

BIODIVERSITY AND EXOTIC SPECIES INVASION IN SOUTHERN APPALACHIAN  
RIPARIAN PLANT COMMUNITIES

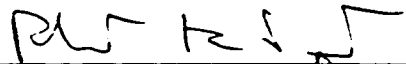
By  
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A dissertation submitted to the faculty of the University of North Carolina at Chapel Hill  
in partial fulfillment of the requirements for the degree of  
Doctor of Philosophy in the Curriculum in Ecology.


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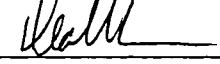
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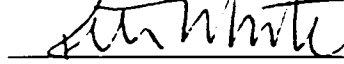
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## ABSTRACT

Rebecca L. Brown:

Biodiversity and exotic species invasion in southern Appalachian riparian plant communities

(Under the Direction of Robert K. Peet)

Although traditional ecological theory suggests that species-rich communities should be difficult to invade because resource use complementarity among the numerous species leaves fewer resources for the potential invader, the opposite has been found in many natural communities. I propose that the relationship between diversity and community invasibility depends on the degree to which community composition is driven by immigration versus extinction processes. Such processes include moderate disturbance and propagule pressure, which increase immigration, whereas competition and environmental stress limit community composition by creating local extinctions or inhibiting new species colonization. I expect that high rates of propagule pressure combined with disturbance due to flooding cause riparian plant communities to be disproportionately driven by immigration processes.

I tested relationships between native and exotic species diversity of vascular plant species and assessed patterns in riparian vegetation composition using multi-scale vegetation plots stratified by geomorphic position in riparian areas and adjacent forested uplands of the Little Tennessee, Upper New, and Nolichucky Rivers in Western North Carolina. I used

geomorphic position as a surrogate for flood intensity, with the more frequently flooded geomorphic positions hypothesized to be more strongly immigration-driven.

Native and exotic species richness were positively correlated with flooding in riparian zones. At the 100-m<sup>2</sup> scale, the relationship between native and exotic species richness in riparian areas was positive, whereas there was no relationship in uplands. However, at the 0.01-m<sup>2</sup> scale, there was a negative relationship between native and exotic diversity in riparian areas, likely because of community saturation at small spatial scales.

Species composition varied among the three rivers, likely due to the relative ease of dispersal within a single drainage compared to between watersheds, but was consistently correlated with geomorphic position and soil fertility.

To further substantiate the role of immigration processes in riparian plant communities, I assessed levels of propagule pressure using seed deposition traps stratified across geomorphic positions in riparian zones and found higher abundance and species richness of propagules, and a larger percentage propagules of exotic species with increased flooding. In an independent field experiment I demonstrated that propagule diversity has a positive effect on community diversity.

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Jack Weiss and Tom Philippi provided invaluable statistical support and helped me to learn SAS. Special thanks to Carol Ann McCormick for her knowledgeable advice and to Cottie Pasternak for ongoing assistance. Rogers McVaugh, Guy Nesom, and Ken Wurdack

added to plant identifications. Susan Whitfield's artistic expertise helped with illustrations and slides.

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Financial support was provided by Graduate School at the University of North Carolina, The Ecology Curriculum of the University of North Carolina, Sigma Xi Grants-in-Aid of Research, The USDA Forest Service, The Nature Conservancy, and The Southern Appalachian Botanical Society. Feldspar Corporation donated material for seed traps.

For stimulating discussions about ecology, friendship, and for making graduate school a lot more fun I would like to thank past and present members of the UNC Plant

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To my mother, father, sister, and brother



## PREFACE

Intact riparian areas without anthropogenic disturbance on large rivers in the Southern Appalachians have become alarmingly few and far between due to the concentration of human land uses in them. Those riparian areas that do remain intact are heavily invaded by exotic species. For example, the old-growth floodplains (surrounded by old-growth forest) in Linville Gorge, North Carolina are heavily invaded by *Microstegium vimineum* (Newell 1997), which was likely washed from roadsides or farmland adjacent to the river upstream in the watershed. Because of ridge top roads such as the Blue Ridge Parkway, exotic species have spread to the headwaters of streams with relatively undisturbed watersheds such as Lost Cove Creek in the Grandfather Ranger District. To my knowledge, there are no riparian areas remaining on large rivers in the southern Appalachians (and likely the entire eastern US if not the world) that have not experienced substantial human impacts leading to permanent changes such as biological invasions, hydrologic modification, agricultural development, or construction of transportation corridors.

Perhaps more troubling, most people have very little appreciation for the long-term consequences of human caused habitat destruction and species introductions. Ecologists themselves face enormous uncertainty about the long-term consequences of human activities, which makes it difficult to effectively argue for the preservation of natural ecosystems.

Understanding processes that control natural patterns of species composition, such as the diversity and invasibility of ecological communities, is a necessary first step towards anticipating the long-term ecological impacts of various human activities on biodiversity and better managing it. However, there has been some controversy in understanding these processes due to the presence of two schools of thought in ecology, each having a different view about which major processes structure plant communities. These contrasting processes have been called equilibrium vs. nonequilibrium (Chesson and Case 1986; Huston 1994), niche-assembled vs. dispersal-assembled (Hubbell 2001), and immigration vs. extinction (MacArthur and Wilson 1967; Tilman 1982) among others.

The misapplication of these two sets of processes has led to confusion about patterns seen in experiments as compared to those seen in nature. For example, experiments have shown that diverse communities should be more difficult to invade in theory because of increased complementarity of resource use (Tilman 1997; Crawley et al. 1999; Knops et al. 1999; Levine and D'Antonio 1999; Levine 2000; Naeem et al. 2000; Prieur-Richard et al. 2000; Symstad 2000). However, I have observed that riparian zones in the southern Appalachians are paradoxically both incredibly diverse (at times with more species per 0.01 ha than any other place yet observed in the Carolinas) and have extremely high rates of exotic species invasion. My goal has been to clarify the confusion about the roles of immigration versus extinction processes in ecological communities by suggesting that both affect communities, but at different rates that vary with respect to disturbance, resource supply, and propagule supply. In this dissertation I explore the gradient of conditions that determine which of these two sets of processes drives southern Appalachian riparian areas. I hope that by understanding the conditions in natural communities that influence the

importance of these two sets of processes, we can increase their predictive power, and thus make them more useful tools for managing biodiversity.

