Biotic and abiotic influences on native and exotic richness relationship across spatial scales: favourable environments for native species are highly invasible

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Summary

1. Biological invasions threaten biodiversity, and understanding the factors that influence a community's susceptibility to invasion informs both management of invasive species and conservation efforts towards promoting biodiversity.

2. In this study, we examined the native–exotic richness relationships (NERR) at two spatial scales and asked what variables mediate the relationship between native and exotic species richness in 1-m^2 plots among old fields. We also tested whether the favourable environment and spatial heterogeneity mechanisms alter the relationship between native and exotic richness. Additionally, we identified biotic, abiotic and landscape factors that accounted for patterns of exotic species richness across spatial scales, from 50-m transects (i.e. local scales) to entire old fields (i.e. landscape scales).

3. We found that native and exotic richness were positively related at both local and landscape spatial scales, with the strength of their relationship greater at the landscape scale. In old-field communities with lower foliar cover, native and exotic plant richness were negatively related across 1-m^2 plots, whereas in old fields with higher foliar cover, native and exotic plant richness were positively related across 1-m^2 plots. Overall, predictors of exotic species richness depended on spatial scale: at local scales, native plant richness, light and landscape factors accounted for most of the variation, but biotic factors alone accounted for most of the variation at the landscape scale.

4. Our findings suggest that fields favourable for native species are also suitable for exotic species, and management efforts towards exotic richness should be tailored to spatial scale.

Key-words: exotic richness, favourable environment, invasibility, native richness, spatial heterogeneity, spatial scale

Introduction

Invasion ecologists have long sought to understand the roles of biotic and abiotic factors in rendering some communities more resistant than others to invasion (Elton 1958; Lonsdale 1999). At local scales (< 10 m^2), the number of exotic species is often negatively correlated with native richness, but at landscape or regional scales, this relationship tends to be positive (Fridley *et al.* 2007). Fridley *et al.* (2007) introduced the phrase 'invasion paradox' to describe the situation in which the native–exotic richness relation-

ship (i.e. NERR) can change with spatial scale. But why might the NERR vary with spatial scale?

The probability of successful colonization by exotic species should be lower at local spatial scales with higher numbers of native species because of competition (Elton 1958). The biotic resistance hypothesis therefore predicted that greater richness would lead to lower invasion because the amount of available resources for 'invaders' would be lower as the number of species increased. Elton's 'biotic resistance' hypothesis has generally been supported at local spatial scales, but the opposite has also occasionally been documented (reviewed in Fridley *et al.* 2007).

Two hypotheses have been proposed to explain the positive NERRs at landscape or regional scales: the favourable environment hypothesis and the spatial heterogeneity hypothesis (Stohlgren *et al.* 1999, 2006; Fridley *et al.* 2007).

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The favourable environment hypothesis suggests that coexistence of native and exotic species is promoted in sites where favourable growing conditions (i.e. higher resource availability) generate high species richness of both natives and exotics (Stohlgren *et al.* 1999, 2006). One criticism of the favourable environment hypothesis is that it accounts for differences only in mean conditions between sites and disregards the potential importance of variation within sites (Davies *et al.* 2005, 2007). The spatial heterogeneity hypothesis, by contrast, states that coexistence of native and exotic species richness is generated via habitat heterogeneity or spatial variability in resources or conditions (Davies *et al.* 2005, Davies *et al.* 2005; Stohlgren *et al.* 2006). Therefore, as variability in biotic and/or abiotic factors increases, so do the numbers of both native and exotic species, thus generating strongly positive NERRs.

In this study, we investigate the NERR across spatial scales to test whether the favourable environment and spatial heterogeneity mechanisms alter the relationships between native and exotic richness. Additionally, we examine the role of other biotic, abiotic and landscape-scale factors associated with exotic richness at two spatial scales and discuss how the predictors of exotic richness differ between local scales and landscape scales. Specifically, we used old-field plant communities to ask the following questions: (i) What is the relationship between native and exotic species richness, and does it vary across spatial scales? (ii) Do favourable environments or spatial heterogeneity, or both, explain the relationship between native and exotic species at local scales? (iii) What biotic, abiotic and landscape factors predict exotic plant richness across scales in old-field communities?

