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LETTER

A null model of exotic plant diversity tested with exotic and native species–area relationships

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Abstract

At large spatial scales, exotic and native plant diversity exhibit a strong positive relationship. This may occur because exotic and native species respond similarly to processes that influence diversity over large geographical areas. To test this hypothesis, we compared exotic and native species–area relationships within six North American ecoregions. We predicted and found that within ecoregions the ratio of exotic to native species richness remains constant with increasing area. Furthermore, we predicted that areas with more native species than predicted by the species–area relationship would have proportionally more exotics as well. We did find that these exotic and native deviations were highly correlated, but areas that were good (or bad) for native plants were even better (or worse) for exotics. Similar processes appear to influence exotic and native plant diversity but the degree of this influence may differ with site quality.

Keywords

Diversity, diversity–invasibility hypothesis, ecoregion, environmental conditions, exotic fraction, exotic species, plant invasion, species–area relationship, traits.

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INTRODUCTION

Identifying the processes that determine the distribution and diversity of exotic species is a major area of research in ecology because exotics impose significant economic, social and environmental costs (Miller 1989; Wilcove *et al.* 1998). A seemingly universal pattern is that variation in exotic and native diversity is similar at intermediate to large spatial scales (Lonsdale 1999; Stohlgren *et al.* 1999, 2003, 2005; Levine 2000; Stadler *et al.* 2000; Sax 2002; Davies *et al.* 2005; Gilbert & Lechowicz 2005). This pattern suggests that exotic and native plants are similar and influenced by the same processes (Levine 2000; Stohlgren *et al.* 2003, 2005; Huston 2004; Davies *et al.* 2005). However, the degree of similarity between exotics and natives is not known. If exotics and natives are 'equivalent' then exotic diversity should be consistent with a null model that randomly samples exotics from the overall community. We tested this null model with exotic and native plant species–area relationships in the ecoregions of North America.

We begin with the hypothesis that regional species pools of exotics and natives have the same distribution of traits and that these traits vary with species abundance and range size in the same way for both exotic and native species. For example, a diverse group of 'wide ranging' exotics would occupy the same location in multidimensional trait space as a diverse group of 'wide ranging' native species and these exotics and natives would share traits in common that putatively confer large ranges (e.g. dispersal ability, wide range of temperature tolerances, etc.). If exotic and native species do share similar trait distributions, then the processes that influence the distribution of species over large geographical areas should be roughly equivalent in their effect on exotic and native species. In this case, exotics and natives should each resemble a random subset of the entire flora (Gotelli & Graves 1996). For any given locale, exotic and native species should be 'sampled' with equal probability from the regional species pool. This leads to the prediction that within any locale and at any scale, the exotic ratio (exotic richness/native richness) should remain constant. Furthermore, a locale that is favourable (or unfavourable) to native species will be equally favourable (or unfavourable) to exotic species. For instance, some locales may have high habitat heterogeneity or productivity, resulting in high species richness for both exotics and natives (Davies *et al.* 2005; Stohlgren *et al.* 2005). In this case, exotic and native species should be equally over-represented relative to the regional exotic and native species pools. In contrast, if exotic and native species, on average share few traits in common, areas that are good for natives should not be good for exotics, and exotics and natives should certainly not be equally over- or under-represented.

To evaluate whether exotic and native species have similar traits and are influenced similarly by the processes that affect species' distributions we conducted two tests. First, we test whether within ecoregions the exotic ratio remains constant with increasing area. We can quantify the exotic ratio as a function of area with fitted power law species–area relationships:

$$\frac{S_E}{S_N} = \frac{c_E \cdot A^{z_E}}{c_N \cdot A^{z_N}}, \tag{1}$$

where the subscripts E and N denote exotic and native, respectively, S is species richness, and c and z are fitted parameters. We see that the exotic ratio, S_E/S_N, will remain constant with respect to area when $z_E = z_N$ (i.e. $A^{z_E}/A^{z_N} = 1$). As the parameter z is the slope of the species–area relationship plotted on natural log-transformed axes, the null model predicts that exotic and native species–area relationships will be parallel lines.