The initial purpose of this study was to describe the vegetation of southern Appalachian riparian areas across a wide geographic range and to describe species composition relationships with environmental factors. Providing a more complete description of vegetation patterns and their underlying processes in southern Appalachian riparian plant communities will help to provide data for management and conservation of southern Appalachian riparian areas, which are critically under-studied and under-protected. While surveying southern Appalachian plant communities, I observed the correlations between of diversity, exotic species invasion, and flooding that inspired the theoretical ideas in this study.

Each chapter has been written as a separate paper. In Chapter 1, I propose a conceptual framework called the immigration-extinction gradient, which can be used to help explain the relationship between native species richness and exotic species diversity across an array of different systems, and I show how propagule pressure and disturbance affect position on the gradient. In Chapter 2, I propose that riparian areas of the southern Appalachians are driven by immigration processes, and I use the immigration-extinction gradient to explain relationships that I documented between native and exotic species diversity across geomorphic positions in the southern Appalachians. In Chapter 3, I explore relationships between vegetation and environment in riparian communities of three southern Appalachian rivers, and I classify the riparian vegetation communities on these rivers as a means of organizing and placing in context other research, and as a tool for inventory and monitoring for conservation purposes. In Chapter 4, I document variation in levels of

propagule pressure across geomorphic positions on the three rivers in order to provide further clarification of the variation in immigration processes in riparian plant communities. Finally, in Chapter 5, I show how experimentally manipulated variations in seed abundance and seed richness can affect diversity in artificially generated communities of annual plants.

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## Chapter 1

### THE IMMIGRATION-EXTINCTION GRADIENT

#### ABSTRACT

I propose that communities can be organized along a gradient from immigration- to extinction-driven, and that position along the gradient determines patterns of species diversity and invasibility in the community. Immigration-driven communities are those where processes that allow new species to enter the community are dominant. Such processes include disturbance, propagule pressure, and resource availability. Conversely, extinction-driven communities are those where community membership is limited to a specific pool of well-adapted species. These communities can be limited by competition, high levels of disturbance, or environmental stress. Propagule pressure and disturbance play a major role in positioning communities along this gradient. I present a three-dimensional conceptual model in which the relationship between propagule pressure, disturbance, position on the immigration-extinction gradient, and expected diversity is shown. The most immigration-driven communities on the model are those with chronic, low-intensity disturbance and high propagule pressure.

## INTRODUCTION

There has been ongoing debate about which processes play the most important roles in driving ecological communities. This debate has been referred to in a variety of ways including: equilibrium vs. nonequilibrium dynamics (e.g. Huston 1994 vs. Tilman 1982, 1988); individualistic movement of species vs. communities Gleason (1926) vs. Clements (1916); stochastic vs. deterministic; or niche assembled vs. dispersal assembled (e.g. Hubbell 2001). The general question being debated is whether communities are composed of predictable sets of organisms resulting from balanced interactions either via competition or facilitation (“the balance of nature”), or whether communities are random assemblages of species with individualistic patterns of distribution (Gleason 1926; Nicolson and McIntosh 2002) and little interdependence.

I propose that both views are correct, and that rather than debating which set of processes is most important, ecologists should instead work toward understanding to what extent each set of processes is structuring any given community, and why. I propose that communities be organized along a gradient based on which of these sets of processes structures the community. Position on this gradient could be helpful for understanding some of the great debates in current ecological thinking, such as the relationship between diversity and productivity, or between diversity and invasibility. The negative effects of diversity on community invasibility (Elton 1958; Tilman 1997; Knops et al. 1999; Crawley et al. 1999; Levine and D'Antonio 1999; Levine 2000; Naeem et al. 2000; Prieur-Richard et al. 2000; Symstad 2000) and the positive effects of diversity on productivity due to resource use complementarity (e.g. Tilman et al. 1996; Hector et al. 1999; Kinzig et al. 2001) that have

been debated are only appropriate when considered from the niche-assembled side of the gradient.

For the purpose of this dissertation, I call this gradient the 'immigration-extinction' gradient. The terms immigration and extinction are derived from MacArthur and Wilson's Equilibrium Theory of Island Biogeography (1967), which predicts island biodiversity based on rates of immigration (determined by distance from island to mainland) and local extinction (determined by island size). I propose that communities can be organized on the immigration-extinction gradient on the basis of factors such as disturbance, propagule pressure, competition, and environmental stress.

Extinction processes are those that create local extinctions or prevent new species from entering a community by restricting community membership to a particular subset of the available species pool consisting of well-adapted, compatible, competitive species (Elton 1958). These include competition, disturbance, and environmental stress. Niche space is partitioned among the extant species through either coevolution or an extended period of competitive sorting. The classical climax community described by Clements (1916) belongs in the 'extinction-driven category. In such communities, competition, environmental stress, and recurrent disturbance restrict the pool of species to those species that are locally competitive or that can adapt to the stress or disturbance.