Materials and methods

STUDY SITE AND FIELD SAMPLING

The Three Bend Scenic and Wildlife Management Refuge Area is part of Oak Ridge National Environmental Research Park near Oak Ridge, TN (35-58′N, 84-17′W). The Three Bend Area consists of a mix of hardwood forests and old fields. Old-field communities were agricultural fields until abandonment ca. 1943. Soils at the sites are characterized as Typic Hapludult with a silty clay loam texture. Mean monthly temperatures range from approximately 3 °C in the winter to 31 °C in the summer and mean rainfall is 1322 mm.

SAMPLING BIOTIC AND ABIOTIC VARIABLES

In the summer of 2006, we sampled seventeen old fields ranging from ca. 2000 to 50 000 m^2. We chose these fields based on the presence of well-defined boundaries such as forests or roads. We randomly placed 50-m transects in each field (2–6 transects depending on field area) (Table S1). Along each transect, we placed five 1-m^2 plots 10 m apart starting 10 m from the origin of each transect. Hereafter, we refer to the data from each 50-m transect as local scale, and landscape scale refers to all transects in a single field.

In each 1-m^2 plot, we identified all plant species (Table S2), tallied exotic and native species richness, and percent foliar cover of all vascular plant species during the peak of the growing season. We also estimated above-ground biomass by randomly placing 0·5 m × 1 m subplots within each 1-m^2 plot and clipping all individuals rooted inside to approximately 1 cm from the soil surface. We sorted the biomass into total above-ground biomass (i.e. live plant material) and litter mass (i.e. dead plant material) and then oven-dried the biomass samples for 48 h at 65 °C and weighed them. We also estimated light availability, soil moisture and soil properties (soil pH, soil texture, soil N) in each of the 1-m^2 plots (Table S3). To estimate light availability, we recorded photosynthetic photon flux density with a line-integrating ceptometer (Decagon Accupar; Decagon Devices, Pullman, WA, USA) positioned horizontally at approximately 2 cm above the ground in each 1-m^2 plot. To measure soil moisture, we used a handheld time domain reflectometer with 12-cm probes (Hydrosense; Decagon Devices) in one random location per 1-m^2 plot to estimate percent volumetric water content. We also collected a 10-cm soil core from the centre of each 1-m^2 plot to quantify soil texture (percent sand and clay), bulk density, gravimetric water content, pH and potential net nitrogen (NO_3^- and NH_4^+) mineralization. To estimate potential net nitrogen (NO_3^- and NH_4^+) mineralization (i.e. potential soil N available for plant uptake), we incubated soil subsamples from each 1-m^2 plot for 1 month and compared nitrogen availability of the incubated subsamples with that of subsamples extracted prior to incubation. Soil nitrate (NO_3^-) and ammonium (NH_4^+) in samples were extracted by 2 M KCL and analysed with an autoanalyzer (Lachat Quikchem 8000; Hach Corporation, Loveland, OH, USA).

ESTIMATING LANDSCAPE VARIABLES

We mapped the boundary of each old field with GPS units and used ARCGIS 9.1 (ESRI, Redlands, CA, USA) to calculate field area and perimeter, density of roads within a 250-m buffer from the edge of each field, and type and area of land cover (other fields, forest, water) within a 250-m buffer from the edge of each old field (Table S3). We calculated road density using the Anderson County roads layer from the Tennessee Spatial Data Server (http://www.tngis.org) and retrieved land cover data from the most recent National Land Cover Database (NLCD 2001; http://www.mrlc.gov). We calculated field edge using Patton's Shape Index (Patton 1975) and used field measurements of slope and aspect to calculate heat load (McCune & Keon 2002), an integrative measure of the field exposure to incident sunlight for each field (Table S3). We created four categories of mowing frequency based on Tennessee Wildlife Resource Agency records (J. Evans, pers. comm.) as our disturbance measure. We assigned each field to a mowing intensity ranging from 1 to 4, with one representing monthly mowing and four representing biennial mowing.

