

REPORT

Invasion in space and time: non-native species richness and relative abundance respond to interannual variation in productivity and diversity

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Abstract

Ecologists have long sought to understand the relationships among species diversity, community productivity and invasion by non-native species. Here, four long-term observational datasets were analyzed using repeated measures statistics to determine how plant species richness and community resource capture (i.e. productivity) influenced invasion. Multiple factors influenced the results, including the metric used to quantify invasion, interannual variation and spatial scale. Native richness was positively correlated with non-native richness, but was usually negatively correlated with non-native abundance, and these patterns were stronger at the larger spatial scale. Logistic regressions indicated that the probability of invasion was reduced both within and following years with high productivity, except at the desert grassland site where high productivity was associated with increased invasion. Our analysis suggests that while non-natives were most likely to establish in species rich communities, their success was diminished by high resource capture by the resident community.

Keywords

Diversity, interannual variability, invasion, logistic regression, productivity, relative abundance, repeated measures, resources, species richness, synthesis.

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INTRODUCTION

Elton (1958) is widely credited as the first to hypothesize that plant communities with high species richness should be the most resistant to invasion by new species, and the findings of many experimental studies support this hypothesis (e.g. Robinson *et al.* 1995; Tilman 1997; Knops *et al.* 1999; Levine 2000; Naeem *et al.* 2000; Prieur-Richard *et al.* 2000; Hector *et al.* 2001; Lyons & Schwartz 2001; Troumbis

et al. 2002; but see Palmer & Maurer 1997). However, in many observational studies, communities with high species richness tend to be the most invaded (e.g. Pickard 1984; PlantyTabacchi *et al.* 1996; Stohlgren *et al.* 1998; Wisser *et al.* 1998; Levine & D'Antonio 1999; Lonsdale 1999; Smith & Knapp 1999; Stohlgren *et al.* 1999; Levine 2000; Stohlgren *et al.* 2003).

Much attention has focused on explaining this apparent contradiction through understanding the mechanisms

underlying the diversity–invasibility relationship. Elton (1958) did not explicitly suggest a mechanism by which increasing species richness would decrease invasion, but others have hypothesized that increased diversity should lead to increased resource capture by the community, thus leaving fewer resources available to a potential invader (e.g. MacArthur 1970; Tilman 1982). While resource availability is often controlled in experimental studies, observational studies cannot control natural variation in resources or other extrinsic factors (e.g. disturbance and dispersal vectors) that may influence native and invader diversity alike (Levine & D'Antonio 1999; Naeem *et al.* 2000). Temporal variation in resource availability may also influence invasion. Where resources vary seasonally or interannually, invasive species may find windows of opportunity when the native community is not fully utilizing available resources (Davis *et al.* 2000; Shea & Chesson 2002). Finally, processes acting at different spatial scales may result in scale-dependent relationships between diversity and invasion (Lonsdale 1999; Stohlgren *et al.* 1999, Brown & Peet 2003).

Observations of plant communities recorded over multiple years at Long-Term Ecological Research (LTER) sites offer ideal datasets to investigate how exotic species invasions vary interannually, and at multiple spatial scales. To date, few long-term datasets have been investigated to elucidate patterns of invasions into natural systems (but see Meiners *et al.* 2004). Above-ground annual net primary productivity (ANPP) is an easily measured integration of the resources (e.g. light, nutrients, water and space) captured by a plant community, and has been monitored in conjunction with species composition at many LTER sites. Here we used data from four North American LTER sites to investigate how invasion into natural systems was influenced by resident species richness, as well as by temporal and spatial variation in resource capture by the community (i.e. ANPP). First, we examined the relationship between native species richness and invasion to put our analysis in the context of past studies, utilizing repeated measures analyses to account for co-variation within repeatedly measured plots. Next, we performed repeated measures logistic regression analysis to investigate whether total species richness or resource capture by the community could predict an increase in invasion from the previous year, and in the following year. Throughout, we examined two measures of invasion into a community: the establishment of new invaders (using non-native richness as a metric), and the proliferation of invaders (using relative abundance of non-natives as a metric). Lastly, because multiple community types were monitored within each LTER, we examined these relationships at two spatial scales: both within and across plant communities at each LTER site.

We found that while native and non-native richness were almost always positively correlated, native richness and

non-native relative abundance tended to be negatively correlated. Thus, we infer that native species richness may interact differently with the processes that control the establishment vs. proliferation of non-natives. Further, when we included both productivity and species richness in the same statistical model, we found that interannual variation in resource capture was a consistent negative predictor of invasion in subsequent years, while species richness did not maintain an independent influence over invasion. Our results indicate that while similar factors may promote high species richness of natives and non-natives alike, high resource capture by the resident community has the potential to prevent the proliferation of non-native species.