Conversely, immigration processes are those that allow a broader subset of species to establish (MacArthur and Wilson 1967; Shmida and Ellner 1984; Gaines and Roughgarden 1985). These include propagule pressure, the diversity and abundance of incoming propagules (Williamson and Fitter 1996), and disturbance (Connell 1978; Huston 1994), which reduces competitive intensity. Note that disturbance plays a dual role on the

immigration-extinction gradient, both eliminating some species (extinction) and facilitating the invasion of new species (immigration) by freeing up resources (sensu Davis et al. 2000), as posited by the Intermediate Disturbance Hypothesis (Connell 1978). An immigration-driven community is one in which membership is not restricted because pressure from outside propagules is so high that a few establish in otherwise poor conditions, or because factors like disturbance disrupt the processes that would otherwise restrict membership. In other words, an immigration-driven community might either be “undersaturated in terms of niche space” (Gaines and Roughgarden 1985) or subject to “mass effects” (Shmida and Ellner 1984; Shmida and Wilson 1985) from outside propagules. In either case, the immigration-driven community is far more susceptible to invasion than the extinction-driven community.

The position of communities on the immigration-extinction gradient can vary temporally and spatially across the landscape. For example, an early successional community is more immigration-driven than a later successional community in which competitive sorting has taken place, as described in the “competitive sorting model of succession” (Magalef 1963; Margalef 1968). In this model, the species composition of the initial community is largely a matter of chance. Over time, as competition between species increases, poor competitors are forced out and the composition of the community becomes more predictable and more extinction-driven (Peet 1992). The spatial variation of communities across the immigration-extinction gradient depends on spatial patterns of disturbance, propagule pressure, and environmental stress.

Propagule pressure is an important characteristic of immigration-driven communities that is often overlooked because it is difficult to quantify. Nevertheless, relative propagule



pressure levels can be estimated for many areas at both local and landscape scales. A number of studies have documented patterns in seed distribution relative to topography and availability of seed transport mechanisms such as rivers and animals ( Carlquist 1967; Howe and Smallwood 1982; Harvey 2000; Schneider and Sharitz 1988; Skoglund 1990; Nilsson and Grelsson 1995). There are two components of propagule pressure that have potentially different effects on the community: species richness and density of seed per species (Williamson and Fitter 1996). The more seeds available per species, the more effective that species will be at establishment, even in non-ideal environments (i.e. ‘mass effect’; Shmida and Ellner 1984). However, the more species of propagules there are available to a community (regardless of abundance of propagules per species), the greater the likelihood that more species will establish in the community. For the purpose of this model, I am considering the two components in unison. By high propagule pressure I mean that more individuals of more species can establish in a community, whereas low propagule pressure means that fewer individuals of fewer species can establish.

## CONCEPTUAL MODEL

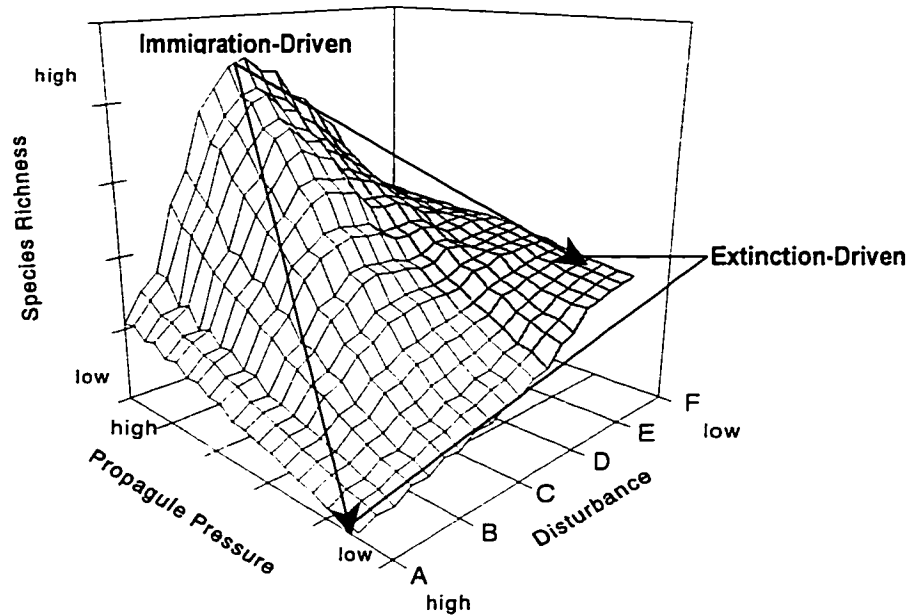
Disturbance and propagule pressure interact because disturbance creates openings and makes resources available in a community, thereby allowing incoming propagules to establish. If we jointly consider the propagule pressure and disturbance gradients (Figure 1.1), predicted species richness becomes a three-dimensional response with relative low points where there is low propagule pressure and either high disturbance (due to the destruction caused by disturbance) or very low disturbance (due to competition). At high levels of propagule pressure, there is a unimodal relationship between species richness and

disturbance, whereas at low levels of propagule pressure, species richness increases monotonically with decreasing disturbance. The positive effect of disturbance on species number described by the Intermediate Disturbance Hypothesis is a limiting case that occurs only when there are sufficient propagules to take advantage of the reduced level of competition created by the disturbance (Figure 1.1A). When the highest levels of disturbance are ignored, there is a gradient from immigration- to extinction-driven communities (Figure 1.1B). Extremely high disturbance and high environmental stress create an extinction-driven community. With higher propagule pressure there is an increase in species despite concurrent extinction processes (such as where disturbance is very high or very low) due to mass effects (Shmida and Ellner 1984).