STATISTICAL ANALYSES

To examine the NERR at local and landscape scales, we performed linear regressions using cumulative native plant richness to predict cumulative exotic plant richness across 50-m transects (n = 50) and old fields (n = 17) (Table S3). In addition, we assessed variation in the NERR among old fields using a similar sampling approach to that of Davies *et al.* (2007), regressing exotic plant richness against native plant richness for the 1-m^2 plots within each of the 17 old fields.

We also examined the support for the favourable environment or spatial heterogeneity hypotheses as influences on NERR within old-field communities. To test the favourable environment and spatial heterogeneity hypotheses, we used a stepwise linear regression with

the slope of NERR (generated across 1-m² plots within each old-field community) as a continuous response variable and the mean and variation (estimated as the coefficient of variation) in biotic (total aboveground biomass and foliar cover) and abiotic (soil VWC, soil pH, soil N, soil bulk density, litter mass) variables at the landscape scale as potential predictor variables. Prior to regression analyses, we created a correlation matrix among mean and variance in biotic and abiotic factors to assess potential covariation among factors. We tested for significant correlations between all predictor variables using Pearson's correlation coefficients. Predictor variables with significant correlation coefficients ($-0.75 > r > 0.75$) were not used in the same model (Kumar, Stohlgren & Chong 2006). We generated NERR slopes, the correlation matrix and the multiple linear regressions with JMP 6.0 (SAS Institute Inc., Cary, NC, USA).

To elucidate which factors might influence exotic plant richness and assess whether those factors varied across spatial scales, we conducted variable selection procedures using all possible regression methods at both local and landscape scales. At both local and landscape scales, we included the measured biotic (native plant richness, total above-ground biomass, exotic cover) and abiotic variables (light availability, soil moisture, soil N, soil bulk density, soil texture, litter mass, heat load) as well as landscape variables (field density, forest density, road density, field edge, mowing regime; Table S3) in our model selection procedure. To estimate biotic variables at the transect and old-field scale (e.g. total species richness, above-ground biomass, etc.), we summed values from all of the 1-m² plots in each transect and old field. To estimate abiotic variables (e.g. light availability, soil N), we averaged the values from each 1-m² plot for each transect and old field.

We used the Akaike Information Criterion adjusted for small sample size (AIC_c; Burnham & Anderson 2002) to evaluate multiple regression models predicting exotic species richness at the local and landscape scales. We tested for collinearity among biotic (native plant richness, total above-ground biomass, exotic cover), abiotic (light availability, soil moisture, soil N, soil bulk density, soil texture, litter mass, heat load) and landscape (field density, forest density, road density, field edge, mowing regime) variables at the landscape scale as potential predictor variables. We tested for collinearity among biotic, abiotic and landscape predictors using the same procedure employed during NERR analyses. All regression analyses were performed using SAS 9.1.3 (SAS Institute, Inc.).

We used Moran's I_{std} correlograms to test for spatial autocorrelation in the residuals of the best models (based on biotic, abiotic and landscape predictors) for exotic and native plant species richness at the local and landscape scales. If we found significant autocorrelation in the environmental model residuals, we constructed spatial models and environment + spatial models to account for this autocorrelation (Borcard & Legendre 2002; Borcard *et al.* 2004). Finally, we found no evidence of spatial autocorrelation in exotic richness at either local or landscape scales (Fig. S1), so we do not discuss it further.

Results

We encountered 157 plant species in the old fields assessed here. Of these, 106 species were native, 36 were exotic and 15 could not be identified to species. At the 1-m² plot scale, the number of native species ranged from 4 to 9 (4.3 ± 0.12) and the number of exotic species from 3 to 20 (9 ± 0.19). At the local scale (50-m transect), the number of native species ranged from 12 to 33 (19.7 ± 0.67) and the number of exotic

species from 3 to 15 (8.5 ± 0.37). At the landscape scale (old-field scale), the number of native species ranged from 17 to 46 (30.9 ± 1.86) and the number of exotic species from 7 to 20 (11.7 ± 0.82).

