

# REPORTS

*Ecology*, 84(1), 2003, pp. 32–39  
© 2003 by the Ecological Society of America

## DIVERSITY AND INVASIBILITY OF SOUTHERN APPALACHIAN PLANT COMMUNITIES

REBECCA L. BROWN<sup>1,3</sup> AND ROBERT K. PEET<sup>2</sup>

<sup>1</sup>*Curriculum in Ecology, CB#3275, The University of North Carolina at Chapel Hill, Chapel Hill, North Carolina 27599-3275 USA*

<sup>2</sup>*Department of Biology, CB#3280, The University of North Carolina at Chapel Hill, Chapel Hill, North Carolina 27599-3280 USA*

**Abstract.** We propose that the relationship between diversity and community invasibility depends on the degree to which community composition is driven by immigration processes. When immigration is enhanced by high propagule pressure or low-intensity disturbance, the relationship between diversity and exotic species invasion should be positive. Only when such immigration processes are limited should competitive interactions lead to a negative correlation between diversity and invasibility. Moreover, competition should be more apparent at smaller scales where individual plants compete directly for space; thus, diversity and invasibility are more likely to be negatively correlated at small spatial scales. We tested these predictions by comparing exotic and native species diversity of vascular plants across five spatial scales in riparian and upland plant communities in the southern Appalachians. We found a positive relationship between species diversity and exotic invasion in riparian areas at large scales (100 m<sup>2</sup>), which graded into a negative relationship at small scales (0.01 m<sup>2</sup>). In uplands, there was a slight positive relationship between native and exotic species diversity at both scales of observation. Overall, riparian areas had more exotic and native species than upland areas, and both native and exotic species diversity increased with flood frequency within the riparian zone.

**Key words:** disturbance; diversity; exotic species; immigration–extinction gradient; invasibility; propagule pressure; riparian plant communities; spatial scale; species richness.

### INTRODUCTION

Traditional theory suggests that species-rich communities should be more difficult to invade than species-poor communities owing to more complete use of resources (i.e., resource complementarity; Trenbath 1974) and more intense competition (Elton 1958, Levine and D'Antonio 1999). However, available data do not consistently support this prediction. Relatively species-rich communities have been variously reported to experience high and low levels of exotic species invasion, with experimental studies often reporting a negative relationship (Tilman 1997, Knops et al. 1999, Naeem et al. 2000, Prieur-Richard et al. 2000) and observational studies often reporting a positive relationship (Stohlgren et al. 1998, Wisser et al. 1998, Lonsdale 1999, Stohlgren et al. 1999, Kalkhan and Stohlgren

2000). The growing problem of exotic species invasions and the uncertainty over the functional significance of species diversity make clarification of the relationship between species richness and invasibility particularly important.

Levine (2000) has suggested that the inconsistency observed in exotic plant invasion into species-rich communities is a consequence of the scale of observation. When Levine examined the occurrence of native and exotic species on tiny islands along a 7-km stream reach in California, he found a positive correlation, which he attributed to propagule pressure (the abundance and diversity of propagules entering a community). However, when he experimentally added propagules to microcosms in a single large riffle, he found that, at the small spatial scale of his microcosms (0.035 m<sup>2</sup>), high richness was correlated with greater resistance to invasion. These results are consistent with Wilson and Watkins (1994) and Wilson et al. (1995), who found plant niche limitation in grasslands to operate only at small scales where herbs compete directly and where there is no room for substitution among ecological equivalents.

Manuscript received 8 November 2001; revised 22 May 2002; accepted 5 June 2002; final version received 1 July 2002. Corresponding Editor: T. J. Stohlgren.

<sup>3</sup> Present address: Patrick Center for Environmental Research, The Academy of Natural Sciences, 1900 Benjamin Franklin Parkway, Philadelphia, Pennsylvania 19103 USA. E-mail: brown@acnatsci.org

Davis et al. (2000) and Wardle (2001) have offered an alternative explanation for the inconsistent relationship between richness of native and exotic species. They suggest that the underlying mechanism controlling invasibility of a community is net resource availability. They proposed that any increase in net resource availability due to factors such as disturbance (a destruction in biomass that frees resources and reduces demand) or direct fertilization would facilitate invasion, independent of species diversity. Their ideas are consistent with Huston's (1994) prediction that highest species diversity and exotic invasion both should occur on productive sites where moderate disturbance frees resources for invaders.