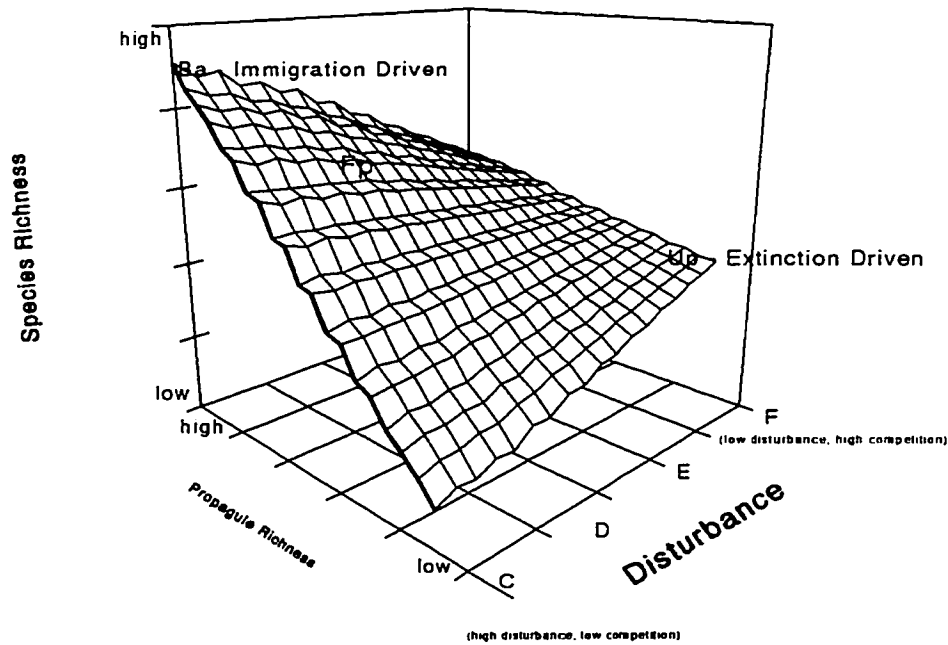
Figure 1.1 is similar to Grime's model of species richness in herbaceous vegetation (Grime 1979; Lord and Lee 2001) in that it shows the role of propagule availability on a disturbance gradient. The models differ when propagule pressure is low, and species persistence is more important in determining community structure than is establishment of new individuals with the result that species richness is highest on the least disturbed sites where species have been able to persist.

**Figure 1.1.** A) The interacting effect of propagule pressure and disturbance on species richness showing how the strength of the unimodal relationship between species richness and disturbance varies with propagule pressure. B) An enlarged portion of the shaded area in Figure 1.1A (C to F on the disturbance axis) with the highest levels of disturbance removed so as to show a gradient from immigration- to extinction-driven communities.

A.



B.



### *Predictions based on the Immigration-Extinction Gradient*

Logical consequences that result from viewing communities as distributed along the immigration-extinction gradient are shown in Table 1.

(1) On sites with high propagule pressure and low disturbance, exotic species and native species not optimally adapted to a site (i.e. transients sensu Grime 1998) can be expected to arrive and be maintained through mass effects (Shmida and Ellner 1984; Pulliam 1988). On these sites we would expect both species richness and invasibility to be high.

(2) In contrast, under conditions of low disturbance and moderate propagule pressure (that adequate to replace existing species), competitive processes are more important in determining community composition. Under these circumstances, equilibrium models based on resource availability and competition (sensu Tilman 1982) are more effective for predicting community structure.

(3) When propagule pressure is limiting and disturbance low, the community is structured by whatever species arrive, and competitive models only work to the extent that the most competitive of what arrives may dominate, but the optimal competitor may never arrive. Thus, the community might be maintained in a recruitment-limited state of competitive disequilibrium (Gaines and Roughgarden 1985; Clark et al. 1998; Hubbell et al. 1999). In this low propagule pressure scenario, diversity could be higher or lower than the equilibrium level predicted by competitive models, with resultant community composition less predictable.

**Table 1.1.** Processes which influence community composition at various propagule pressure and disturbance levels.

	<i>Disturbance High (intense, frequent)</i>	<i>Medium</i>	<i>Low (mild, rare)</i>
<i>High propagule pressure (high diversity and abundance of propagules of species from inside and outside the system)</i>	Some transients but mainly only species that can tolerate high disturbance	High invasion rates, transients and immigrants form a large component of species diversity	Mass effects Competitive effects are important but transients contribute to species diversity
<i>Medium propagule pressure (enough propagules to replace species already in system)</i>	Only species that can tolerate disturbance persist	Moderate species diversity with some augmentation of competitive species by ruderals due to disturbance and propagule availability	Competitive equilibrium – diversity determined by habitat factors such as resource levels
<i>Low propagule pressure (recruitment limited, not enough propagules to replace species already in system)</i>	Few to no species present (since no replacement for those damaged by disturbance)	Few species (since little replacement after disturbance), very much a recruitment limited system	Competitive equilibrium with some empty niches as best adapted species may be recruitment limited

## DISCUSSION

The idea that plant communities might be sorted in terms of their ambient levels of propagule pressure is critical to the immigration-extinction gradient, as it is to the Equilibrium Theory of Island Biogeography (MacArthur and Wilson 1967), Supply-side Ecology (Gaines and Roughgarden 1985), and the metapopulation concept of source-sink populations (Pulliam 1988). Nevertheless, it is often ignored because propagule pressure is typically considered a stochastic and unpredictable phenomenon. However, there may be large, measurable, and predictable variations in propagule pressure at both large and small scales as one moves across the landscape. At small scales the existing species and microtopographic features can influence propagule pressure, whereas at large scales factors such as topography, presence of different types of transport corridors, edge effects, human activities, and animal activities may all influence the amount of propagule pressure predicted to occur at a given site. A better understanding of the factors that affect propagule pressure in communities would help ecologists to have a better understanding of how communities are assembled.

The immigration-extinction gradient provides a method for organizing communities that unifies some divergent theoretical approaches. The predictions that follow from investigation of community variation relative to the immigration-extinction gradient approach are not new; they draw from examinations of previously tested theories including the Intermediate Disturbance Hypothesis, the Competitive Exclusion Principle, and the Equilibrium Theory of Island Biogeography. From as far back as Clements's climax communities (1916) and Gleason's Individualistic Hypothesis (1926), ecologists have been aware that there are two general sets of processes at work structuring communities:

competitive exclusion and immigration. The immigration–extinction gradient helps us to examine real communities found in a wide array of environments and to consider which processes are most important for them.