NERR ACROSS SPATIAL SCALES

Native and exotic plant richness were significantly positively correlated at all spatial scales (local scale: $R^2 = 0.13$, $n = 50$ $P = 0.012$; landscape scale: $R^2 = 0.42$, $n = 17$, $P = 0.004$; Fig. 1). Although the overall NERR at the local scale (50-m transect) was positive across the 17 old fields ($n = 50$), it varied within each field: it was positive in two fields, negative in two fields and not statistically related in the remaining 13 fields (note NERR slope values in Fig. 2).
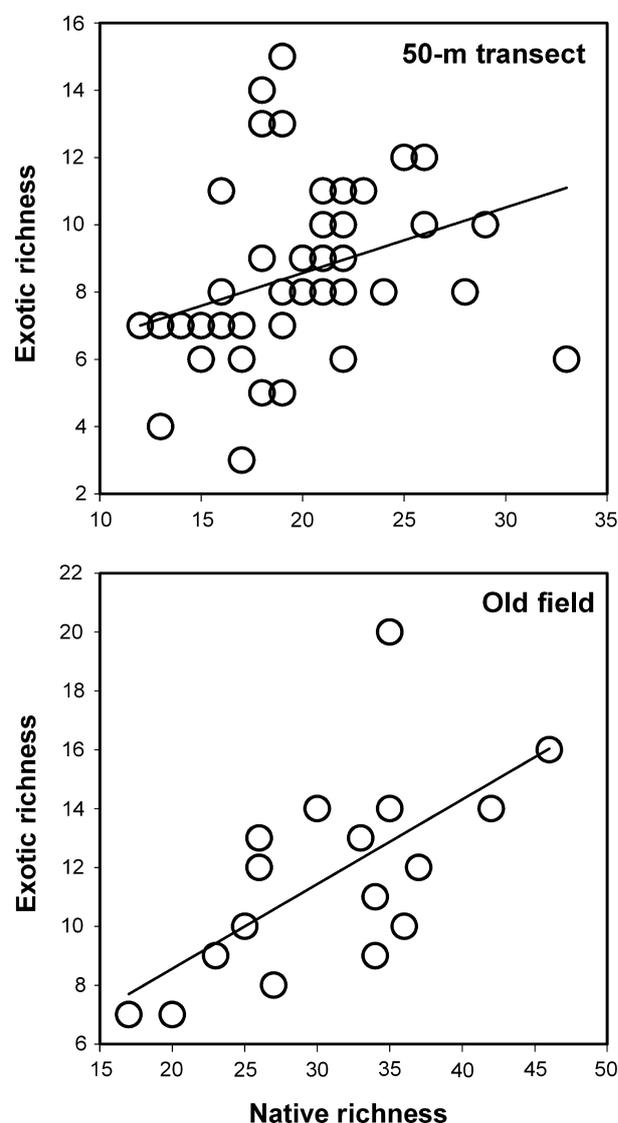