METHODS

Study sites

We used datasets from four LTER study sites located in grassland and desert biomes in North America: Cedar Creek LTER (CDR), Kellogg Biological Station LTER (KBS), Konza Prairie LTER (KNZ) and Jornada Basin LTER (JRN) as summarized in Table 1. We used records of ANPP and species composition from plots established in natural herbaceous communities in the absence of resource additions or direct experimental manipulations of species composition. Each site contained multiple community types which were distinguished based on differences in dominant vegetation, successional age or disturbance regime. Community types at CDR are a successional sequence of old-fields abandoned between 1927 and 1989. KBS community types consist of six replicate old-fields abandoned in 1989, arrayed throughout the landscape. At KNZ, community types vary in the fire-return frequency of 1, 2, 4, or 20 years, which was experimentally maintained. At JRN community types differ in the dominant species of vegetation among three desert grassland sites. More detailed information about these sites can be found in the references in Table 1 or at the LTER home-page: <http://www.lternet.edu>.

Definition of native vs. non-native species

Species were defined as non-native at the state level based primarily on the USDA list of Introduced Plants of North America (http://plants.usda.gov/cgi_bin/noxious.cgi). These designations were checked against species lists compiled from local floras available for each site. The lists differed on only two occasions and the designation in the local flora was then used. In these two cases the species were native to one location in North America but were non-native to the particular study site in this analysis.

Table 1 Summary information for the four datasets used in our analyses

Study site	Description	Community types (<i>n</i>)	Years	<i>N</i>	Plot size (m ²)	<i>S</i> _{Nat}	<i>S</i> _{Non}	Mean ANPP (g m ⁻²)	Reference
Cedar Creek LTER, MN (CDR)	Old-fields	Successional chronosequence (14)	1988–1996	4	0.3	113	40	119	Inouye <i>et al.</i> 1987
Jornada LTER, NM (JRN)	Chihuahuan desert	Playa grassland and bajada grassland (2)	1990–1998	147	1.0	200	8	153	Huenneke <i>et al.</i> 2001
Kellogg Biological Station LTER, MI (KBS)	Old-fields	Successional chronosequence (6)	1989–2001	3	1.0	81	103	428	Huberty <i>et al.</i> 1998
Konza Prairie Biological Station LTER, KS (KNZ)	Tall-grass prairie	Watersheds with burn frequencies of 1, 2, 4 or 20 years (4)	1984–2001	90	0.1 (ANPP), 10 (S)	416	60	398	Briggs & Knapp 1995

The abbreviation used throughout the paper for each long-term ecological research (LTER) site is in parentheses. ‘Description’ refers to the LTER as a whole. ‘Community types’ describes the characteristics that defined different community types within each LTER. ‘Years’ refers to when the data utilized in this paper were collected. ‘*N*’ refers to the number of plots sampled within each community type in each year. *S*_{Nat} refers to the total number of native species encountered in the dataset, a measure of the native species pool. *S*_{Non} refers to the total number of non-native species encountered in the dataset, a measure of the non-native species pool. ‘Mean ANPP’ refers to the average annual net primary productivity of all plots in all years for each site, scaled to grams per meter squared. The ‘Reference’ describes how productivity and species composition were characterized at each site.

Productivity and species richness

Methods for determining ANPP and species composition varied among sites, as did the plot size, and the level of replication within community type (see Table 1, Inouye *et al.* 1987; Briggs & Knapp 1995; Huberty *et al.* 1998; Huenneke *et al.* 2001). ANPP at all sites but JRN was estimated by destructive harvest at the time of peak biomass. Harvested biomass was sorted to determine species composition and total species richness, except at KNZ where adjacent 10 m² permanent plots were surveyed for species composition on a percent cover basis (Briggs & Knapp 1995). ANPP at JRN was calculated using non-destructive measures of percent cover and height of each species, which were then compared to destructively harvested samples to obtain regression relationships (Huenneke *et al.* 2001). In this case, three measurements were performed throughout the year, and ANPP was calculated by summing the seasonal growth increments for each species. Biomass and species composition of non-vascular plant species were excluded from all analyses.