Finally, we must recognize, as did Davis et al. (2000), that communities are dynamic. They shift along the immigration-extinction gradient as disturbance regimes and propagule pressure change due to factors such as human activities. On a global scale, the increase of disturbance and fragmentation by humans and the transport of species from their natural habitats have pushed communities toward the immigration side of the immigration-extinction gradient with the consequence that exotic species invasion and species turnover rates have increased significantly.

## Chapter 2.

### DIVERSITY AND INVASIBILITY OF SOUTHERN APPALACHIAN PLANT COMMUNITIES

#### ABSTRACT

I propose that the relationship between diversity and community invasibility depends on the degree to which community composition is driven by immigration versus extinction processes. When immigration processes such as propagule pressure and moderate disturbance dominate, I predict a positive relationship between diversity and exotic species invasion. Only when immigration is low relative to extinction processes such as competition should species saturation produce a negative correlation between diversity and invasibility. Moreover, saturation should be more likely to be observed at smaller scales where individual plants compete directly for space.

I tested these predictions by comparing exotic and native species diversity of vascular plants across 5 spatial scales in riparian and upland plant communities in the southern Appalachians. I found a positive relationship between species diversity and exotic invasion in the propagule-rich 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, the positive relationship between native and exotic species diversity became stronger as the scale of observation decreased. 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.

## 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 apparent ease of exotic plant invasion into species-rich communities varies with 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 ( $0.035 \text{ m}^2$ ), 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 species-rich grasslands to operate only at small scales where herbs compete directly and where there is no room for substitution among ecological equivalents.

Davis et al. (2000) and Wardle (2001) have offered an alternative explanation for the inconsistent relationship between richness of native and exotic species. They suggested that the underlying mechanism controlling invasibility of a community is net resource availability (i.e. the resources not in use by plants in a community). 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 versus immigration processes clarifies the basis for 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 moderate disturbance facilitate entry of new species into the community and are here called immigration processes, whereas phenomena such as competition and chronic environmental stress selectively remove or limit less competitive species and are here called extinction processes. Where extinction dominates leading to resource complementarity or space limitation, which is particularly likely at small scales owing to direct plant interactions, I 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 (Lord and Lee 2001), diversity and invasibility should be high and positively related.

Riparian corridor vegetation can experience a broad range of immigration and extinction pressures. Propagule pressure varies dramatically with flood frequency and flow conditions, largely because floodwaters carry seeds from diverse habitats located throughout a watershed (Johansson et al. 1996). Similarly, disturbance frequency and competitive intensity vary with the amount of flood scour and sediment deposition. In this study I take advantage of a large dataset spanning much of the variation in southern Appalachian forests of North Carolina to test for a large geographic region the expectation that the relationship between exotic and native species richness will be significantly more pronounced in immigration controlled riparian systems than the more stable, mature (relatively extinction-controlled) uplands. I then look in greater depth at riparian systems spanning a range of geomorphic surfaces correlated with flood disturbance frequency and presumably propagule pressure. I 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 where immigration processes are important. In the adjacent uplands I expect lower diversity and invasion due to a lack of immigration processes and the presence of extinction processes related to competition.

I test Levine's 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 5 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 invisibility could be positively correlated owing to both being correlated with site fertility (Burke and Grime 1996; Proulx et al. 1998; Huston 1994), I evaluate the role that soil fertility plays on invasibility in our system. Specifically, I assess the relationship between soil pH on exotic species diversity in riparian and upland areas.

## METHODS

### *Vegetation Plots*

Species richness and exotic invasion of vascular plant species were compared in southern Appalachian riparian and upland areas using data from 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 in stream order from 3 to 5 (Strahler 1964). Within riparian areas, plots were stratified across geomorphic positions (including uplands) using a total of 21 transects across the three rivers. Additional plots were added from the Carolina Vegetation Survey database.

A total of 105 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 I used for our analysis range from 100-m<sup>2</sup> to

0.01-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-year 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 every year, floodplains with approximately 1 to 5-year flood intervals, and terraces with greater than 5-year flood intervals (Osterkamp and Hupp 1984). Flood frequency was determined from the height of the plot above the river, river width, and gauging station data. Uplands include all sites not exposed to flooding. For this analysis I 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, I 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 soil below the leaf litter (the 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 4 samples for a 1000-m<sup>2</sup> plot). Soil analyses were conducted by Brookside Laboratory, New Knoxville, Ohio, using Mehlich III extraction. Results included cation exchange capacity, pH, estimated nitrogen release (N), easily extractable phosphorus (P), exchangeable cations (Ca, Mg, K, Na), percent base saturation (%Ca, Mg, K, Na), extractable micronutrients (ppm B, Fe, Mn, Cu, Zn, Al), soluble sulfur, and bulk density

values . Ultimately I 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). I used four measures to assess the level of exotic species invasion: exotic species richness (for a range of scales 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 of percent covers of exotic species per 100-m<sup>2</sup> (called exotic percent cover), and percent flora exotic (calculated by dividing species richness of exotic plants by total plot species richness at 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 using code written by Jack Weiss of the Curriculum in Ecology at the University of North Carolina. For pairwise combinations of geomorphic positions, observations were randomized among the positions and the difference between the two randomly assigned groups was calculated. This procedure was repeated

10,000 times to generate an empirical null distribution, which was used to calculate a P-value for the actual difference between the groups. The difference was considered significant if the P-value was less than 0.05/28 (95% probability 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 (Scharf et al. 1998). 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, I 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 (0.01-m<sup>2</sup>) plots (there were only 12 upland plots with any exotic species found at the 0.01-m<sup>2</sup> scale, whereas there were 238 plots with exotics at 100-m<sup>2</sup>). If native species competitively inhibit invasive species, this is most likely to be observed at small scales where plants directly interact, with high numbers 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 (given that plots were selected to have a relatively homogenous within plot community), such that the relationship between exotic species richness at the 100-m<sup>2</sup> scale and native species richness at 0.01-m<sup>2</sup> can assay of the effects of diversity at small scales on invasion despite the scale differences.