Fig. 1. The relationship between exotic species richness and native species richness across spatial scales. Cumulative exotic richness is positively related to cumulative native species richness at local (top panel) and landscape (bottom panel) scales. Significant ($P < 0.05$) relationships are shown with a regression line.
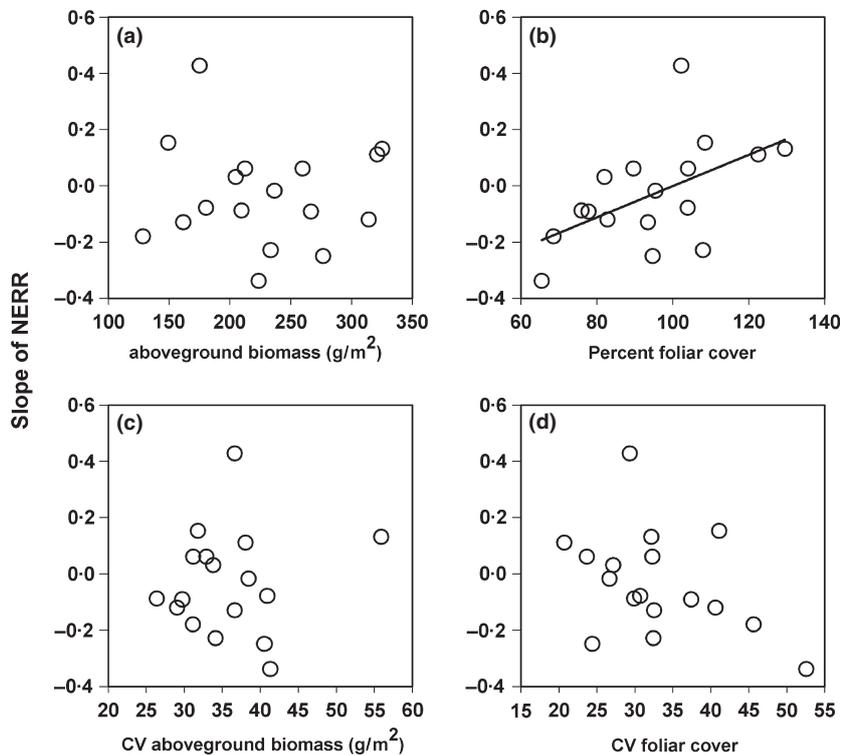
Fig. 2. The relationship between the slope of the native–exotic richness relationship across 1-m² plots in individual old fields and mean field above-ground biomass (a), mean field foliar cover (b), heterogeneity (CV) in above-ground biomass (c) and heterogeneity (CV) in foliar cover (d). Significant ($P < 0.05$) correlations are shown with a regression line.

FAVOURABLE ENVIRONMENT HYPOTHESIS VS. SPATIAL HETEROGENEITY HYPOTHESIS

Our data support the favourable environment hypothesis but not the environmental heterogeneity hypothesis. Mean foliar cover at the landscape scale was positively correlated with the slope of the NERR ($R^2 = 0.29$, $P = 0.03$; Fig. 2b), but heterogeneity in foliar cover was not related to the NERR slope (Fig. 2d). In addition, neither mean productivity nor heterogeneity in productivity (measured as CV of above-ground biomass) affected NERR (Fig. 2a, c) across old fields. Furthermore, the slope of the NERR was not correlated with either the mean or heterogeneity of any of the measured abiotic resources or conditions at the landscape scale.

BIOTIC, ABIOTIC AND LANDSCAPE PREDICTORS OF EXOTIC PLANT RICHNESS

Native plant richness, light availability and road density were important predictors of exotic richness in multiple regression models at both local and landscape scales. Together, these variables accounted for 45% and 85% of the variation in exotic plant richness at local and landscape scales, respectively (Table 1).

At the local scale, biotic, abiotic and landscape factors accounted for similar amounts of variation in exotic plant richness. For example, as native plant richness (partial $R^2 = 0.13$) and light availability (partial $R^2 = 0.17$) increased so did exotic plant richness. On the other hand, road density (partial $R^2 = 0.15$) surrounding old fields was

Table 1. Comparison of the best models for predicting exotic species richness at local (50-m transect), and landscape (old field) scales. Local and landscape-scale models included biotic, abiotic and landscape predictors

Variable	d.f.	Parameter	Variable P	Partial R^2	Model R^2	Model P
Landscape scale						
Intercept	1	5·647	0·0979	–	0·93	0·0402
Native richness	1	0·318	0·0219	0·7254		
Road density	1	−0·004	0·0956	0·1261		
Soil moisture	1	−0·288	0·1784	0·083		
Light availability	1	5·51	0·3327	<0·0001		
Local scale						
Intercept	1	8·942	0·0004	–	0·58	<0·0001
Light availability	1	6·42	0·0004	0·1672		
Road density	1	−0·003	0·0003	0·1465		
Native richness	1	0·168	0·0127	0·1253		
Field density	1	−0·078	0·0698	0·0953		
Soil clay	1	−0·122	0·0354	0·0408		

negatively correlated with exotic plant richness. As the density of surrounding fields increased, exotic plant richness in local communities decreased (Table 1).

