Do Non-native Plant Species Affect the Shape of Productivity-diversity Relationships?

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ABSTRACT.—The relationship between ecosystem processes and species richness is an active area of research and speculation. Both theoretical and experimental studies have been conducted in numerous ecosystems. One finding of these studies is that the shape of the relationship between productivity and species richness varies considerably among ecosystems and at different spatial scales, though little is known about the relative importance of physical and biological mechanisms causing this variation. Moreover, despite widespread concern about changes in species' global distributions, it remains unclear if and how such large-scale changes may affect this relationship. We present a new conceptual model of how invasive species might modulate relationships between primary production and species richness. We tested this model using long-term data on relationships between aboveground net primary production and species richness in six North American terrestrial ecosystems. We show that primary production and abundance of non-native species are both significant predictors of species richness, though we fail to detect effects of invasion extent on the shapes of the relationship between species richness and primary production.

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INTRODUCTION

Empirical patterns between species richness and production are complicated and causation is postulated to run both directions (Waide et al., 1999; Tilman et al., 2001). One view is that in terrestrial ecosystems the amount of available energy is the major determinant of species diversity (Rosenzweig and Abramsky, 1993; Rosenzweig, 1995). For this reason, the relationship between aboveground annual net primary productivity and species richness has been studied in a variety of ecosystems. Numerous studies in plant communities have shown a relationship between productivity and species richness within and between ecosystems (Waide et al., 1999; Mittelbach et al., 2001); that this relationship, if present, may commonly take as many as four different shapes (positive, negative, U-shaped or hump-shaped; Figs. 1a–1d); and that the form of the relationship may vary with the scale of investigation (Gross et al., 2000; Chase and Leibold, 2002). A number of factors have been proposed to explain this variation (Rosenzweig and Abramsky, 1993; Chapin et al., 1997; Gough et al., 2000) including soil fertility, climate, disturbance regime and herbivory, but the relative importance of these different factors to the shape of productivity-richness relationships remains unclear.

Further, many ecosystems are undergoing invasion by non-native species. Though observational studies have shown that diverse plant communities also tend to contain many exotic species (Levine and D’Antonio, 1999; Lonsdale, 1999; Stohlgren et al., 1999) and severe effects of exotic species are evident in case studies of particular ecosystems (e.g., Vitousek and Walker, 1989), it is unclear whether the number of exotic species affects productivity or other ecosystem processes in predictable ways across ecosystems (Levine and D’Antonio, 1999). If exotic species do affect productivity in systematic ways, this could be an unrecognized cause of the variation in productivity and species richness relationships observed among different ecosystems. Here, we explore the influence of non-native species on the shape of the relationship between plant species richness and aboveground net primary production and how these relationships differ in space and time, using long-term data from temperate grassland, wetland, and desert sites in North America.

We hypothesized that non-native species could affect the form of the relationship between productivity and richness in two ways. First, if non-native species characteristically affect primary production in predictable ways, then we expect that invasion extent (a general notion of the relative abundance of non-native species—see discussion below) and production will be correlated (e.g., Vitousek and Walker, 1989; D’Antonio and Vitousek, 1992; Cleland et al., 2004). Second, we hypothesized that invasive species may cause a qualitative change in the shape of the relationship between primary production and species richness if communities with a high abundance of non-native species are characteristically more or less productive than those lacking non-native species. This might occur if, as ecosystems become increasingly invaded, invasion extent increasingly determines species richness, altering the relationship between species richness and production. To our knowledge, this is the first development of this idea.