I used 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. I used the `bsqreg` quantile regression routine in Stata (StataCorp 2001) to create bootstrapped estimates of the regression slope and intercept at the median and 90<sup>th</sup> percentile (with 10,000 bootstrapped replicates). I 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.

To determine the role of flood dispersal processes as compared to local resource levels or site productivity on invasibility, I 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 (Davis et al. 2000; Huston 1994), so I 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 I restricted the riparian sites to floodplains, excluding scour bars because they have substantially higher light levels (another factor that may influence invasion), whereas floodplains and upland forests (both with closed canopies) have more similar light levels. I also excluded terraces because they are transitional between riparian and upland habitats and rarely, if ever flood.



## RESULTS

### *Comparisons of Riparian and Upland Areas*

Riparian areas have significantly higher species diversity of both native and exotic species ( $P < 0.0001$ ) than upland areas, with 55.19 native species per 100-m<sup>2</sup> compared to 31.28 species, and 8.05 exotic species compared to 0.20 (statistical differences in Table 2.1). Thus, riparian zones have around 40 times greater mean exotic species per plot (around 8 more species on average) than upland areas. Upland areas had much lower percent flora exotic and percent cover exotic compared to riparian areas (Table 2.1). Exotic species are also more frequently found in riparian zones, with 92.4% of riparian plots containing exotic species compared to only 24.7% of the upland plots (Chi-square test of  $p_{\text{upland}} = p_{\text{riparian}}$ :  $P < 0.0001$ , Chi-square = 209.45,  $df = 1$ ).

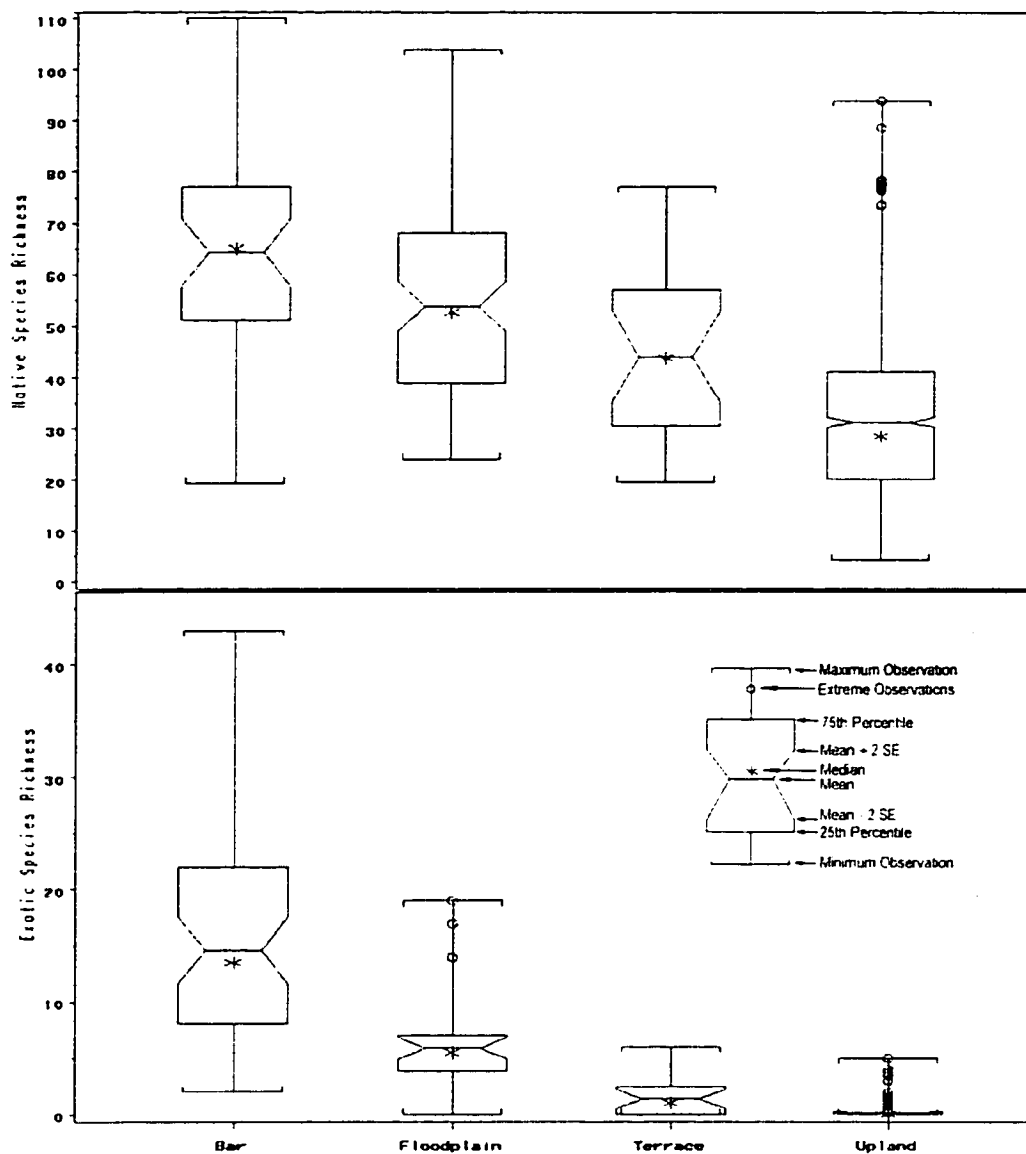
### *Comparisons Across Geomorphic Positions*