Biotic rather than abiotic predictors accounted for most of the variation in exotic plant richness at the landscape scale. Exotic plant richness was positively associated with native richness, accounting for 70% of the total variation, and road density and soil moisture were negatively related to exotic plant richness, accounting for 13% and 8% of the variation in exotic plant richness. Finally, exotic plant richness was positively related to light availability, but the latter was a poor predictor, accounting for <1% of the variation in exotic plant richness (Table 1).

Discussion

NERRS ARE POSITIVELY ASSOCIATED ACROSS SPATIAL SCALES

In this study, the NERR was positive at both local and landscape scales, but the strength of this relationship was greater at landscape scales than at local scales. It is not surprising that at larger spatial scales NERR are positively associated, but encountering such a relationship at smaller spatial scales (i.e. transects) across old fields is not as common (Fridley *et al.* 2007; Belote *et al.* 2008). This fact suggests the mechanisms shaping the NERR might vary among systems and depend on context.

FAVOURABLE ENVIRONMENTS SHAPE THE NERR

We found support for the favourable environment hypothesis shaping NERR across a foliar cover gradient. Mean foliar cover at the landscape scale was the most important factor mediating the slope of the NERR within old fields, and in no case did heterogeneity account for any variation in the NERR, as the spatial heterogeneity hypothesis would predict. In contrast to a study by Shea & Chesson (2002), we documented that the slope of NERR is not scale dependent but is affected by the favourableness of an environment. In fact, environmental variation (i.e. across old-field communities) shaped the NERR rather than a change in spatial scale. Recently, in a related study, Davies *et al.* (2007) found that a gradient in foliar cover shaped the NERR in a serpentine grassland system. However, Davies *et al.* (2007) reported positive NERR in communities with low cover and negative NERR in communities with greater foliar cover in serpentine systems in the western United States, which contrasts with our result. In that serpentine system, Davies *et al.* (2007) used foliar cover as a proxy for productivity and attributed differences in NERR to the notion that productive sites have negative NERR because they are homogeneous, but low productivity sites have positive NERR because they are heterogeneous. There are at least two reasons why our results are not congruent with theirs. First, foliar cover might not be a good proxy for productivity in our system, and in fact, mean foliar cover and mean above-ground biomass (i.e. productivity) are uncorrelated ($P = 0.14$). Moreover, fields with greater foliar cover need not be more homogeneous in terms of biotic and abiotic factors as suggested by Davies *et al.* (2007). In fact, we did not find fields with greater foliar cover to be more homogeneous in terms of biotic or abiotic factors (data not shown). Second, it could be that in productive systems, such as ours, heterogeneity is not a prerequisite for coexistence among native and exotic species. Unlike the serpentine communities of Davies *et al.* (2007), local old-field plant communities are not saturated across a foliar cover gradient. As a result, native species may exert weak effects on the establishment of exotic species. For instance, most NERRs (negative or positive) within fields were weak and non-significant, indicating that local old-field communities can still accommodate more species.

LANDSCAPE, BIOTIC AND ABIOTIC FACTORS INFLUENCE EXOTIC RICHNESS IN LOCAL SCALES

At the local spatial scale, abiotic, biotic and landscape variables accounted for similar amounts of variation in exotic plant richness. Local communities with greater light availability had more exotic plant species than did local communities with lower light availability. Light availability in transects is negatively correlated with litter mass accumulation, which has been shown to impede successful colonization of exotic plant species by affecting seedling establishment (Rasran, Vogt & Jensen 2007). Also, transects within old fields that had higher densities of other fields and roads in their vicinity harboured fewer exotic plant species than transects nested within fields surrounding by fewer roads or other fields.