Differences in measurement scale (i.e. plot size) represent a challenge for synthesis efforts, especially because species richness cannot be scaled in a linear manner. Past meta-analyses of relationships between productivity and diversity have used species-area relationships to normalize species richness measures to a common plot size in order to combine data from diverse locations into one statistical analyses (i.e. Gross *et al.* 2000). Here we chose to conduct statistical analyses for each site separately and make

qualitative comparisons among sites in order to avoid any bias that might result from scaling species richness measures.

Relative abundance of non-natives

We used relative abundance of non-natives (%NN) as our measure of the degree to which non-natives had proliferated in the community. Where biomass was destructively harvested, %NN was defined as the proportional biomass of non-native species compared to total plot biomass. At JRN and KNZ, species composition was determined on a percent cover basis, thus %NN was calculated as relative cover of non-natives.

Statistical analyses

Both data management and statistical analyses were performed using SAS version 8.01 (SAS Institute, Inc., Cary, NC, USA). We performed all statistical analyses at the grain of plot and at two spatial scales. At the large scale we investigated the relationships among all community types within each LTER, while at the small scale we investigated the relationships within each community type.

In the JRN dataset, there were a number of extreme values of ANPP for particular years. Inspection revealed that *Yucca* spp. had flowered in these plots during these years, translocating belowground stored reserves to create an inflorescence of relatively high biomass. Because translocation of stored reserves does not necessary reflect

annual estimates of productivity, these plots were excluded from all subsequent analyses.

To analyze the relationship between native and non-native richness, and between native richness and %NN we performed a repeated measures analysis akin to regression using the PROC MIXED procedure. This procedure utilized maximum likelihood analysis to determine whether one variable predicted a significant proportion of variance in the other, and correctly partitioned the co-variance due to repeatedly sampled plots (Little *et al.* 2002). Because the PROC MIXED procedure does not calculate measures of association, Spearman rank-correlations between native and non-native species richness, and between native richness and %NN, were calculated for each study site. The non-parametric measure of association, ρ (rho), is reported.

To determine if inter-annual variation in ANPP or total species richness could predict the success of non-natives we performed repeated measures multiple logistic regressions using the PROC GENMOD procedure (Allison 2001). Logistic regression determines the likelihood of possible outcomes for a binary dependent variable (in this case either an increase or no-increase in invasion) along a range of the continuous independent variable. The technique for performing logistic regression in PROC GENMOD utilized generalized estimating equations to account for co-variance among repeatedly measured plots. Here we allowed ANPP and total species richness to vary together in the same multiple logistic regression model, analogous to multiple linear regression. Preliminary tests for co-linearity between ANPP and total species richness found low condition indices between the two factors. This is not surprising considering that other analyses have found large variation in the functional shape of the productivity–diversity relationship at these sites, and predominantly non-significant relationships (J. Drake *et al.*, unpubl. data). The Z -statistic was calculated to assess significance of each parameter at the $P < 0.05$ threshold. There is no true r^2 statistic for logistic regression. We used the PROC LOGISTIC procedure to calculate the C -statistic; this is directly related to the area under the receiver–operator curve and reflects the ability of the model to correctly predict the outcome across the range of the independent variables. C varies between 1.0 (100% correct predicted outcomes) and 0.5 (no better than a coin toss).

For KNZ and JRN, where permanent plots were used to determine species composition, it was appropriate to conduct the logistic regressions using non-native species richness as the dependent binary variable, with the addition of ≥ 1 non-native species designated as an increase ($= 1$), or with no-change or a decrease in non-native richness designated as no-increase ($= 0$).

Next, logistic regressions were conducted for all sites using %NN as the dependent binary variable, with $\geq 5\%$

increase in non-native abundance designated as an increase ($= 1$), and $< 5\%$ increase designated as no-increase ($= 0$). This threshold was chosen objectively to mirror the 0.05 significance level the scientific community generally accepts as statistically significant. While all analyses were performed at the plot grain, the ‘subject’ of the repeated measures procedure reflected the smallest experimental unit which was repeatedly measured. At JRN and KNZ where permanent plots were utilized, plot was the subject of the analyses. Because CDR and KBS destructively harvested different plots each year to determine species composition, the subject for these analyses was the field.

RESULTS

Relationship between native species richness and invasion

At the large scale (LTER site), native and non-native species richness were positively correlated (Fig. 1) and highly significant ($P < 0.001$ at all sites). The measures of association between native and non-native richness were relatively low at all sites; values of ρ varied from a low of 0.12 at KNZ to a high of 0.34 at KBS. At CDR, JRN and KBS there was a negative correlation between native species richness and %NN (Fig. 1), whereas the relationship was non-significant at KNZ. Again, the values of ρ were low (-0.18 to -0.34).

