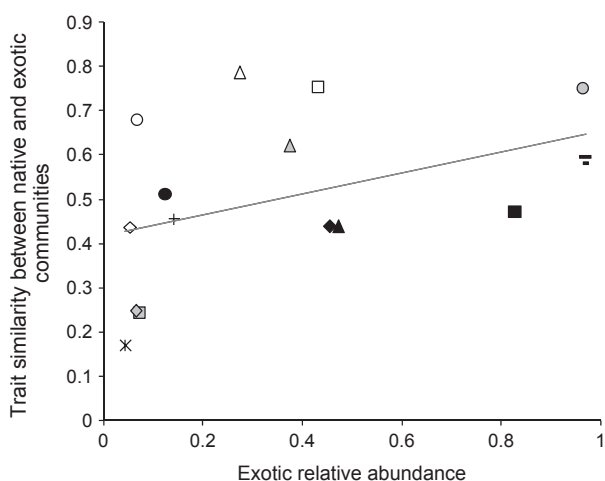


Fig. 3. Trait similarity between native and exotic communities is positive related to exotic relative abundance across sites. Each datum represents the mean value across all years of an experiment. Symbols indicate experiments as in Fig. 2. Fertilization did not alter the relationship between trait similarity and exotic abundance (Table S5); hence, these data are averaged across control and fertilized plots. Trendline shows best linear fit through the data.

In particular, exotic relative abundance varies more among and within sites with different management regimes than in response to N enrichment, highlighting the importance of land-use history in predicting establishment and dominance of exotic species (Von Holle & Motzkin 2007).

Our multivariate analysis found that native and exotic portions of the plant community differed in their suite of functional traits (Question 2). This is consistent with the concept that limiting similarity is an important force in community assembly across a wide variety of herbaceous plant communities. Alternatively, the strong trait differences observed between native and exotic communities in this data set may not be due to a signal of competitive exclusion, but instead result from phylogenetic differences between native and exotics, such that the two groups have intrinsically different suites of traits (Daehler 1998; Cadotte, Hamilton & Murray 2009). Many exotic species have been introduced by humans to provide forage or other utility, which could contribute to trait differences between native and exotic species (Mack & Lonsdale 2001). In addition, exotic species may be more likely to establish if they have traits associated with good colonization ability, such as high reproductive allocation or small seed size, regardless of traits related to resource use (Baker 1974; Turnbull, Rees & Crawley 1999; Milbau *et al.* 2003). To isolate the effects of limiting similarity during community assembly, one would need to standardize for colonization differences of the species in the potential species pools. Seed-sowing experiments accomplish this, but lack the realism associated with naturally assembled communities.

Environmental context also strongly contributed to the results, as the identity of traits that differed between native and exotic communities varied among sites (Question 3, Table 2). This signal suggests environmental or habitat filtering, i.e. the suite of traits present at each site was a subset of the larger species pool, likely due to environmental constraints (Diaz, Cabido & Casanoves 1998; Weiher & Keddy 1999; Cornwell, Schwilk & Ackerly 2006). Taken together, our analysis demonstrates how forces of divergence (limiting similarity) and convergence (habitat filtering) can act simultaneously during community assembly, as evidenced by natural patterns of functional trait abundance. For instance, in our overall analysis, native species were more likely to be perennial, while exotic species were more likely to be annuals, but at JRG, these traits did not distinguish between the native and exotic plant communities. The species in the sandstone grassland community at JRG are overwhelmingly likely to be annual as opposed to perennial. Instead, height in the canopy predicted the significant difference in the traits of the native and exotic communities; the exotic species that dominated the biomass at JRG also reached taller parts of the canopy. At this site, exotic and native species may also have differed in phenology, rooting depth or another unmeasured trait. Similarly, at CDR, perennial species dominated among both natives and exotics, such that the annual/perennial split evident at other sites was not an important contributor to the difference between native and exotic plant communities. Prior efforts to identify the traits of successful invaders by analysing regional lists of native and

exotic species (reviewed by Pyšek & Richardson 2007) support the conclusion that traits of successful invaders vary among locations. For instance, Cadotte & Lovett-Doust (2001) found that exotic species in the south-western region of Ontario, Canada, were more likely to be annual or biennial, while Thompson, Hodgson & Rich (1995) found that exotic species in Great Britain, Ireland and the Netherlands were more likely to be perennial and clonal, and Sutherland (2004) found that exotic species in the United States were less likely to be clonal.