To clarify, we present this second “curvature hypothesis” with an illustration to show how a change in the shape of a productivity-diversity relationship could depend on the shape prior to invasion and the degree to which the system has been invaded (Fig. 1). In this figure, every point represents the species richness and productivity of a plot at some point in time. Filled symbols represent plots that are never invaded while open symbols represent eventually invaded plots. Circles represent plots that are presently un-invaded while triangles represent invaded plots. By comparing the plots in the first row with plots in the
positive  negative  U-Shaped  hump

Fig. 1.—Commonly observed relationships between species richness and primary productivity are (A) positive, (B) negative, (C) U-shaped or (D) hump-shaped. We hypothesize that invasion by non-native species will change these relationships in predictable ways if invaded communities are characteristically more productive than un-invaded communities and if non-native species richness is additive to native species richness (E-H) or diminishes total species richness (I-L). Data in the figure were simulated to illustrate the hypothesis by adding an evenly distributed random variable between 0 and 8 to the specified linear or quadratic model. Filled symbols represent plots that are never invaded; open symbols are plots that are eventually invaded (i.e., invaded in panels E-L). Circles represent un-invaded plots; triangles represent invaded plots. The reverse pattern could occur where invaded communities are characteristically less (rather than more) productive than wholly native communities. The important assumption of this hypothesis is that the effect of invasion on production is consistent across plots.

second row, one sees how the relationship between production and species richness would be affected by invasion of non-native species that increase species richness. By comparing the plots in the first row with plots in the third row, one sees how the relationship between production and species richness would be affected by invasion of non-native species that decrease species richness. Thus, if communities with non-native species were more productive than communities lacking non-native species, and if invasion increased species richness (i.e., if both species richness and productivity are generally additive), relationships that were positive or U-shaped would remain unchanged (Figs. 1e, g), one that is negative would become U-shaped (Fig. 1f), and a previously hump-shaped relationship would exhibit no relationship after heavy invasion (Fig.1h). Alternatively, if non-native species diminished total richness through direct or indirect inter-specific interactions, we expect a positive relationship would become hump-shaped (Fig.1i), negative or hump-shaped relationships would not change (Fig. 1j, l) and a U-shaped relationship would subsequently show no
Species richness was estimated by plot from harvested or adjacent plots (see Methods). Species were designated as native or non-native using USDA and site-specific species lists (see Methods). N is the total number of years and community type combinations; $S_{nat}$ is the number of native species while $S_{non}$ is the number of non-native species.

<table>
<thead>
<tr>
<th>Study site</th>
<th>Site description</th>
<th>Community type (number of different community types)</th>
<th>Years</th>
<th>N</th>
<th>Size of sampling units</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cedar creek LTER, MN</td>
<td>Tallgrass prairie</td>
<td>Succession chronosequence (1)</td>
<td>1988–1996</td>
<td>9</td>
<td>0.3 m²</td>
</tr>
<tr>
<td>Jornada LTER, NM</td>
<td>Desert</td>
<td>Playa, creosote bush, grassland, mesquite and tarbrush (5)</td>
<td>1990–1998</td>
<td>45</td>
<td>1.0 m²</td>
</tr>
<tr>
<td>Kellogg biological station LTER, MI</td>
<td>Old-fields</td>
<td>Succession chronosequence (1)</td>
<td>1989–2001</td>
<td>12</td>
<td>1.0 m²</td>
</tr>
<tr>
<td>Konza prairie biological station LTER, KS</td>
<td>Tallgrass prairie</td>
<td>Burn frequencies of 1, 2, 4, 20 y (4)</td>
<td>1993–1998</td>
<td>24</td>
<td>0.1 m² (ANPP), 10.0 m² (SR)</td>
</tr>
<tr>
<td>Pearl river, LA</td>
<td>Wetland</td>
<td>Plots along a salinity gradient (5)</td>
<td>1994</td>
<td>5</td>
<td>1.0 m²</td>
</tr>
<tr>
<td>Short grass steppe LTER, CO</td>
<td>Short grass steppe</td>
<td>Prairie grassland (1)</td>
<td>1992–1998</td>
<td>7</td>
<td>0.25 m²</td>
</tr>
</tbody>
</table>

relationship (Fig. 1k). If invaded plots are characteristically less productive rather than more productive, the hypothesized relationships change accordingly. In this paper we report the results of some initial tests of the idea that invasion extent changes the relative frequencies of the different productivity-species richness relationships found across ecosystems. Consequently, our null hypothesis is that there will be no difference.