The nature of the relationship between landscape factors and exotic richness produced some interesting patterns. For example, transects nested within small old fields tended to have fewer exotic plant species compared to transects found within larger old fields (Fig. S2). Recent studies have demonstrated that regional richness can be the strongest predictor of local (1-m^2 plot scale) plant richness after accounting for environmental variation (Harrison 1999; Freestone & Harrison 2006). Generally, species richness in a variety of local communities is linearly related to regional richness when immigration effects override species interactions (Witman, Etter & Smith 2004; He *et al.* 2005; Fox & Srivastava 2006). We found regional exotic plant richness (i.e. old field) to be positively related to local exotic plant richness (i.e. plot, $P < 0.0001$, $R^2 = 0.77$) (Fig. S2). Likewise, exotic plant species richness in the 1-m^2 plots is positively related to exotic plant richness at the 50-m transect scale ($P < 0.0001$, $R^2 = 0.74$), which is also positively related to exotic richness at a regional scale ($P = 0.008$, $R^2 = 0.54$) (Fig. S2). Consequently, the total number of exotic plant species in a field strongly predicts exotic richness at local scales across old-field communities, demonstrating the importance of regional processes at local scales.

BIOTIC FACTORS INFLUENCE EXOTIC RICHNESS AT LANDSCAPE SCALES

Exotic richness at the landscape scale is a better predictor of exotic plant richness at local scales, suggesting that exotic plant immigration within transects exceeds immigration from other fields or via roads. At the largest spatial scale, landscape scale, native plant richness was the best predictor of exotic plant richness. This result is similar to those of other studies (Stohlgren *et al*. 1999, 2006; Fridley *et al*. 2007; Belote *et al*. 2008) that found NERR strongly positively correlated at larger spatial scales. Stohlgren *et al*. 2006 documented native and exotic species relationships increasing in strength from local to regional scales across 37 vegetation types ranging from desert shrublands to tallgrass prairies as well as from low elevation grasslands to forests and high elevation tundras. Despite the fact that our study was conducted in a single community type (old fields in the Southeast) and/or single land-use history, our findings provide additional support to previous studies showing that 'the rich gets richer' (Stohlgren *et al*. 2006). At larger spatial scales, both favourable environment and spatial heterogeneity are thought to contribute to higher NERR.

Conclusions

Our findings demonstrate that old-field communities with more native plant species are likely to have more exotic plant species than are communities with fewer native plant species at both local and landscape scales. The mechanism driving the NERR within old fields (across 1-m^2 plots) in our system is not productivity or variation in productivity as has been found in other studies (Davies *et al*. 2007). Instead, variation in mean foliar cover seems to be correlated with NERR: fields with greater foliar cover were more likely to generate positive NERR slopes than were fields with lower foliar cover. In fact, native plant richness was the best predictor of exotic plant richness at the landscape scale, but also an important predictor at local spatial scales. Furthermore, exotic plant richness, abiotic and landscape variables were also associated with exotic plant richness at local scales. Finally, management efforts to control colonization by exotic plant species will likely have to focus on resource availability at local spatial scales, yet preservation of native biodiversity will be guided by decisions regarding exotic species colonization from local to landscape scales.

Acknowledgements

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Supporting Information

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

Table S1. Table listing site name, field identification number, number of transects per old-field community, and area in m^2 of all old-field communities.

Table S2. Table listing the family, scientific name and nativity of 95 plant specimens identified across old-field communities.

Table S3. Table listing variables measured and measurement methods.

Figure S1. Moran's I_{std} correlograms of spatial autocorrelation for exotic richness at local (50-m transect) (a) and landscape (old-field) (b) scales.

Figure S2. Linear regression of exotic richness at 1-m^2 plots vs. exotic richness at the landscape scale (a), exotic richness at 1-m^2 plots vs. exotic richness at the local scale (50-m transect) (b), and exotic richness local scale vs. exotic richness at the landscape scale (old field) (c).

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