Contrary to our expectation, fertilization did not alter trait similarity between native and exotic communities, suggesting that fertilization does not alter the strength of competitive interactions contributing to limiting similarity between native and exotic communities (Question 4). This could indicate that limiting similarity is maintained as species shift from competition for nutrients to competition for light or other resources, so that the signal of limiting similarity is robust across this range of nutrient availability. In a study of herbaceous wetland vegetation, species had a wider range of functional traits in areas with high nutrient availability, particularly phosphorus (Weiner, Clarke & Keddy 1998). In these nutrient-rich areas, there was also increased competition among species for light and other resources, providing support for the idea that competitive interactions control the level of limiting similarity during community assembly, even as the identity of the limiting resource varies (Grime 2006).

In contrast to our expectation that high trait similarity between native and exotic communities would lower exotic abundance (Question 5), we found that experiments with higher trait similarity were the most invaded (Fig. 3). Much of the experimental work relating community composition to invasion has found that high species or functional group diversity in the native community prevents invasion (e.g. Dukes 2001; Prieur-Richard *et al.* 2002; Maron & Marler 2007). Greater resource uptake by diverse communities (Hooper *et al.* 2005) or higher likelihood of good competitors (Wardle 2001) are the hypothesized mechanisms to underlie these patterns, in which case limiting similarity theory would predict that functionally similar species should contribute the greatest resistance to exotic invaders. Fewer studies have actually addressed this hypothesis, by focusing on functional identity separately from functional diversity. Some experimental studies have found that the greatest biotic resistance against invaders was provided by functionally similar native species (e.g. Fargione, Brown & Tilman 2003; Hooper & Dukes 2010). This is not always the case (e.g. Symstad 2000; Von Holle & Simberloff 2004; Emery 2007), indicating the importance of factors other than limiting similarity in these systems.

We interpret the positive relationship between trait similarity and exotic relative abundance in the studies in this data set as evidence that to reach high levels of abundance, exotic species must have traits that pre-adapt them to the environmental conditions in the invaded habitat. These traits are likely to be the same ones prevalent in the native community. At first, this seems to contradict both limiting similarity theory and Darwin's naturalization hypothesis – that introduced species are less likely to establish in places with closely related species. It is

important to note, however, that Darwin's naturalization hypothesis is based on phylogenetic relatedness rather than resource consumption. The concept of phylogenetic niche conservatism assumes that closely related species will be more likely to share similar traits (Wiens & Graham 2005) and hence use similar resources. Observations of plant species distributions in environmental niche space support this concept (Prinzinger 2001), but levels of niche conservatism can vary with taxonomic group and the trait of interest (reviewed in Ackerly 2003). This may explain why some studies find that species are more likely to be invasive when their new habitat lacks closely related species (Strauss, Webb & Salamin 2006), while others find the reverse (Duncan & Williams 2002). The question of whether phylogenetic relationships constrain native and exotic trait composition will be an important future research direction as trait data bases become increasingly available, and sequence archives make it increasingly possible to quantitatively estimate phylogenetic relatedness across large data sets.