Species–area relationships are excellent for this test because they are influenced by environmental conditions and species' traits (Shmida & Wilson 1985; Rosenzweig 1995; Keeley 2003; Keeley & Fotheringham 2003; Horner-Devine *et al.* 2004). Subsequently, if exotics and natives differ we expect their species–area relationships to differ as well.

Second, we examine the relationship between the deviations of exotic and native species–area relationships across all six ecoregions. The number of species found in any location or sample commonly deviate from the species–area relationship. These deviations may reflect how species respond to local site factors such as productivity and habitat heterogeneity (for review, see Rosenzweig 1995; Brown & Lomolino 1998). As we have argued above, if exotics and natives are 'equivalent', then native and exotic deviations from the species–area relationship will be proportionally identical. For example, if any given site has 30% more native species than predicted by the species–area relationship, then the same site should also have 30% more exotic species. Thus, we predict that deviations from the species–area relationship for exotics and natives will be proportionally identical with a positive slope of 1.

To summarize, a null model corresponding to the hypothesis that exotic and native plants are 'equivalent' predicts that: (i) exotic and native species–area relationships are parallel on log-transformed axes; and (ii) the deviation of sites from these relationships should be identical between exotics and natives.

METHODS

Constructing the species–area relationships

We tested our predictions with data on the richness of exotic and native plant species in the states and provinces of the USA and Canada (Kartesz & Meacham 1999). The data set was compiled using local and regional floras and herbarium records. To our knowledge, this is the most comprehensive compilation of exotic and native plant incidence currently available for North America and includes both rare and common species.

We divided the states and provinces (hereafter states) of the USA and Canada into ecoregions before exploring the scaling of diversity with area. Environmental factors, species' traits and evolutionary processes have been linked to rates of species accumulation and to sizes of species pools (Shmida & Wilson 1985; Rosenzweig 1995; Keeley 2003; Keeley & Fotheringham 2003; Horner-Devine *et al.* 2004). If these factors differ between ecoregions so will species–area relationships. For this reason we compare exotic and native species–area relationships within the same ecoregion. Ecoregions included eastern deciduous forest (AR, CT, DC, IN, KY, MA, MI, NY, OH, PA, RI, TN, VA and WV), eastern mixed hardwoods (AL, FL, GA, MS, NC and SC), western coniferous forest (BC, ID, OR and WA), boreal forest (MB, NB, NL, ON, PE, QC and SK), grassland (IA, KS, MO, NE, ND, OK, SD and TX) and desert (AZ, NV, NM, UT and WY) (Bailey 1998). We excluded states that were primarily tundra or where no single ecoregion dominated.

We followed standard methodology to quantify species–area relationships by grouping states and provinces in each ecoregion into contiguous pairs, then triplets, quadruplets, etc. (Rosenzweig 1995; Scheiner *et al.* 2000). We employed all possible contiguous groupings in all ecoregions except eastern deciduous forests, where we randomly selected a subset (*c.* 400) of all possible combinations (*c.* 1000). We regressed log-transformed species-richness on log-transformed area (km^2) to fit a power function to the species–area relationship (McGuinness 1984; Rosenzweig 1995).

The species–area relationship and the exotic ratio

We tested this predicted equality of z-values, and thus constancy of exotic ratio using two methods. First, we used a paired t-test of native vs. exotic z-values within each of our six ecoregions to determine whether exotic slopes were significantly 'greater' or 'less' than native slopes. Second, we used a randomization to test whether native and exotic slopes are significantly 'similar' within ecoregions (Sokal & Rohlf 1995; Resampling Stats, version 4.1, Resampling Stats, Inc. Arlington, VA, USA). We randomly generated six pairs of slopes (from our 12 slopes) without replacement and then calculated the mean absolute difference between pairs. We repeated the process 10 000 times to generate a probability distribution for the mean absolute difference. If our observed mean absolute difference between native and exotic slopes within ecoregions was <97.5% ($P < 0.05$, two-tailed test) of the random pairings, we concluded that native and exotic slopes were more similar within ecoregions than expected by chance and thus were statistically similar.