Native species richness, exotic species richness, exotic percent cover, and percent flora exotic all generally decreased from frequently flooded to less frequently flooded sites in riparian zones, and the frequency of plots with exotic species was significantly lower in less frequently flooded sites (Chi-square = 217.53,  $P < 0.0001$ ,  $df = 3$ ) as shown in Table 2.1 and Figure 2.1. The decreases in native and exotic species across bars (most flooded), floodplains, terraces (least flooded), and uplands (not flooded) were significant for all variables except exotic percent cover and native species richness (Table 2.1). For exotic percent cover, the differences between bars and floodplains and between floodplains and terraces were insignificant. The lack of significance for bars is probably the effect of

**Table 2.1.** Summary data for native and exotic species for riparian and upland plots and across geomorphic positions (results in bold are means  $\pm$  1 SE). P-values shown are the results of the randomization test for pair-wise differences among geomorphic positions. A \* indicates statistical significance at the 95% probability level with a Bonferroni correction.

	<i>Frequency Exotics Present</i>	<i>Mean Native Species Richness</i>	<i>Mean Exotic Species Richness</i>	<i>% Cover of Exotics</i>	<i>% Flora exotic</i>
<i>All Upland (n=1075)</i>	266 plots (24.74%)	<b>31.28 <math>\pm</math> 0.44</b> Bar P<0.001* Floodp. P<0.001* Terrace P<0.001*	<b>0.20 <math>\pm</math> 0.02</b> Bar P<0.001* Floodp. P<0.001* Terrace P<0.001*	<b>0.20 <math>\pm</math> 0.03</b> Bar P<0.001* Floodp. P<0.001* Terrace P<0.001*	<b>0.52 <math>\pm</math> 0.05</b> Bar P<0.001* Floodp. P<0.001* Terrace P<0.001*
<i>All Riparian (n=105)</i>	97 plots (92.38%)	<b>55.19 <math>\pm</math> 1.96</b> Upland P<0.001*	<b>8.05 <math>\pm</math> 0.72</b> Upland P<0.001*	<b>22.08 <math>\pm</math> 2.73</b> Upland P<0.001*	<b>11.59 <math>\pm</math> 0.79</b> Upland P<0.001*
<i>Bar (n=35)</i>	35 plots (100%)	<b>61.18 <math>\pm</math> 3.61</b> Floodp. P=0.128 Terrace P=0.006	<b>13.77 <math>\pm</math> 1.55</b> Floodp. P<0.001* Terrace P<0.001*	<b>16.38 <math>\pm</math> 2.90</b> Floodp. P=0.020 Terrace P=0.021	<b>17.43 <math>\pm</math> 1.35</b> Floodp. P<0.001* Terrace P<0.001*
<i>Floodplain (n=56)</i>	56 plots (96.40%)	<b>54.58 <math>\pm</math> 2.57</b> Terrace P=0.058	<b>6.29 <math>\pm</math> 0.59</b> Terrace P<0.001*	<b>30.57 <math>\pm</math> 4.46</b> Terrace P=0.004	<b>10.29 <math>\pm</math> 0.87</b> Terrace P<0.001*
<i>Terrace (n=16)</i>	10 (62.50%)	<b>44.20 <math>\pm</math> 4.32</b>	<b>1.69 <math>\pm</math> 0.47</b>	<b>4.83 <math>\pm</math> 3.56</b>	<b>3.33 <math>\pm</math> 1.12</b>

**Figure 2.1.** Native and exotic species richness per 100-m<sup>2</sup> over three geomorphic positions. Because there were many more upland plots, and many of them had no exotics, the mean for exotic species richness in uplands is close to zero and the variance is smaller than the other geomorphic positions. Extreme values are those outside the interquartile range.



frequent abrasive flooding and the consequent rocky substrate 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 (Figure 2.1).