A conceptual framework based on the relative strength of extinction vs. immigration processes clarifies the inconsistent relationship between diversity and invasibility. Immigration and extinction processes are widely appreciated to be major determinants of community composition and structure (MacArthur and Wilson 1967). Processes such as propagule pressure and resource release through low-intensity disturbance facilitate entry of new species into the community and are here called immigration processes, whereas phenomena such as competition, extreme disturbance, and chronic environmental stress selectively remove or limit less competitive species and are here called extinction processes. Where competition-driven extinction dominates, leading to resource complementarity or space limitation, which is particularly likely at small scales owing to direct plant interactions (Huston 1999), we should expect the negative correlation between diversity and invasibility predicted by classical theory. In contrast, where immigration rates are high, owing to either high propagule pressure or low competition for resources (e.g., Lord and Lee 2001), diversity and invasibility should both be high and positively related.

In riparian corridors, vegetation propagule pressure can be exceptionally high because floodwaters carry seeds from diverse habitats located throughout a watershed (Johansson et al. 1996). Similarly, disturbance frequency can be enhanced and competitive intensity decreased by flood-induced scouring and sediment deposition. In this study, we take advantage of a large data set spanning the variation in southern Appalachian forests of North Carolina to compare the relationship between exotic and native species richness in immigration-controlled riparian systems and mature (relatively extinction-controlled) uplands. We then look in greater depth at riparian systems spanning a range of geomorphic surfaces correlated with flood disturbance frequency and presumably propagule pressure. We expect that exotic species richness (our measure of invasibility) will be highest and the relationship between exotic and native richness will be positive and strong in the most frequently flooded areas. In the adjacent uplands, we expect lower diversity and invasion due to more limited immigration and control of community

composition by extinction processes, such as competition.

We test Levine's (2000) assertion that the relationship between native and exotic species should be negative at small scales and positive at large scales by examining the relationship between exotic and native species across five spatial scales ranging logarithmically from 0.01 m<sup>2</sup> to 100 m<sup>2</sup> for the southern Appalachians as a whole and for riparian areas in that region. Because community diversity and invasibility could be positively correlated owing to both being correlated with site fertility (Huston 1994, Burke and Grime 1996, Proulx and Mazumder 1998), we also evaluate the role that soil fertility plays on invasibility in our system. Specifically, we assess the relationship between soil pH and exotic species diversity in riparian and upland areas.

## METHODS

### *Vegetation plots*

Species richness and exotic species invasion of vascular plants were compared in southern Appalachian riparian and upland areas using the Carolina Vegetation Survey database, including riparian data collected on segments of three rivers: the Little Tennessee, the New, and the Nolichucky. These river segments were selected because they represent a range in land use, history, and geology, but have similar volumes of water flow, and dams have not significantly altered their flow regimes. Included riparian areas range from 3 to 5 in stream order (Strahler 1964). Within riparian areas, plots were stratified across geomorphic positions (including uplands) using a total of 21 cross-river transects.

A total of 107 riparian and 1075 upland plots were included in the study. Plots were located in areas with natural vegetation and a minimum of human disturbance (though forested plots were often relatively mature second growth). All plots were recorded using a nested quadrat system with 5–6 scales of observation arranged along a logarithmic scale from 0.01 m<sup>2</sup> to 1000 m<sup>2</sup>. In many of the riparian zones, the geomorphic position sampled was not large enough for 1000-m<sup>2</sup> plots, so the scales we used for our analysis range from 0.01 to 100 m<sup>2</sup>. Percent cover by species was recorded at the 100-m<sup>2</sup> scale following the Carolina Vegetation Survey protocol (Peet et al. 1998). Although both herbs and trees were recorded, the vast majority of species were herbaceous.

Riparian areas include all plots within the 100-yr flood zone. Within riparian areas, species richness and exotic invasion were compared across three geomorphic positions: bars, floodplains, and terraces. The geomorphic positions were classified on the basis of flood frequency with bars flooding more often than once per year, floodplains with ~1–5-yr flood intervals, and terraces with >5-yr flood intervals (Osterkamp and Hupp

TABLE 1. Summary data for native and exotic species in southern Appalachian riparian and upland plots and across geomorphic positions.