**METHODS**

**DATA**

We used data from five United States Long Term Ecological Research (LTER) Network sites and from the Pearl River Wetland in Louisiana. Each had simultaneous measures of aboveground net primary productivity (ANPP) and species composition (Table 1). Methods for determining productivity and species composition differed among sites, as did the scale at which they were measured. Although previous analyses of productivity-richness relationships have standardized heterogeneous data to a common grain (e.g., Gross et al., 2000), we chose not to make any adjustments to avoid introducing bias as a result of scaling. This choice is justified as we do not perform statistical contrasts between sites.

For each site, species were defined as non-native according to the USDA list ofIntroduced Plants of North America (http://plants.nrcs.usda.gov/cgi_bin/topics.cgi?earl=noxious.cgi). These designations were compared with species lists for local floras at each site (Table 1). Where the USDA and local lists differed, the designation in the local flora was used, in recognition that a species native to one location in North America might be non-native in another. Nonetheless, the lists only differed for two species overall.

Our concept of invasion extent refers to the relative contribution of all non-native species (not only noxious invaders) to the total measure of an ecosystem process. A good measure
of invasion extent will consistently represent the influence of non-native species and should be easily interpreted. Additionally, the effects of invasion extent should be empirically detectable in terms of testable predictions about ecological interactions and underlying physiological processes. To determine the appropriate measure of invasion extent, we considered using four plot-level measures: absolute non-native species richness, proportional non-native species richness, absolute abundance of non-native species and proportional abundance of non-native species. Absolute non-native richness and absolute non-native abundance are components of total richness and ANPP, respectively, potentially creating difficulties in interpreting statistical patterns between species richness and ANPP. Therefore, these measures of invasion extent were not suitable for our analysis. In the past, using proportional richness of non-native species has yielded spurious results when correlated with variation in native richness (as discussed in Levine and D’Antonio, 1999). For this reason, we also rejected proportional richness of non-native species as a measure of invasion extent. Moreover, because many interspecific interactions (e.g., competition) are mediated by proportional biomass, we expect that ecosystem-level effects of non-native species are likely to be proportional to relative abundance of non-native species. Therefore, we determined that proportion of total community abundance (biomass or cover) contributed by non-native species (hereafter %NN) satisfied these criteria and was the most appropriate measure of invasion extent for our analyses.

For three of the sites (Cedar Creek, Kellogg Biological Station, and Short Grass Steppe), aboveground biomass was destructively harvested as a surrogate for net primary production, and the biomass sorted to species to determine species composition (see methods citations in Table 1). Proportion of non-native species was defined as the ratio of the biomass of non-native species to total biomass of all species in the plot. Biomass was measured non-destructively three times each year at the Jornada Basin site in order to capture production by plants with differing phenologies and species composition was estimated as relative proportion of biomass (see Hueneke et al., 2001 for detailed methods). The Jornada dataset contained a number of outlying values of ANPP due to flowering events of yuccas (Yucca glauca); flowering reflects translocation of stored reserves in addition to annual production, so these plots were excluded from the analysis. For the Konza Prairie site, percent cover of