A prior analysis of this data set found that N enrichment generally reduced species richness and this effect differed among functional groups; in particular, native, perennial and N-fixing species were more likely to be lost than exotic, annual or non-N-fixing forb species (Suding *et al.* 2005). The analysis presented here was focused on shifts in trait abundance as opposed to species richness and interestingly found that fertilization did not alter the multivariate distribution of functional traits within these communities (with the exception of CDR as discussed previously). These seemingly disparate findings are a result of differences in the way the analyses were conducted. First, the majority of species in our data base are relatively rare, and rare species are more likely to be lost with fertilization (Suding *et al.* 2005) and owing to random demographic stochasticity exacerbated by environmental fluctuations (Hubbell 2001). The data set analysed by Suding *et al.* (2005) focused on the traits of subdominant and rare species and tested whether the probability of species loss with N enrichment was related to functional traits and rarity. A species-level approach is particularly relevant for predicting impacts of environmental change on species diversity. In the analysis here, we asked instead whether the relative abundances of traits (rather than the number of species with particular traits) were shifted by fertilization, in order to focus on the mechanisms associated with convergence and divergence during community assembly. While many studies have shown that N-fixing forb species are likely to be lost with N enrichment (e.g. Stevens *et al.* 2006), they were a low-abundance component of both native and exotic plant communities in our analysis. As a result, this trait did not contribute to the difference in traits between native and exotic communities. Further, because trait abundances in the exotic and native communities were normalized and considered separately, this analysis did not ask whether overall community composition shifted with N enrichment. There are strong multivariate trait correlations in our data set (Fig. 2) and as a result, a shift in the relative abundances of native vs. exotic abundances would likely reveal overall shifts in community-wide trait composition. Putting the results of Suding *et al.* (2005) and this analysis together, we see that N enrichment

caused loss of species with particular functional traits, but because the species lost were rare, their loss did not significantly change functional composition within native and exotic portions of the community.

A potential criticism of this analysis is that it relies on categorical functional traits that may only loosely correlate with strategies of resource capture that provide a mechanism for limiting similarity. Analyses of continuous trait differences between native and exotic species are also limited in their ability to infer mechanisms related to community assembly, however, for several reasons. First, analyses are often performed for regional floras such that species may occupy different spatial locations and hence not compete with one another for resources. Second, none of these analyses have considered species abundances despite the growing recognition that abundance-weighted analyses may better reflect the importance of traits for ecosystem processes (Garnier *et al.* 2004; Díaz *et al.* 2007). Third, because it is difficult to obtain complete continuous trait data for a large number of species, many species from a community may be omitted from an analysis. The categorical functional traits we used in this analysis are considerably easier to accumulate as they can often be extracted from local floras, increasing the likelihood of having full trait coverage for a large data set (Pakeman *et al.* 2008). Further, this synthesis of experiments from naturally assembled communities provides an important link to other regional-scale analyses of categorical trait differences in native and exotic species pools (e.g. Thompson, Hodgson & Rich 1995; Cadotte & Lovett-Doust 2001; Sutherland 2004; reviewed in Pyšek & Richardson 2007).

In conclusion, our analysis demonstrated that native and exotic communities differed in their suite of functional traits across a wide range of herbaceous-dominated ecosystems, regardless of N availability. There was considerable variability among sites in the response of exotic relative abundance to fertilization, with strong responses at only a few sites driving the overall positive response. Together, these results are consistent with patterns that would be expected to arise via limiting similarity and environmental filtering during community assembly and suggest these processes were robust across a range of ecosystems dominated by herbaceous vegetation. The data set used for these analyses was comprised of naturally assembled communities. As a consequence, other factors such as historical legacies of human introduction or phylogenetic correlations with traits relating to colonization or long-distance dispersal could have contributed to some of the differences in trait distributions among exotic and native communities. Regardless, our analysis presents some of the best evidence of trait differences between natives and exotics expressed at the community level, across a wide variety of habitats.

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Supporting Information

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

Table S1. Table of type 3 tests of fixed effects for factors included in a mixed effects model predicting exotic relative abundance based on SITE and N fertilization status.

Table S2. Results from a multivariate PERMANOVA analysis performed at two scales, testing how ORIGIN and N fertilization influence the relative abundances of functional traits among seven SITES containing exotic species.

Table S3. Relative abundance of each trait within the native and exotic communities in each experiment.

Table S4. Traits that differ between the native and exotic plant communities at each site.

Table S5. Pearson correlation coefficients between each trait and PCA axis scores displayed in Fig. 2.

Table S6. Statistical output for linear mixed model analysis predicting exotic relative abundance.

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