Plot type	No. plots	No. plots with exotics (%)	Species richness		Exotic cover (%)	Percentage flora exotic
			Natives	Exotics		
A) Mean values ( $\pm 1$ SE)						
All upland	1075	266 (24.74)	31.28 $\pm$ 0.44	0.20 $\pm$ 0.02	0.20 $\pm$ 0.03	0.52 $\pm$ 0.05
All riparian	107	99 (92.52)	55.19 $\pm$ 1.96	8.05 $\pm$ 0.72	22.08 $\pm$ 2.73	11.59 $\pm$ 0.79
Bar	35	35 (100)	61.18 $\pm$ 3.61	13.77 $\pm$ 1.55	16.38 $\pm$ 2.90	17.43 $\pm$ 1.35
Floodplain	56	54 (96.43)	54.58 $\pm$ 2.57	6.29 $\pm$ 0.59	30.57 $\pm$ 4.46	10.29 $\pm$ 0.87
Terrace	16	10 (62.50)	44.20 $\pm$ 4.32	1.69 $\pm$ 0.47	4.83 $\pm$ 3.56	3.33 $\pm$ 1.12
B) Pairwise differences ( <i>P</i> values)						
All upland plots vs.						
All riparian plots			<0.001†	<0.001†	<0.001†	<0.001†
Bar plots only			<0.001†	<0.001†	<0.001†	<0.001†
Floodplain plots only			<0.001†	<0.001†	<0.001†	<0.001†
Terrace plots only			<0.001†	<0.001†	<0.001†	<0.001†
Differences between riparian plots						
Bar plots vs.						
Floodplain plots			0.128	<0.001†	0.020	<0.001†
Terrace plots			0.006	<0.001†	0.021	<0.001†
Floodplain plots vs.						
Terrace plots			0.058	<0.001†	0.004	<0.001†

Note: Values of *P* shown are the results of the randomization test for pairwise differences among geomorphic positions.  
 † Statistical significance at the 95% probability level with a Bonferroni correction.

1984). Flood frequency was determined from the height of the plot above the river, river width, and gauging station data. Uplands included all sites not exposed to flooding. For this analysis, we used 56 floodplain plots, 35 bar plots, 16 terrace plots, and 1075 upland plots. Of the upland plots, 32 were sampled as components of the 21 cross-river transects. Because analyses run using these 32 upland plots yielded similar results to the analyses run using all 1075 plots, we report only results with all upland plots so as to maximize the generality of the uplands results.

To assess the effect of soil fertility on exotic species richness, soil samples were collected from the top 10 cm of mineral soil (A horizon) in the center of each 100-m<sup>2</sup> plot. Soil samples were averaged for plots with more than one soil sample from the A horizon (typically four samples for a 1000-m<sup>2</sup> plot). Soil analyses were conducted by Brookside Laboratory, New Knoxville, Ohio, using Mehlich III extraction. We selected soil pH as a surrogate for soil fertility, as it had the strongest correlation with vegetation composition and herbaceous cover.

Exotic species were identified using the USDA Plants Database (USDA 2001). We used four measures to assess the level of exotic species invasion: exotic species richness per unit area ( $\log_{10}$  scale from 0.01 m<sup>2</sup> to 100 m<sup>2</sup>), frequency of plots with exotic species present in each geomorphic class at 100 m<sup>2</sup>, total percent cover of exotic species calculated by summing the percent cover per 100 m<sup>2</sup> for each exotic species (exotic percent cover), and percentage flora exotic ( $100 \times$  exotic species richness per 100 m<sup>2</sup>/total species richness per 100 m<sup>2</sup>).

### Statistical analyses

Distribution-free randomization methods were used for statistical comparisons. Traditional parametric regression methods were not used because both native and exotic species richness data were heteroscedastic (Levene's test for homogeneity of variance: Native  $F = 9.50$ ,  $P < 0.0001$ ; Exotic  $F = 113.62$ ,  $P < 0.0001$ ) and were not normally distributed (Kolmogorov Smirnov test for normality: Native  $D = 0.08$ ,  $P < 0.01$ ; Exotic  $D = 0.39$ ,  $P < 0.01$ ). In particular, the absence of exotic species in many of the plots (resulting in a zero exotic value) made it impossible to transform the data to normality.

Two-group randomization tests were used to compare native species richness, exotic species richness, exotic percent cover, and percent flora exotic across the four geomorphic positions and in riparian and upland areas. For pairwise combinations of geomorphic positions, observations were randomized among the positions and the difference between the two randomly assigned groups was calculated with 10 000 repeats to generate an empirical null distribution. Significance was assessed at the 95% confidence level (with a Bonferroni adjustment). The differences in frequencies of plots with exotic species present were compared across the four geomorphic positions and between riparian and upland areas using chi-square goodness-of-fit tests.

Variation in the relationship between native and exotic species richness in riparian and upland zones was compared across spatial scales using quantile regression because it facilitates analysis of the upper or lower limits of a variable rather than the mean or median

(Scharf et al. 1998). In the case of exotic species, the upper limit of the exotic species richness variable may be more relevant than the mean because exotic species are unlikely to have fully saturated a site due to dispersal limitations. Values less than the maximum may simply reflect sites that are still in the process of being colonized by exotics. We used the *bsqreg* quantile regression routine in Stata (StataCorp 2001) to create bootstrapped estimates of the regression slope and intercept at the median and 90th percentile (with 10 000 bootstrapped replicates). We selected the maximum percentile that can be selected for our sample size of riparian plots following the conservative procedure described in Scharf et al. (1998):  $n > 10/(1 - q)$ , where  $n$  is the number of plots and  $q$  is the quantile. Terraces were excluded from this analysis because these fall between riparian and upland positions and do not flood.