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**Table 1.**—Extended

<table>
<thead>
<tr>
<th>$S_{Nat}$</th>
<th>$S_{Non}$</th>
<th>Range ANPP (g/m²)</th>
<th>ANPP method</th>
<th>Methods reference</th>
<th>Native flora (Site-Specific) reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>113 (+ 13 unk)</td>
<td>40</td>
<td>1.69–1149.07 Above ground clippings</td>
<td>Inouye et al. 1987</td>
<td><a href="http://www.lter.umn.edu/">http://www.lter.umn.edu/</a></td>
<td></td>
</tr>
<tr>
<td>200 (+ 75 unk)</td>
<td>8</td>
<td>0–1105.7 Estimate using regressions based on plant volume</td>
<td>Hueneke et al. 2001</td>
<td><a href="http://jornada-wwm.nmsu.edu/">http://jornada-wwm.nmsu.edu/</a></td>
<td></td>
</tr>
<tr>
<td>80 (+22 unk)</td>
<td>91</td>
<td>24–1380.7 Above ground clippings</td>
<td>Huberty et al. 1998</td>
<td><a href="http://iter.kbs.msu.edu/">http://iter.kbs.msu.edu/</a></td>
<td></td>
</tr>
<tr>
<td>416 (+22 unk)</td>
<td>60</td>
<td>158.7–1278.3 Above ground clippings</td>
<td>Briggs &amp; Knapp 1995</td>
<td><a href="http://www.konza.ksu.edu/">http://www.konza.ksu.edu/</a></td>
<td></td>
</tr>
<tr>
<td>55 (+2 unk)</td>
<td>3</td>
<td>181.6–4394.8 Nondestructive, estimated from light penetration</td>
<td>Grace &amp; Guntenspergen 1999</td>
<td>James Grace, pers. comm.</td>
<td></td>
</tr>
<tr>
<td>58 (+4 unk)</td>
<td>5 (1 unk)</td>
<td>1.36–138.46 Above ground clippings</td>
<td>Milchunas et al. 1990</td>
<td><a href="http://sgs.cnr.colostate.edu/">http://sgs.cnr.colostate.edu/</a></td>
<td></td>
</tr>
</tbody>
</table>
each species was estimated in permanent plots. Adjacent plots were harvested destructively to determine ANPP. For the Pearl River site, productivity was determined non-destructively (for methods see Grace and Guntenspergen, 1999) and species composition was determined as percent cover within each plot. For these sites, we used percent cover as a fraction of total vegetation cover for our measure of %NN. Non-vascular plant species were excluded from our analyses because they were not consistently identified at all sites.

STATISTICAL ANALYSIS

All analyses were performed using SAS statistical software (SAS version 8.01, SAS Institute, Inc.). All but the Pearl River site contained data from multiple years. In previous analyses, representative years have been chosen for sites where multiple years of data were available (e.g., Gross et al., 2000). However, because of large inter-annual variability in productivity and diversity, it is difficult, and perhaps misleading, to choose only one year of data for analysis. For this reason we chose to use all years of available data. We tested for temporal correlation in ANPP or species richness (S) in consecutive years using mixed model repeated measures ANOVAs for years by community type (PROC MIXED, with year as the repeated measure). Significant correlation was detected in 33 out of 102 y pairs. We address the high level of inter-annual variability in these data in another paper (Cleland et al., 2004).

We used Spearman rank correlations between %NN and ANPP over all plots by site to test the hypothesis that invaded plots are characteristically more or less productive than non-invaded plots.

To examine the shapes of relationships between ANPP and S, and to quantify the influence of %NN and ANPP on S, we performed stepwise multiple regressions with S as the dependent variable along with four independent variables: ANPP (linear), the square of ANPP (quadratic), the natural logarithm of ANPP (log) and %NN. While alternative modeling approaches (e.g., nonparametric regression) might detect subtler relationships, this is the conventional method for modeling patterns in primary productivity and species richness (e.g., Mittelbach et al., 2001) and allows comparison with other studies. Our approach simply extends this method to include a covariate for the influence of non-native species. Every model that resulted from regression was categorized into one of two groups, those in which the proportion of non-native species was a significant (α = 0.05) predictor of S, and those in which it was not. To test the hypothesis that non-native species affect the shape of productivity-richness relationships, we used a Fisher’s exact test (Zar, 1999) to compare the frequency distributions of the shapes of the relationship (positive, negative, U-shaped, hump-shaped and not significant) for groups where %NN was and was not a significant predictor of S.

When the quadratic transformation of ANPP was significant, we identified the maximum or minimum of the model equation and ascertained if it fell within the observed range of productivity to determine if the shape of the relationship was truly hump-shaped or U-shaped. We used multiple regressions because our interest in the shape of productivity-richness relationships is primarily phenomenological, rather than mechanistic. Use of variable transformations allowed us to fit a wide variety of shapes including the monotonic, hump and U-shaped relationships commonly reported (e.g., Mittelbach et al., 2001). A stepwise procedure was used because we made no a priori hypothesis about the shape of the relationship, which was allowed to vary with the particular transformation of ANPP selected. The significance level criterion for a variable to enter the model or to stay in the model with each iteration was α = 0.05.