At the smaller scale (within individual community types), non-significant relationships between native richness and non-native richness or %NN predominated (because of the large number of community types, the results are tallied in Fig. 2). However, trends were similar to those observed at the larger spatial scale; when the relationship was significant between native and non-native richness, it was always positive, and negative relationships between native richness and %NN were more common than positive ones (Fig. 2). For example, the unburned (20 years fire interval) community at KNZ showed a significant positive relationship between native and non-native richness ($\rho = 0.23$, $P < 0.001$) and negative relationship between native richness and %NN ($\rho = -0.18$, $P < 0.001$).

Inter-annual variation in ANPP, total species richness and invasion

At the large scale, results of the repeated measures logistic regressions showed a significant negative relationship between ANPP and the likelihood that %NN would increase from the previous year at KBS and KNZ, but showed a positive relationship between ANPP and an increase in %NN at JRN (Fig. 3a–c, Table 2a). At KBS and KNZ, ANPP continued to be a negative predictor of %NN even in the subsequent year, while at JRN this relationship

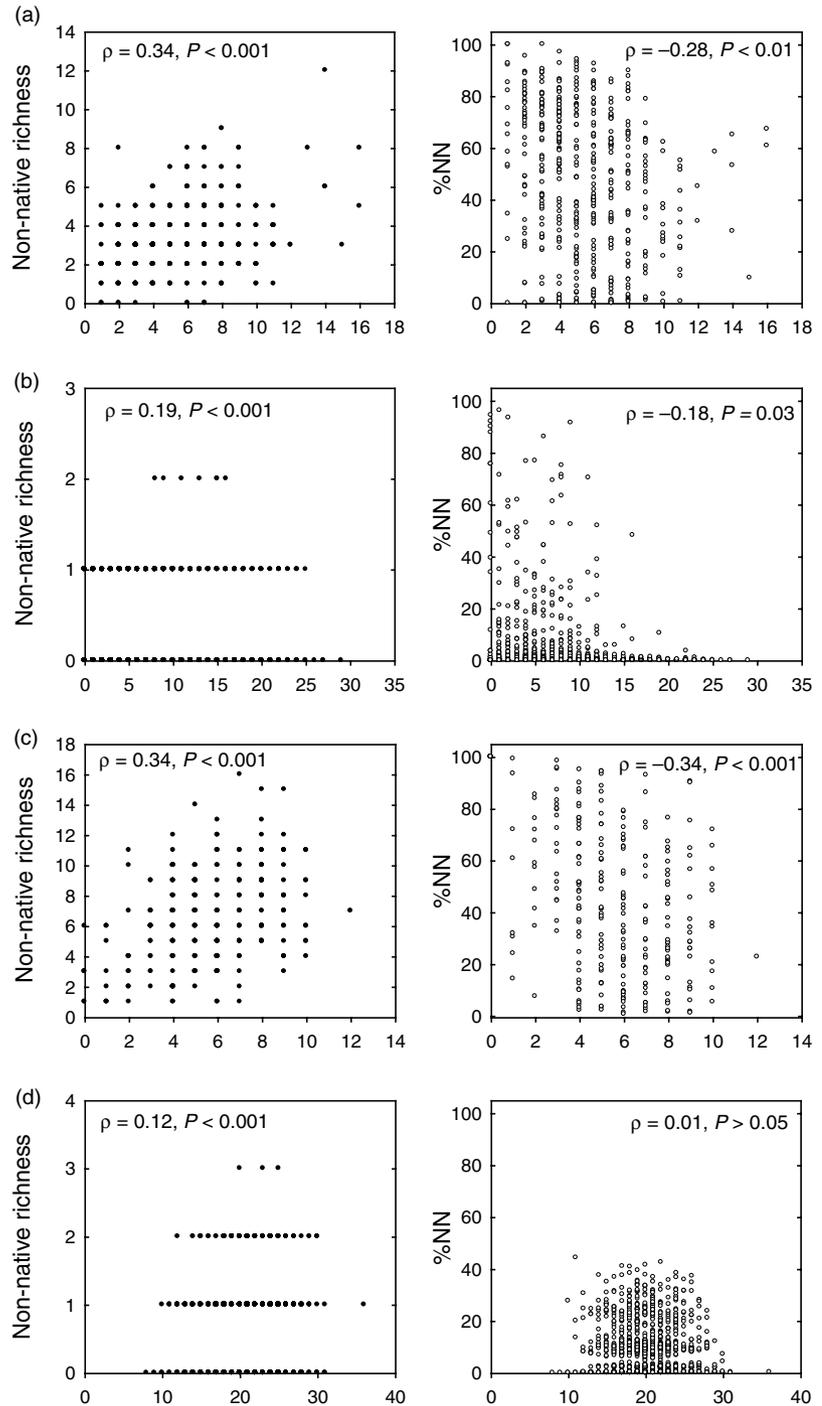


Figure 1 Relationships between native and non-native species richness (filled circles), and between native richness and relative abundance of non-natives (%NN; open circles) at (a) Cedar Creek (CDR), (b) Jornada Basin (JRN), (c) Kellogg Biological Station (KBS) and (d) Konza Prairie (KNZ). ρ -Values represent the non-parametric measure of association from Spearman rank correlations. P -values < 0.05 are statistically significant and were determined using a repeated measures procedure described in the Methods.

became negative (Table 2c). Total species richness was positively and significantly related to the probability that %NN would increase at KNZ (Table 2a), but did not significantly predict a change in %NN in the following year at any site (Table 2c).