In addition to comparing native and exotic species richness at the same scales, we also examined the effect of native species richness at small scales on exotic species richness at the 100-m<sup>2</sup> scale because exotic species abundance was generally too low for exotics to occur within the small number of species in the smallest scale plots (only 12 0.01-m<sup>2</sup> plots as compared 238 100-m<sup>2</sup> upland plots contained exotics). If native species competitively inhibit invasive species, this is most likely a consequence of small-scale competitive processes wherein plants directly interact with high numbers of species in small areas, suggesting intense competition. Native species richness at the 0.01-m<sup>2</sup> scale is likely to influence the invasion of exotics throughout the 100-m<sup>2</sup> plot (plots were selected to be relatively homogenous), such that the relationship between exotic species richness at the 100-m<sup>2</sup> scale and native species richness at the 0.01-m<sup>2</sup> scale can provide an assay of the effects of diversity at small scales on invasion.

To determine the role of flood dispersal processes as compared to local resource levels or site productivity on invasibility, we compared the effect of soil fertility and percent cover of native species on exotic species richness in riparian and upland areas. Soil fertility can affect both native species richness and the invasibility of a site (Huston 1994, Davis et al. 2000), so we compared the effect of soil pH (related to soil fertility) on exotic species richness in floodplain and upland areas to determine whether it influences the observed patterns of exotic species invasion. For this comparison, we restricted the riparian sites to floodplains (excluding terraces, which rarely or never flood, and scour bars, which have the potentially confounding influence of substantially higher light levels).

## RESULTS

### *Comparisons of riparian and upland areas*

Riparian areas have significantly higher species diversity of both native and exotic species ( $P < 0.0001$ )

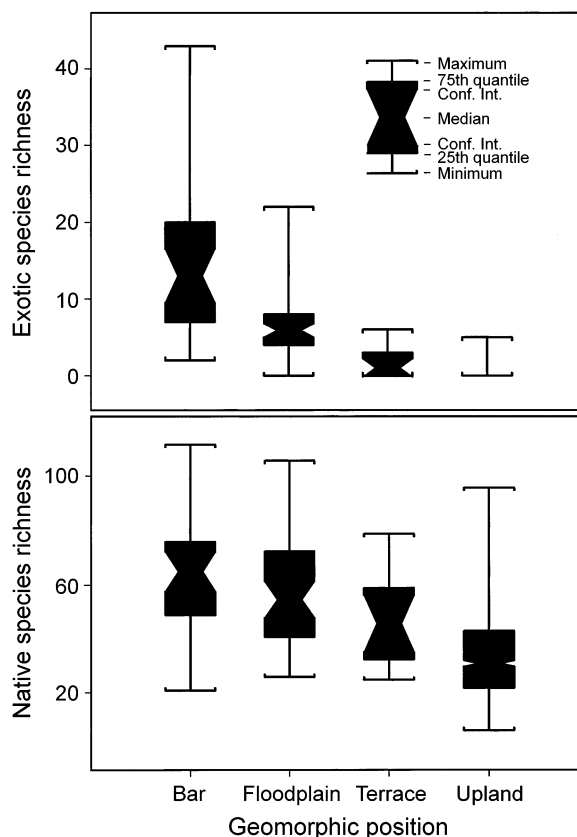


FIG. 1. Boxplots showing native and exotic species richness per 100 m<sup>2</sup> over four geomorphic positions in southern Appalachian riparian and upland areas. Because there were more upland plots compared to other geomorphic positions, and most upland plots had no exotic species, the median upland exotic species richness is zero with a relatively small variance.

than upland areas, with 55.19 vs. 31.28 native species/100 m<sup>2</sup>, and 8.05 vs. 0.20 exotic species (see Table 1 for statistical differences). Thus, riparian zones have roughly 40 times greater mean exotic species per plot (~8 more species on average) than upland areas. Upland areas had much lower percent flora exotic and percent cover of exotics compared to riparian areas (Table 1). Exotic species are also more frequently found in riparian zones, with 92.4% vs. only 24.7% of plots containing exotics (chi-square test of  $p_{\text{upland}} = p_{\text{riparian}}$ :  $P < 0.0001$ , chi-square = 209.45, df = 1).