The average amount of variation explained by a predictor is an indication of the importance of that factor in predicting S. The ratio of partial R² to the full model R²...
indicates the relative importance of a variable compared with other independent variables. Mean and standard errors of the partial $R^2$ and $R^2$ ratios were computed on arcsine-square root transformations of the data. Reported values have been back-transformed.

**RESULTS**

The correlations between %NN and ANPP were commonly, but not always, significant (Table 2). The presence of significant correlations confirms our hypothesis that non-native species might alter or contribute to productivity in ways that are predictable within systems. However, the sign of the relationship was not consistent among sites, indicating that there is no general pattern in the relationship between invasion extent and productivity. ANPP, ANPP$^2$ and $\log_e$(ANPP) were significant predictors of $S$ in 15.7%, 17.6%, and 48.0% ($N = 102$) of comparisons, respectively, although non-significant relationships were most common. These results correspond to 24.5% of comparisons exhibiting positive relationships, 21.6% exhibiting negative relationships, 14.8% exhibiting hump-shaped relationships and 39.2% exhibiting no discernible relationship between ANPP and $S$ (Fig. 2). After all significant predictors had been entered in models, %NN was a significant predictor of $S$ in 13.7% ($N = 14$) of all comparisons. In six of these cases, %NN and $S$ were positively correlated; two cases were negatively correlated; and one plot exhibited a hump shaped relationship (Fig. 2). Rarely were both %NN and ANPP significant predictors of $S$. The unique variation in $S$ explained by each significant variable was generally low (average partial $R^2 < 12%$; Table 3). Additionally, the ratio of partial $R^2$ to model $R^2$ was relatively high (average ratio >75%). Thus, only a small part of the variation in $S$ was explained by ANPP or invasion extent, and generally the first variable selected dominated the final model.

We failed to reject the null hypothesis that the relative frequencies of the shapes of the relationship between ANPP and $S$ were different in situations where %NN was a significant predictor of $S$ versus those where it was not a significant predictor of $S$ ($P = 0.44$, $N = 102$). Thus, we found no evidence for the hypothesis that non-native species have an effect on the form of productivity-richness relationships in these systems.

**DISCUSSION**

The effects of non-native species on plant communities and ecosystem processes have often been dramatic (Simberloff, 1981; Parker et al., 1999). The invasion of non-native species sometimes has resulted in the re-structuring of large-scale patterns in ecological processes, especially when non-native species modify the physical structure of the ecosystem (Levinton, 1994) or interrupt natural cycles such as fire frequency (D’Antonio, 2000). We hypothesized that as ecosystems became increasingly invaded, invasion extent would increasingly determine species richness, possibly replacing the dependence of species richness on production. Thus, we expected that sites in which %NN was a predictor of species richness would differ from sites where it was not in the distribution of patterns in the relationship between species richness and productivity. We found no support for this
hypothesis; however, our analysis shows that the effects of non-native species also might be subter, depending on the phenomenon and scale of interest. This finding is consistent with the suggestion of Ortega and Pearson (2005) that strong and weak invaders will have qualitatively different effects on species distributions and ecosystem processes.
Table 3.—Mean and standard error for partial $R^2$ and the ratio of partial $R^2$ to model $R^2$ for each significant predictor variable across all sites. Mean partial $R^2$ values indicate the average importance of the variable in explaining the variation in species richness. The ratio indicates the relative importance of the variable compared with other variables in the model. Statistics were computed on the arcsin-square root transformations; reported values have been back-transformed.

<table>
<thead>
<tr>
<th>Variable</th>
<th>$\text{mean}_{\text{partial}} +/- \text{SE}$</th>
<th>$\text{mean}_{\text{partial/model}} +/- \text{SE}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>%NN</td>
<td>0.074 +/- 0.003</td>
<td>0.770 +/- 0.078</td>
</tr>
<tr>
<td>ANPP</td>
<td>0.113 +/- 0.003</td>
<td>0.839 +/- 0.051</td>
</tr>
<tr>
<td>ANPP$^2$</td>
<td>0.069 +/- 0.002</td>
<td>0.941 +/- 0.050</td>
</tr>
<tr>
<td>$\log_{10}$(ANPP)</td>
<td>0.116 +/- 0.005</td>
<td>0.844 +/- 0.021</td>
</tr>
</tbody>
</table>