Where permanent plots were monitored at JRN and KNZ, it is not surprising that total species richness was a positive predictor of the arrival of a non-native species as compared with the previous year, indicating that species richness increased with addition of a new non-native species, rather

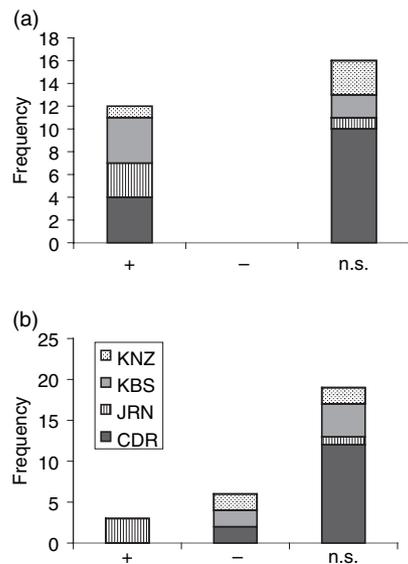


Figure 2 Distribution of significant positive, negative or non-significant repeated measures analyses of association within community types for each site (a) between native and non-native richness, and (b) between native richness and relative abundance of non-natives (%NN). Relationship was determined to be significant statistically if $P < 0.05$, and ecologically significant if $p \geq \pm 0.15$.

than as a function of turnover (Table 2b). However, it is interesting to note that at JRN, total species richness was a negative predictor of the probability that a new non-native species would arrive in the subsequent year (Table 2d).

At the smaller scale (within community types across years), only one community type out of 33 showed any significant relationship between ANPP or total species richness and the success of non-natives. At KNZ the unburned community had a significant negative relationship between ANPP and %NN as compared with both the previous and the following year ($P = 0.04$, $N_{\text{plots}} = 30$, data not shown).

DISCUSSION

Native richness has opposite relationship with non-native richness vs. relative abundance

Native and non-native species richness were positively and significantly correlated when observed across community types (large spatial scale). This is consistent with the findings of past observational studies, and with the hypothesis that both groups respond in the same way to extrinsic factors (Levine & D'Antonio 1999; Levine 2000). The strong positive relationship between native and non-native richness across community types at the extent of LTER sites supports the hypothesis that both native and non-native species richness are responding to environmental factors