### *Comparisons across geomorphic positions*

Native species richness, exotic species richness, exotic percent cover, and percent flora exotic all generally decreased from frequently flooded bars to less frequently flooded terraces in riparian zones (Table 1, Fig. 1). All pairwise differences between geomorphic positions were significant for all variables, except exotic percent cover and native species richness (Table 1). For exotic percent cover, the lack of significance for bars is probably the effect of frequent, abrasive

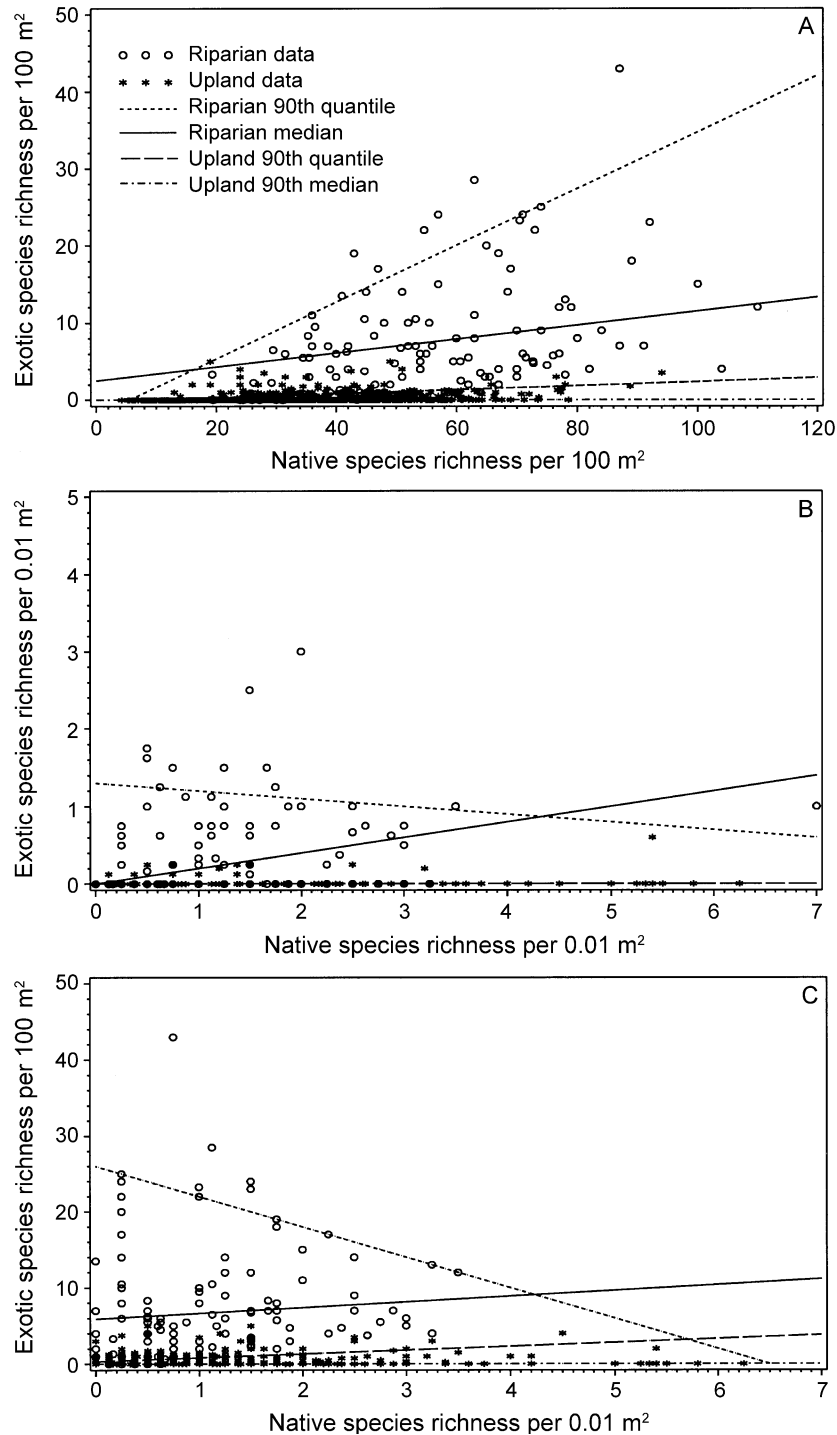


FIG. 2. The relationship between native and exotic species richness in riparian and upland plots: (A) at the 100-m<sup>2</sup> scale, (B) at the 0.01-m<sup>2</sup> scale, and (C) a comparison of native species richness at 0.01 m<sup>2</sup> and exotic species richness at 100 m<sup>2</sup>.

flooding that prevents any species, including exotics, from having high cover values in bars, regardless of species richness or invasion rates. For native species richness, terraces were not significantly different from

floodplains or uplands (Fig. 1). The frequency of plots with exotic species was significantly lower in less frequently flooded sites (chi-square = 217.53,  $P < 0.0001$ ,  $df = 3$ ).