Site-deviations from the species–area relationship

To test the prediction that native and exotic deviations from the species–area relationship will be proportionally identical (and in the same direction) we regressed deviations from the exotic species–area relationship against deviations from the native species–area relationship using Type II (Reduced Major Axis) regression (Sokal & Rohlf 1995). We used only individual states for this test because groupings of multiple states within a given ecoregion are not independent from other groupings containing one or more of the same states. Equal exotic and native deviations indicate equal proportional deviation from the log–log species–area relationship. Thus, we predict a positive regression slope of one. If the regression was indeed significantly positive with a slope of 1 we concluded that exotic and native deviations were proportionally identical.

RESULTS

General trends

Species–area relationships for natives and exotics in all ecoregions were reasonably fit by power functions (Fig. 1). The z-values ranged widely for both exotics and natives (0.145–0.574) and were greatest for grasslands and lowest for western coniferous forests (Table 1). The relative ranking of z-values among ecoregions was the same for both exotics and natives (Table 1). The z-values for eastern deciduous and western coniferous forests were typical for mainlands whereas the other z-values (particularly grassland and dessert) were greater (Rosenzweig 1995). Exotic fraction (S_E/S_{total}, sensu Lonsdale 1999) ranged from a low of 11% for deserts to a high of 30% for eastern deciduous forests (Table 1).

Testing the predictions

The difference between exotic and native z-values ($z_E - z_N$, Table 1) for each ecoregion was near zero with the exception of grasslands ($z_E - z_N = -0.137$), and exotic and native z-values were not significantly different (t-ratio $= 0.080$, $P = 0.53$). In addition, the randomization test showed that the z-values were significantly similar between exotics and natives within ecoregions ($P < 0.05$). Regressing exotic species–area relationship deviations on

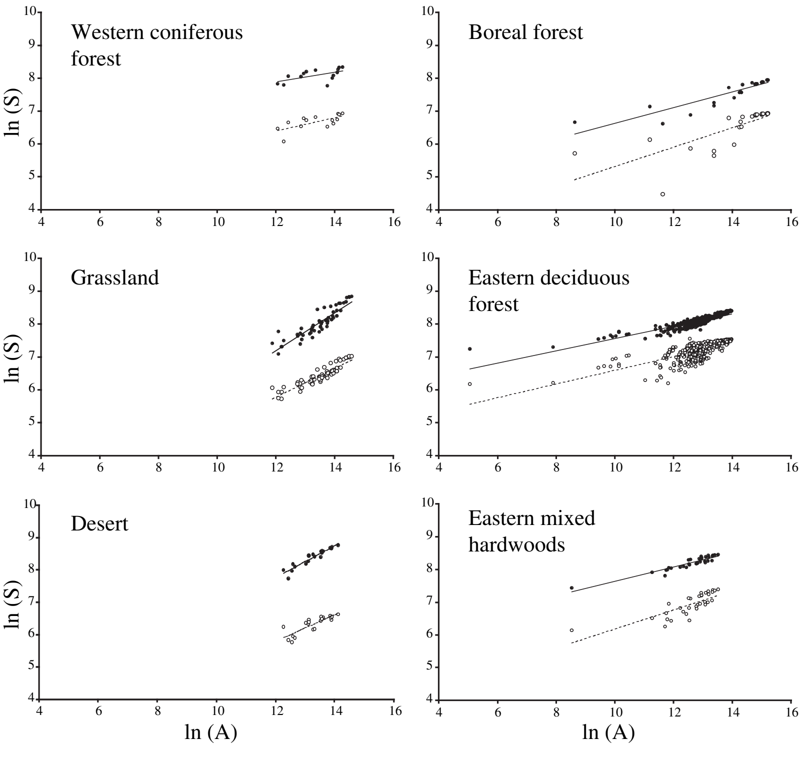

Figure 1 Species–area relationships for exotic plants (open circles) and native plants (closed circles) in six ecoregions of the USA and Canada. Note that the x-axis and y-axis are natural log transformed and that the units of area are km^2.