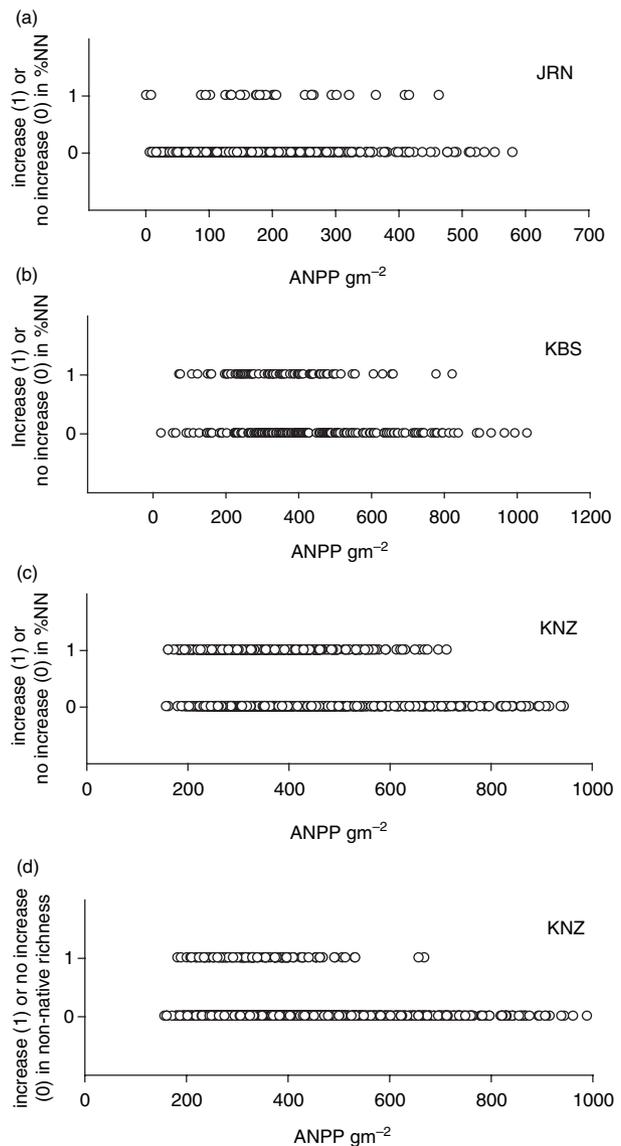


Figure 3 (a)–(c) Repeated measures multiple logistic regressions test the ability of above-ground annual net primary productivity (ANPP) to predict an increase ($\geq 5\%$) or no-increase ($< 5\%$) in relative abundance of non-natives (%NN) as compared with the previous year. (d) Where permanent plots were monitored, logistic regressions were used to ask whether ANPP could predict the arrival of a new non-native species (+1 non-native species) as compared with previous year. Only significant relationships as compared with the previous year are shown, summary statistics for relationships with both the previous and following years are detailed in Table 2.

that differentiate community types at larger spatial scales (Sax & Gaines 2003). The weaker relationships we found within community types may reflect more complex relationships at smaller spatial scales, where competition and other interactions among species structure local community

Table 2 Summary statistics for the repeated measures multiple logistic regressions testing the ability of ANPP and total species richness to predict (a) an increase in %NN and (b) the arrival of a new non-native species within the same year, and in the following year (c) and (d)

	C-statistic	ANPP			Total species richness		
		+/-	Z	P	+/-	Z	P
(a)							
CDR	0.56	-	-1.3	n.s.	+	1.59	0.112
JRN	0.69	+	3.73	> 0.001	+	0.34	n.s.
KBS	0.63	-	-5.05	> 0.001	-	-0.78	n.s.
KNZ	0.62	-	-4.66	> 0.001	+	3.53	> 0.001
(b)							
JRN	0.75	+	1.69	0.090	+	8.84	> 0.001
KNZ	0.73	-	-3.13	0.002	+	5.79	> 0.001
(c)							
CDR	0.55	+	0.23	n.s.	-	0.02	n.s.
JRN	0.60	-	0.83	n.s.	-	-0.03	n.s.
KBS	0.68	-	-2.07	0.039	+	1.50	0.133
KNZ	0.71	-	-1.86	0.062	+	1.66	0.096
(d)							
JRN	0.65	-	-2.35	0.019	-	-4.97	> 0.001
KNZ	0.64	-	-2.96	0.004	+	1.66	0.003

We report the functional relationship between the variables (positive or negative), the Z-statistic, and C-statistic as a measure of model-fit, as described in the Methods. Result was significant when $P < 0.05$. Moderately significant, $P > 0.05$ and < 0.10 , and marginally significant, $P > 0.10$ and < 0.15 , results are reported to elucidate non-significant trends. n.s. denotes $P > 0.15$.

composition (Lonsdale 1999; Sax & Gaines 2003). Alternatively, the smaller sample sizes utilized in community level analyses may have had limited statistical power to detect relationships.

In contrast to patterns of non-native richness, we found negative correlations between native richness and the relative abundance of non-natives, particularly at the sites which had the most significant positive relationships between native and non-native richness (CDR, KBS, and the unburned community at KNZ). This suggests that different processes may control the establishment vs. proliferation of non-natives. For example, environmental fluctuations may facilitate establishment (Davis *et al.* 2000) while simultaneously reducing the population growth rate in the long run (Lewontin & Cohen 1969).