TABLE 2. Summary of quantile regression results for the relationship between native and exotic species richness across spatial scales.

Scale	Riparian						Upland					
	Median			90th quantile			Median			90th quantile		
	Slope	P	R	Slope	P	R	Slope	P	R	Slope	P	R
A) Exotic species richness at the same scale as native species												
100 m <sup>2</sup>	<b>0.086</b>	<b>0.034</b>	0.048	<b>0.368</b>	<b>0.003</b>	0.16	NA	NA	NA	<b>0.027</b>	<b>&lt;0.001</b>	0.173
10 m <sup>2</sup>	0.063	0.323	0.022	<b>0.250</b>	<b>0.022</b>	0.13	NA	NA	NA	<b>0.020</b>	<b>&lt;0.001</b>	0.130
1 m <sup>2</sup>	0.061	0.159	0.036	0.240	0.123	0.05	NA	NA	NA	<b>0.019</b>	<b>&lt;0.001</b>	0.118
0.1 m <sup>2</sup>	<b>0.159</b>	<b>&lt;0.001</b>	0.103	0.067	0.853	0.003	NA	NA	NA	0	1.000	0
0.01 m <sup>2</sup>	<b>0.200</b>	<b>0.036</b>	0.050	-0.087	0.694	0.002	NA	NA	NA	NA	NA	NA
B) Exotic species richness at 100 m <sup>2</sup> vs. native species richness at different scales												
100 m <sup>2</sup>	<b>0.086</b>	<b>0.034</b>	0.048	<b>0.368</b>	<b>0.003</b>	0.164	NA	NA	NA	<b>0.027</b>	<b>&lt;0.001</b>	0.173
10 m <sup>2</sup>	<b>0.250</b>	<b>0.032</b>	0.039	0.286	0.198	0.069	NA	NA	NA	<b>0.051</b>	<b>&lt;0.001</b>	0.143
1 m <sup>2</sup>	0	1.000	0	0.291	0.499	0.016	NA	NA	NA	<b>0.105</b>	<b>0.032</b>	0.122
0.1 m <sup>2</sup>	0	1.000	0	-1.37	0.188	0.020	NA	NA	NA	<b>0.286</b>	<b>&lt;0.001</b>	0.097
0.01 m <sup>2</sup>	0.750	0.486	0.002	<b>-4.00</b>	<b>0.027</b>	0.053	NA	NA	NA	<b>0.500</b>	<b>0.001</b>	0.061

Notes: Values in boldface indicate statistical significance at the 95% probability level. NA = cases with too few exotics in upland areas to run the median relationship.

*Comparisons of riparian and upland areas across spatial scales*

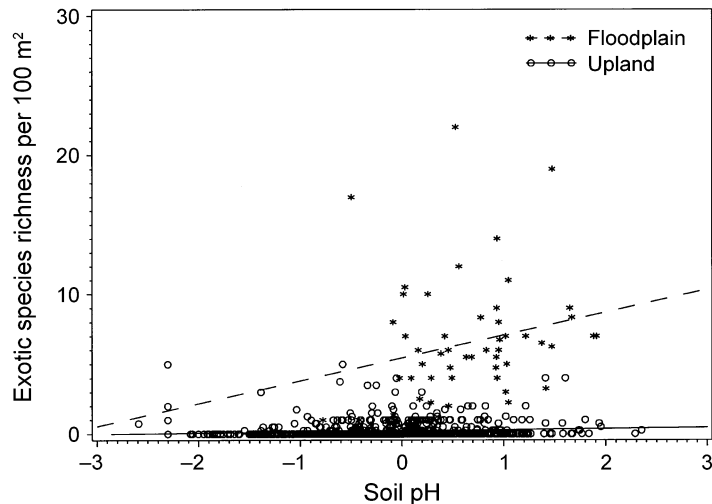
In riparian areas at the 100-m<sup>2</sup> scale, there was a significant positive relationship between native and exotic species richness at the 90th quantile and an insignificant relationship at the median (Fig. 2). This relationship gradually declined as scale decreased to 0.01 m<sup>2</sup> (Table 2), where the relationships at both the median and 90th quantile were insignificant in riparian areas. When we compared native species richness at 0.01 m<sup>2</sup> with exotic species richness at 100 m<sup>2</sup>, there was a significant negative relationship between native and exotic species richness in riparian areas at the 90th quantile. Overall, in riparian areas we saw a positive relationship between diversity and invasion at large scales, and either no relationship or a negative relationship at small scales depending on which scale we used to count exotic species (Table 2).