Table 1 Species–area relationship parameters fit from the power function $S_i = c_i A^{z_i}$, the difference between exotic and native z-values ($z_E - z_N$), ecoregion species richness (i.e. total number of species in the ecoregion) and the ratio of exotic to total exotic and native diversity (exotic fraction) for each of six ecoregions

	z-values			c-values		Ecoregion species richness		
Ecoregion	Exotics	Natives	$z_E - z_N$	Exotics	Natives	Exotics	Natives	Exotic fraction
Grassland	0.437	0.574	− 0.137	1.705	1.348	1120	6839	0.14
Desert	0.409	0.494	− 0.085	2.425	6.241	753	6404	0.11
Boreal forest	0.294	0.239	0.055	10.802	69.29	1018	2828	0.27
Eastern mixed hardwoods	0.292	0.218	0.074	26.212	234.206	1612	4676	0.26
Eastern deciduous forest	0.209	0.187	0.022	90.477	294.447	1905	4525	0.30
Western coniferous forest	0.199	0.145	0.054	54.636	471.963	1020	4196	0.20

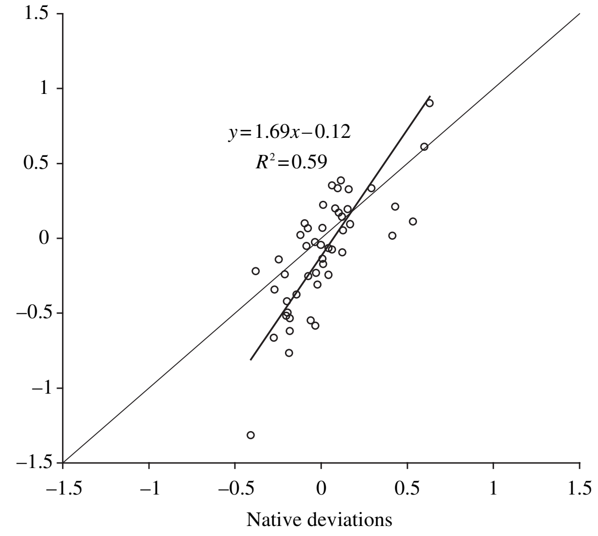

Figure 2 Exotic vs. native plant species–area curve deviations (from natural log-transformed data) for the states and provinces of the USA and Canada. Type II regression revealed a slope (solid line) of 1.69 (± 0.32 95% CI, $P < .0001$), which is significantly greater than the prediction of 1 (dotted line).

native species–area relationship deviations with reduced major axis regression yields a highly significant positive relationship with a slope of 1.69 (± 0.32 95% CI, $r^2 = 0.59$, $P < 0.0001$, Fig. 2).

DISCUSSION

General patterns

To the best of our knowledge this is the first study to describe large-scale species–area relationships for exotic species within North American ecoregions. Both the native and exotic z-values we quantified were within the range of those reported elsewhere, particularly those from large spatial scales (reviewed in Rosenzweig 1995). Nonetheless, desert and grassland z-values were in the upper range of reported values probably because these ecoregions sampled many distinct habitat types (Rosenzweig 1995).

Our measures of exotic fraction are strikingly consistent with those of Lonsdale (1999), who grouped similar ecoregions on a worldwide basis (e.g. all temperate forests). Of the ecoregions considered by both Lonsdale (1999) and ourselves, temperate forests had the highest exotic fraction (20–30%) and deserts had the lowest (11%). Surprisingly, boreal forests are also heavily invaded (27%). These results may reflect increased propagule pressure associated with human activity and large coastlines (Lonsdale 1999). Additionally, temperate and boreal forests cover large fractions of habitat worldwide and therefore have large exotic source pools and are also large targets for incoming propagules.

How similar are exotic and native species?

We asked if processes that influence the distribution of species over large geographical areas equivalently affected exotic and native species. If so, a null model where exotics are a random subset of the entire community should explain the relationship between exotic and native diversity. The null model predicts that exotic and native diversity will be proportionally similar (i.e. the exotic ratio will be constant) at multiple spatial scales. We tested this prediction by comparing species–area relationship z-values and state-level deviations of exotic and native species. The z-values of native and exotic species–area relationships were both indistinguishable (paired t-test) and similar (randomization test) (Table 1). We acknowledge that our power for these tests is limited because of small sample size (i.e. six ecoregions). Within ecoregions, statistical tests are not available to determine the probability that pairs of z-values differ, because data points within ecoregions are not independent. Hence, the differences in z-values in some ecoregions such as Grassland (Table 1) could result from real differences between the exotic and native community. Nevertheless, while exotic and native *z*-values are similar 'within' ecoregions, *z*-values ranged widely 'among' ecoregions (0.15–0.57, Table 1). This suggests that native and exotic species respond similarly to factors specific to different ecoregions. Lonsdale (1999) found that while exotic and native diversity shared a strong positive relationship globally, exotics had a lower *z*-value than natives. However, Lonsdale (1999) used combined data from multiple ecoregions that included smaller scale data than this study. Therefore, our results are not directly comparable.