Our findings also shed light on the different results found by observational vs. experimental studies. Most observational studies use species richness of invaders as a measure of community invasibility and find positive relationships between native and non-native species richness (e.g. Pickard 1984; Knops *et al.* 1995; Pysek & Pysek 1995; PlantyTabacchi *et al.* 1996; Stohlgren *et al.* 1998; Wisser *et al.* 1998; Lonsdale 1999; Smith & Knapp 1999; Stohlgren *et al.* 1999; Levine 2000; Stohlgren *et al.* 2003; Meiners *et al.* 2004; but see the results in Stohlgren *et al.* 1999 for the prairie grasslands at the 1 m² scale). In contrast, many experimental studies use invader biomass (or some other measure of success) as a measure of

community invasibility and find negative relationships between species diversity and invader success (Pickard 1984; Knops *et al.* 1999; Hector *et al.* 2001; Kennedy *et al.* 2002; Troumbis *et al.* 2002).

While the simple difference in measuring invader abundance vs. richness can be an important factor in predicting the relationship with native species richness, there are likely to be additional factors that influence the functional shape of these relationships. Some experimental studies finding a negative relationship between community diversity and invasibility may be limited in their ability to generalize because they are based only on the success of only one invading species (Robinson *et al.* 1995; Lyons & Schwartz 2001; Dukes 2002) or of only a few invading species (Levine 2000; Naeem *et al.* 2000; Prieur-Richard *et al.* 2000). Further, some experimental studies have measured the species richness of invaders and found both positive (Palmer & Maurer 1997; Crawley *et al.* 1999; Foster *et al.* 2002) and negative (Tilman 1997; Knops *et al.* 1999; Hector *et al.* 2001; Troumbis *et al.* 2002) relationships with species richness of the resident community.

In observational datasets it is difficult to determine whether invaders are responding to, or influencing, the characteristics of the resident community. The negative correlations we found between native richness and the relative abundance of non-natives may reflect the impact of invasion in areas where invaders have become abundant. It is possible that we are seeing the first

stages of impact, where the relative abundance of natives is reduced, but local extinctions have not taken place. A qualitative comparison of the richness and abundance of non-native species across sites (Fig. 1) supports this interpretation. The two sites that have the highest richness and abundance of non-native species (CDR and KBS) are also the two sites where significant negative relationships were found between native richness and non-native abundance. This was also true within sites. For example, the unburned community type at KNZ had the highest richness and abundance of non-natives and was the only community type with a significant negative relationship between native richness and non-native abundance.

Variability in productivity–diversity relationships creates temporal opportunities for invasion?

Elton's (1958) hypothesis that diverse plant communities should be less invaded because of more complete use of resources by the community implicitly assumes a positive relationship between diversity and resource capture. Thus, positive correlations are expected between ANPP and species richness; however, at these sites the relationship between ANPP and species richness is highly variable in both space and time, and is most often non-significant (Gross *et al.* 2000, J. Drake *et al.*, unpubl. data). We hypothesized that the high interannual variation in ANPP and total species richness would provide temporal opportunities for non-natives to invade (Davis *et al.* 2000; Shea & Chesson 2002).

Species richness predicts variable relationships with invasion in subsequent years

When species richness and ANPP varied together in the same statistical model, interannual variation in species richness was seldom a predictor of an increase in invader abundance. Only at KNZ did total species richness predict an increase in %NN. However, where permanent plots were monitored (JRN and KNZ) there were significant relationships between total species richness and the likelihood of the arrival of a new non-native species in a plot in comparison to both the previous and following year. At KNZ total species richness was a positive predictor of establishment of non-natives as compared with the previous and following year. At JRN, interannual variation in total species richness was a positive predictor of an increase in non-native richness as compared with the previous year, and a negative predictor of an increase in non-native richness the following year.

It is likely that richness of natives and non-natives responded similarly to factors which structured species

composition at these sites. Most non-natives at JRN and other Chihuahuan desert sites are annual species which appear in years with high rainfall, when a number of native annuals are also likely to appear (Guo & Brown 1996). Both groups increase total species richness in the year they appear, and in the following year the disappearance of these annuals causes a decline in total species richness, non-native richness and %NN. In contrast, Smith & Knapp (1999) showed that the positive relationship between native and non-native richness observed at KNZ was strongly influenced by underlying patterns of disturbance, with grazing enhancing both native and exotic richness and increased fire frequency suppressing both. These effects are likely to persist into subsequent years through effects of litter production and lowered light availability (Briggs & Knapp 1995), or because the physical presence of the resident plants prevents seed dispersal or establishment of newly arriving non-native species (Von Holle *et al.* 2003).