The relationship between native and exotic species invasion in upland areas at the 100-m<sup>2</sup> scale had a far lower slope than riparian areas, although there was a slight positive relationship at the 90th quantile, which remained at smaller scales. In general, there were far fewer exotic species in uplands plots, and little relationship between native and exotic species diversity.

*The effect of soil pH on exotic species richness in floodplains and uplands*

Soil pH had a positive effect on exotic species diversity in floodplains and little effect in uplands (Fig. 3). For any given pH, exotic species richness was higher in floodplains than uplands, suggesting that differences in soil fertility between floodplain and upland plots do not explain the observed differences in exotic species richness.

FIG. 3. The relationship between exotic species richness per 100 m<sup>2</sup> and soil pH in floodplain and upland plots.



## DISCUSSION

Riparian areas had greater cover, frequency, and species richness of exotic plants than upland areas. Within riparian areas, native and exotic species richness were both correlated with flooding. Upland areas had few exotic species (only 12 of the 1075 upland plots had >2 species/100 m<sup>2</sup> with 5 species maximum, whereas riparian areas had up to 43 exotic species/plot). Even comparisons of upland and riparian sites with similar soil pH showed fewer exotics on the uplands, suggesting that the differences cannot be explained by fertility differences alone. The low level of exotic species invasion in upland relative to riparian areas may be a consequence of low propagule pressure (and consequent dispersal limitation) of exotics, combined with lower disturbance frequency in upland sites.

At large scales (100 m<sup>2</sup>), there was a much stronger positive relationship between native and exotic species diversity in riparian areas than in upland areas. The differences in exotic species richness between riparian and upland areas were not explained by differences in soil fertility (pH) alone, and were pronounced even in comparisons of closed-canopy floodplain and upland forests where light availability was relatively similar. These results are consistent with the hypothesis that flooded areas are more immigration-driven than uplands due to a combination of increased disturbance, increased resource availability, and greater rates of propagule influx.

Levine's (2000) observation of a negative relationship between diversity and invasibility at small scales could be due in part to a sampling effect with the most diverse plots having the species most likely to competitively exclude invaders (Wardle 2001). In observational studies, however, a negative relationship between diversity and invasibility cannot be attributed to sampling effect because the presence of a competitive dominant would reduce both native and exotic species diversity (Wardle 2001). The negative relationship we observed between native richness at the 0.01-m<sup>2</sup> scale and maximal exotic richness at the 100-m<sup>2</sup> scale in riparian areas is consistent with Levine's findings and suggests that community saturation is more likely to occur at small scales. This negative relationship may occur because plants compete more directly for space and resources at small scales (Huston 1999). An alternative, related explanation is that at small scales, the small plot size relative to the size of the plants physically limits the number of plants that can fit, and high diversity of native or exotic species means that the maximum number of plants is already present. Thus, at the maximum quantile, there should always be a negative relationship between native and exotic diversity with very small plots (relative to plant size).

Recognition of an immigration-extinction framework leads to a prediction that, in immigration-driven

communities, there will be a positive relationship between native and exotic species richness reflecting the correlation in the influx of the two types of propagules. In extinction-driven systems, other factors, such as competition, dominate with the result that there is no basis for expecting a consistent relationship between native and exotic species other than resource complementarity, which is yet to be documented in natural systems and has not been strongly documented in experiments (Levine and D'Antonio 1999, Wardle 2001). Recognition of an immigration-extinction gradient complements the work of Davis et al. (2000) and Levine (2000) by recognizing the importance of both contributions while providing a larger framework for assessing the likelihood of invasion by exotic species.

Elton's well-known prediction (1958) that more diverse communities should be more difficult to invade was not born out, except possibly at the smallest scales in riparian zones. The results suggest that site factors such as disturbance, resource availability, and the availability of propagules, which positively influence native species richness, also have a positive influence on exotic species richness, rather than diversity or competitive exclusion per se limiting invasibility.