We found that the relative abundance of non-native species was occasionally a significant factor explaining species richness and that it was correlated with productivity at four out of six sites, but did not affect the frequency of different patterns of the productivity-richness relationship. Thus, ecosystem-scale responses to invasion can be equivocal: the effects of non-native species, though discernible (we detected statistically significant relationships), may not have great ecological significance (the relative frequency of different productivity-richness patterns did not change). Given that our findings result from a study of six different systems, we think it unlikely that these findings are idiosyncratic.

Our results indicate that a standard shape for the relationship between primary productivity and species richness does not exist among the six sites included in this study. We found similar numbers of positive, negative, and non-significant relationships, but few hump-shaped relationships and no U-shaped relationships, which makes our findings roughly consistent with past studies (Waide et al., 1999; Mittelbach et al., 2001). Why do observed productivity-richness relationships differ among sites and years? Artifacts of statistical techniques (Mittelbach et al., 2001), magnitude of spatial extent (Gross et al., 2000; Mittelbach et al., 2001) and physical or biological mechanisms such as disturbance or consumer pressure (Worm et al., 2002) have all been proposed as potential explanations. In this study we investigated for the first time the influence of the relative abundance of non-native species on productivity-diversity relationships. Generally, either %NN or some transformation of ANPP was important for predicting $S$, but not both. We expected invaded sites to exhibit different productivity-richness relationships than non-invaded sites. However, we found no evidence of this in our study. Nonetheless, invasion extent was an important factor in predicting species richness approximately 14% of the time.

While dominance by non-native species did not alter the overall shape of the relationship between productivity and species richness, there were interesting differences among sites, both in the pattern of the productivity richness relationship and in the influence of non-natives. In Jornada Basin, invasion extent was positively correlated with ANPP. In this desert ecosystem most non-natives are annual species that appear in years with high rainfall, when a number of native annuals are also likely to appear (Guo and Brown, 1996). This explains the high abundance of positive productivity-richness relationships where invasion extent was also a predictor of total species richness. In contrast, invasion extent was negatively correlated with ANPP at both Pearl River and Konza Prairie, two sites with high rates of ANPP (see Table 1). It has been suggested that ecosystems with high ANPP may be less invasible than other systems (Tilman, 1997; Smith and Knapp, 1999). At Pearl River, non-native species tend to be found in disturbed areas where both diversity and productivity are low (J. Grace, pers. comm.). At Konza Prairie, native and non-native species richness are positively correlated (Smith and Knapp, 1999). While annual burning suppressed the
species richness of native species and non-native species, non-native species comprised a greater portion of the ANPP in the areas that were annually burned.

Given that invasive species are one of the greatest threats to native biodiversity (Wilcove et al., 1998; Sala et al., 2000), why didn’t we see more of an influence of invasion extent on species richness and productivity relationships? One possibility is that non-native species are not generally functionally different than their native counterparts (Ortega and Pearson, 2005). Previous research has suggested that only a small proportion of non-native species should have large ecosystem effects (Williamson and Fitter, 1996; Vitousek et al., 1997), and that non-natives with novel functional traits are the most likely to influence ecosystem processes (Chapin et al., 1994). Smith and Knapp (2001) found that native species and non-native species at Konza Prairie did not differ in their functional traits. Together, these observations suggest that the reason we did not find large effects of non-natives at this site was their functional similarity.

What can be inferred from these results with respect to the search for general patterns in the impact of non-native species on ecosystem processes? Waide et al. (1999) pointed out that the study of relationships between productivity and species richness intertwines two issues of considerable importance: the conservation of biodiversity (species richness) and the conservation of an ecosystem process (primary production). The role of often undesirable invasive species in this relationship further complicates environmental management. Our study shows that although the presence of non-native species can influence total species richness, the extent of invasion in an ecosystem does not necessarily alter productivity-richness relationships.

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LITERATURE CITED