The null model also predicts that a locale (here a state) will be equally good or bad for both exotic and native species (see also Stohlgren *et al.* 2003). While we found that native and exotic deviations were strongly positively correlated as predicted, the slope was significantly > 1 (Fig 2). This implies that if a state was good for natives it tended to be better for exotics and, conversely, if it was bad for natives it tended to be worse for exotics (Fig. 2). The regression estimate suggests, for example, that if a state had 30% more natives than predicted, it had 38% more exotics. Alternatively, if there were 30% less natives than predicted then there were 52% less exotics. The mechanisms contributing to this pattern remain elusive.

In sum, we found better support for a null model at the ecoregion scale than at the state scale. This suggests that while similar processes structure both native and exotic diversity – and hence the positive relationship between the two – these processes differentially affect exotic species at state scales, and these differences are muted when averaged over larger areas such as entire ecoregions.

Alternatively, different factors could underlie exotic and native diversity. For example, humans could be attracted to diverse ecological communities, while human activity drives the introduction of exotic species (Rejmánek 2003). Such explanations are less parsimonious; however, because they require two simultaneous and equivalent processes.

A number of correlative studies and at least one experimental investigation have found strong evidence suggesting that exotics and natives respond in a similar way to environmental influences (Stohlgren *et al.* 2003, 2005; Jiang & Morin 2004; Davies *et al.* 2005; Gilbert & Lechowicz 2005). However, we are not aware of evidence explicitly linking species' traits to patterns of both exotic and native diversity. Stohlgren *et al.* (2005) found that the same environmental variables (e.g. transpiration, temperature and precipitation) influenced the diversity of exotic and native plants in the counties of the USA. The most important environmental variables were related to favourable conditions such as high productivity (Stohlgren *et al.* 2005). On the contrary, Davies *et al.* (2005) found that habitat heterogeneity was the best predictor of both exotic and native diversity.

We are not the first to use a null model to investigate the relationship between exotic and native diversity. Herben *et al.* (2004) and Fridley *et al.* (2004) use neutral null models where all species in a species pool are assumed to have the same traits to predict patterns of exotic and native diversity. These null models predict a strong positive correlation between exotic and native diversity at large scales. Herben (2005) successfully predicts patterns of exotic diversity on oceanic islands with a null model that randomly draws exotic and native species from a pool of species with variable traits. The biological interpretation of results supporting null models is that exotic and native species pools are comprised of similar species and that environments have similar effects on these species.

The diversity–invasibility hypothesis predicts a negative relationship between exotic and native diversity because high native diversity may reduce the number of open niches available to exotics (Elton 1958; Levine & D'Antonio 1999). While there is support for this hypothesis at local scales in ecological neighbourhoods (see e.g. Levine 2000; Kennedy *et al.* 2002; Fargione & Tilman 2005), this study adds to the growing body of evidence that the opposite pattern is true at intermediate to large spatial scales (Lonsdale 1999; Stohlgren *et al.* 1999, 2003, 2005; Levine 2000; Stadler *et al.* 2000; Sax 2002; Davies *et al.* 2005; Gilbert & Lechowicz 2005).

Overall, our findings agree with recent work that suggests that the spatial distribution of both exotic and native species are structured by similar processes operating in a similar manner on both groups (Lonsdale 1999; Stohlgren *et al.* 1999, 2003, 2005; Levine 2000; Stadler *et al.* 2000; Sax 2001, 2002; Davies *et al.* 2005; Gilbert & Lechowicz 2005). These findings suggest that exotic and native plants share some similar life history trait variation because processes structuring diversity such as habit heterogeneity are likely to depend upon species' traits. However, the degree to which exotics and natives are 'similar plants responding to the same things' remains an open question. Applying a random sampling null model across scales and in a wide variety of investigations can help answer this question.

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