## ACKNOWLEDGMENTS

Thanks to Jason D. Fridley, Peter S. White, Dean L. Urban, Jack Weiss, and members of the University of North Carolina Plant Ecology Lab for providing valuable advice and comments throughout. Tom Stohlgren and Michael Huston provided helpful reviews of the manuscript. Funding for this research has been provided by Sigma Xi Grants-in-Aid of Research, the Southern Appalachian Botanical Society, the Nature Conservancy, the NC Heritage Trust, the USDA Forest Service, the Graduate School at UNC, and the UNC Ecology Curriculum. Special thanks to the Carolina Vegetation Survey (and especially Thomas Wentworth, Mike Schafale, and Alan Weakley) for the use of their data. Jack Weiss and Tom Philippi provided statistical assistance, and Jack Weiss provided code for the randomization tests. We thank New River State Park, The Nantahala Outdoor Center Nolichucky Outpost, Crescent Land Group, and the Hart Family for providing ongoing field support, river access, shuttles, and housing. This research has been made possible by numerous, dedicated field assistants.

## LITERATURE CITED

- Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. *Ecology* **77**:776–790.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* **88**:528–534.
- Elton, C. S. 1958. *The ecology of invasions by plants and animals*. Methuen, London, UK.
- Huston, M. A. 1994. *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press, Cambridge, UK.
- Huston, M. A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* **86**:393–401.
- Johansson, M. E., C. Nilsson, and E. Nilsson. 1996. Do rivers function as corridors for plant dispersal? *Journal of Vegetation Science* **7**:593–598.

- Kalkhan, M. A., and T. J. Stohlgren. 2000. Using multiscale sampling and spatial cross-correlation to investigate patterns of plant species richness. *Environmental Monitoring and Assessment* **64**:591–605.
- Knops, J. M. H., D. Tilman, N. M. Haddad, S. Naeem, C. E. Mitchell, J. Haarstad, M. E. Ritchie, K. M. Howe, P. B. Reich, E. Siemann, and J. Groth. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances, and diversity. *Ecology Letters* **2**:286–293.
- Levine, J. 2000. Species diversity and biological invasions: relating local process to community pattern. *Science* **288**:852–854.
- Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* **87**:15–26.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**:1522–1536.
- Lord, L. A., and T. D. Lee. 2001. Interactions of local and regional processes: species richness in tussock sedge communities. *Ecology* **82**:313–318.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Naeem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* **91**:97–108.
- Osterkamp, W. R., and C. R. Hupp. 1984. Geomorphic and vegetative characteristics along three northern Virginia streams. *Geological Society of America Bulletin* **95**:1093–1101.
- Peet, R. K., T. R. Wentworth, and P. S. White. 1998. A flexible, multipurpose method for recording vegetation composition and structure. *Castanea* **63**:262–274.
- Prieur-Richard, A. H., S. Lavorel, K. Grigulis, and A. Dos Santos. 2000. Plant community dynamics and invasion by exotics: invasion of Mediterranean old fields by *Coryza bonariensis* and *Coryza candensis*. *Ecology Letters* **2**:412–422.
- Proulx, M., and A. Mazumder. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* **79**:2581–2592.
- Scharf, F. S., F. Juanes, and M. Sutherland. 1998. Inferring ecological relationships from the edges of scatter diagrams: comparison of regression techniques. *Ecology* **79**:448–460.
- StataCorp. 2001. *Stata statistical software: release 7.0*. Stata Corporation, College Station, Texas, USA.
- Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* **69**:25–46.
- Stohlgren, T. J., K. A. Bull, Y. Otsuki, C. Villa, and M. Lee. 1998. Riparian zones as havens for exotic plant species. *Plant Ecology* **138**:113–125.
- Strahler, A. N. 1964. Quantitative geomorphology of drainage basins and channel networks. Chapter 4, Pages 39–76 in V. T. Chow, editor. *Handbook of applied hydrology*. McGraw-Hill, New York, New York, USA.
- Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* **78**:81–92.
- Trenbath, B. R. 1974. Biomass productivity of mixtures. *Advances in Agronomy* **26**:177–210.
- USDA, National Resources Conservation Service (NRCS). 2001. The PLANTS database, version 3.1. National Plant Data Center, Baton Rouge, Louisiana, USA. [Online, URL: <http://plants.usda.gov>.]
- Wardle, D. A. 2001. Experimental demonstration that plant diversity reduces invasibility; evidence of a biological mechanism or a consequence of sampling effect. *Oikos* **95**:161–170.
- Wilson, J. B., M. T. Sykes, and R. K. Peet. 1995. Time and space in the community structure of a species-rich limestone grassland. *Journal of Vegetation Science* **6**:729–740.
- Wilson, J. B., and A. J. Watkins. 1994. Guilds and assembly rules in lawn communities. *Journal of Vegetation Science* **5**:590–600.
- Wiser, S. K., R. B. Allen, P. W. Clinton, and K. H. Platt. 1998. Community structure and forest invasion by an exotic herb over 23 years. *Ecology* **79**:2071–2081.