Other factors that vary among sites could influence patterns of both native and non-native richness, such as interactions with herbivores, or dispersal vectors. For instance, several observational studies conducted in riparian areas have found positive correlations between native and non-natives; riparian corridors are likely to be high dispersal zones for natives and non-natives alike, leading to high species richness of both groups (Pysek & Pysek 1995; Planty-Tabacchi *et al.* 1996; Stohlgren *et al.* 1998; Levine *et al.* 2002, Brown & Peet 2003).

High community resource capture prevents invasion

With the exception of JRN, we found that ANPP was negatively related to the chance that invaders would establish or would increase in abundance, both compared with the previous and the following years. In years with high ANPP, resources may have been utilized more fully by the community, or may have led to higher shading by litter in the following year (Briggs & Knapp 1995). Both of these mechanisms could cause lower resource availability for non-native colonists, thereby reducing their chance to establish and proliferate in subsequent years. It is interesting to note that while we often think of non-natives as weedy species with the potential to increase local productivity (e.g. Wardle 2001), our result indicates that the non-native species could not have been responsible for a disproportionate increase in productivity as compared to the natives, otherwise we would have observed a positive relationship between ANPP in the previous year, and increasing relative abundance of non-natives. At JRN where rainfall is scarce and the potential species pool of non-natives is small, the opposite pattern was observed: richness and abundance of non-natives increased in years with high ANPP, and declined again in subsequent years. As with the influence of species richness,

the responses of annual species are likely driving this pattern (Guo & Brown 1996).

Studies which experimentally manipulated species composition have found that increasing species richness leads to lower available resources above and belowground (Tilman *et al.* 1996, Loreau *et al.* 2001), and also to fewer invaders (Hector *et al.* 2001, Kennedy *et al.* 2002). This analysis extends the findings of these previous studies by concluding that when species richness and resource capture are included in the same statistical model, the probability of invasion is better predicted by community resource capture.

Future directions: functional identity of natives and non-natives

Wardle (2001) suggests that the apparent conflict between experimental and observational studies could be explained by the effect of competitive dominants on productivity, i.e. a sampling effect. He argues that in both productivity–diversity and diversity–invasibility experiments, researchers are more likely to include competitive dominants in treatments with high species richness, making the impact on productivity or invasibility an artifact of experimental design rather than a reflection of the impact of species richness. Recent manipulations of dominance through seed addition (Foster *et al.* 2002), or reduction in the biomass of clonal dominants (Smith *et al.* 2004), found that dominance rather than richness, most strongly influenced invasion. However, a study by Tilman (1997) found no effect of species dominance on the success of newly seeded natives into grassland plots. In a study which manipulated species evenness while keeping richness constant, dicot invaders were most likely to invade in plots where monocots dominated the community (Wilsey & Polley 2002), indicating that functional identity of the invader can interact with community characteristics of dominance or evenness to determine the outcome of invasion.

Our analysis examined the responses of non-native species regardless of their functional identity, but the functional traits of native and invasive species may be just as important as species richness in predicting resistance to invasion (Crawley *et al.* 1999; Wardle 2001; Dukes 2002; Fargione *et al.* 2003). Future efforts should address how resource availability interacts with the functional traits of native and non-native species in determining the establishment and proliferation of invasive species.

CONCLUSIONS

This analysis found that the diversity–invasibility relationship was influenced by interannual variation in community resource capture, spatial scale, and the metric by which invasion was defined. Native species richness was consis-

tently positively associated with non-native species richness, but negatively associated with non-native relative abundance. This suggests that different processes may influence the abundance vs. richness of non-native species. Relationships between invasion and productivity or species richness were stronger and more consistent at the larger spatial scale, but the analyses at the smaller scale may have lacked statistical power to detect relationships.

The results of this analysis also showed that resource capture by the resident community could predict the chance of invasion when compared with previous and subsequent years. In three mesic sites invaders were less likely to succeed in years of high resource capture by the resident community (high ANPP). In contrast, at the xeric desert grassland site where resource availability was inherently low, non-native species increased in richness and abundance in years when interannual variation in climate promoted high resource capture by both non-natives and the resident community. Interannual variation in total species richness only predicted an increase in the abundance of non-natives at one site. Our results indicate that shifts in the abundance of non-natives are often negatively predicted by resource capture by the resident community, while the arrival of new species may be related to processes also acting on native species richness – such as dispersal or disturbance.

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