### *Comparisons of Riparian and Upland Areas Across Spatial Scales*

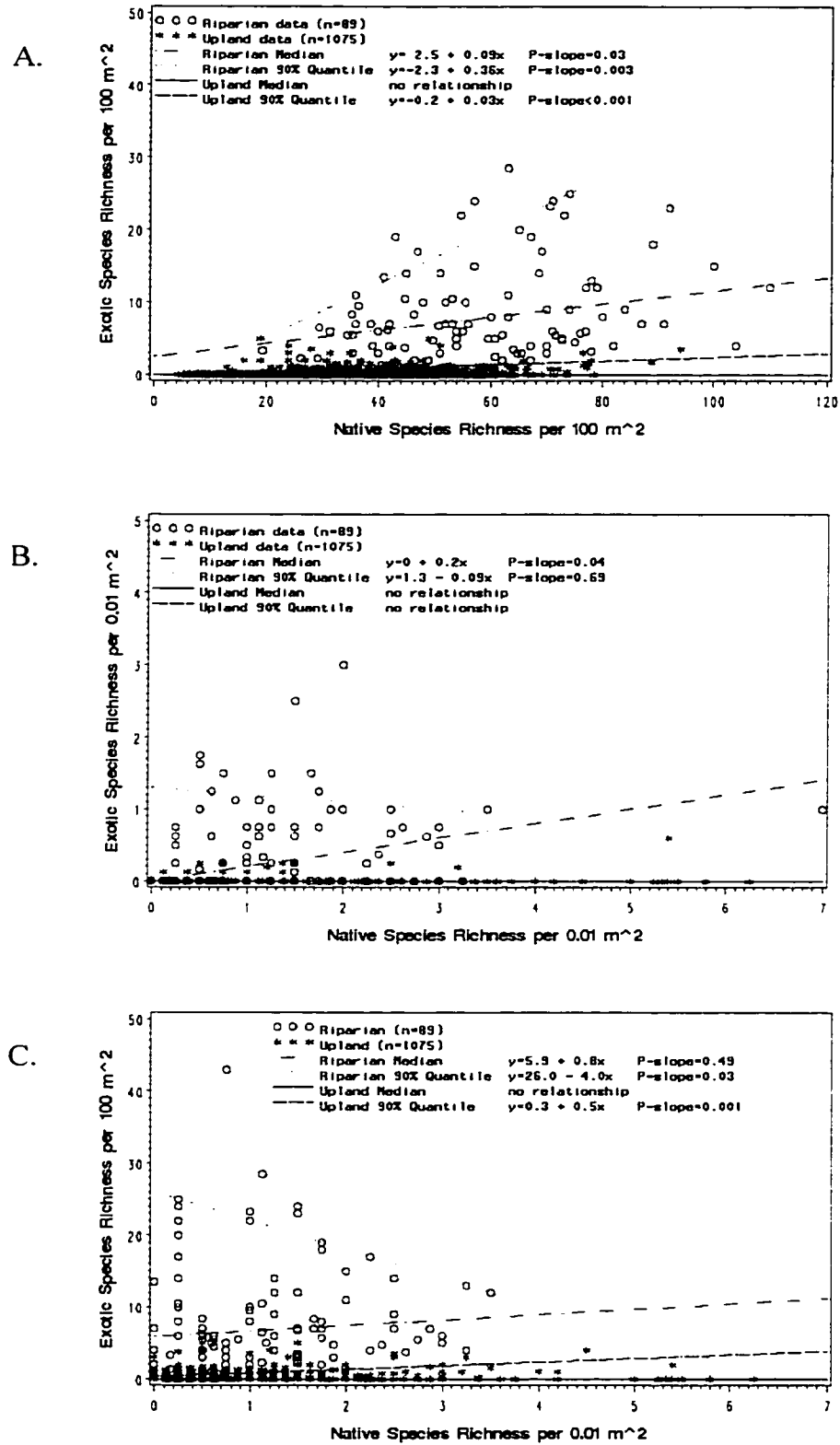
In riparian areas at the 100-m<sup>2</sup> scale, there was a significant positive relationship between native and exotic species richness at the 90<sup>th</sup> quantile and an insignificant relationship at the median (Figure 2.2). This relationship gradually declined as scale decreased until the 0.01-m<sup>2</sup> scale (Table 2.2), where the relationships at both the median and 90<sup>th</sup> quantile were insignificant in riparian areas. When I 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 90<sup>th</sup> quantile. Overall, in riparian areas I saw a positive relationship between diversity and invasion at large scales and either no relationship at small scales or a negative relationship at small scales depending on which scale I used to count exotic species (Table 2.2).

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 90<sup>th</sup> 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. For example, at the smallest scale, only 12 of the 1075 plots had any exotic species.

**Table 2.2.** Summary of quantile regression results for the relationship between native and exotic species richness across spatial scales. Cases with too few exotics in upland areas to run the median relationship are indicated with 'NA'.

<b>Exotic Species Richness at the Same Scale as Native Species</b>								
	<b>Riparian</b>				<b>Upland</b>			
	<i>Median</i>		<i>90<sup>th</sup> quantile</i>		<i>Median</i>		<i>90<sup>th</sup> quantile</i>	
<b>Scale</b>	<i>Slope</i>	<i>P</i>	<i>Slope</i>	<i>P</i>	<i>Slope</i>	<i>P</i>	<i>Slope</i>	<i>P</i>
<b>100 m<sup>2</sup></b>	<b>0.09</b>	<b>0.03</b>	<b>0.36</b>	<b>0.003</b>	NA	NA	<b>0.03</b>	<b>&lt;0.001</b>
<b>10 m<sup>2</sup></b>	0.06	0.32	<b>0.25</b>	<b>0.02</b>	NA	NA	<b>0.02</b>	<b>&lt;0.001</b>
<b>1 m<sup>2</sup></b>	0.06	0.16	0.24	0.123	NA	NA	<b>0.02</b>	<b>&lt;0.001</b>
<b>0.1 m<sup>2</sup></b>	<b>0.16</b>	<b>&lt;0.001</b>	0.07	0.85	NA	NA	0	1
<b>0.01 m<sup>2</sup></b>	<b>0.2</b>	<b>0.04</b>	-0.09	0.69	NA	NA	NA	NA
<b>Exotic Species Richness at 100 m<sup>2</sup> Versus Native Species Richness at Different Scales</b>								
	<b>Riparian</b>				<b>Upland</b>			
	<i>Median</i>		<i>90<sup>th</sup> quantile</i>		<i>Median</i>		<i>90<sup>th</sup> quantile</i>	
<b>Scale</b>	<i>Slope</i>	<i>P</i>	<i>Slope</i>	<i>P</i>	<i>Slope</i>	<i>P</i>	<i>Slope</i>	<i>P</i>
<b>100 m<sup>2</sup></b>	<b>0.09</b>	<b>0.03</b>	<b>0.36</b>	<b>0.003</b>	NA	NA	<b>0.03</b>	<b>&lt;0.001</b>
<b>10 m<sup>2</sup></b>	<b>0.25</b>	<b>0.032</b>	0.28	0.20	NA	NA	<b>0.05</b>	<b>&lt;0.001</b>
<b>1 m<sup>2</sup></b>	0	1	0.29	0.50	NA	NA	<b>0.25</b>	<b>0.032</b>
<b>0.1 m<sup>2</sup></b>	0	1	-1.37	0.19	NA	NA	<b>0.29</b>	<b>&lt;0.001</b>
<b>0.01 m<sup>2</sup></b>	0.8	0.49	<b>-4.0</b>	<b>0.03</b>	NA	NA	<b>0.5</b>	<b>0.001</b>

**Figure 2.2.** 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) as seen in a comparison of native species richness at 0.01-m<sup>2</sup> and exotic species richness at 100-m<sup>2</sup>.



### *The Effect of Soil pH on Exotic Species Richness in Floodplains and Uplands*

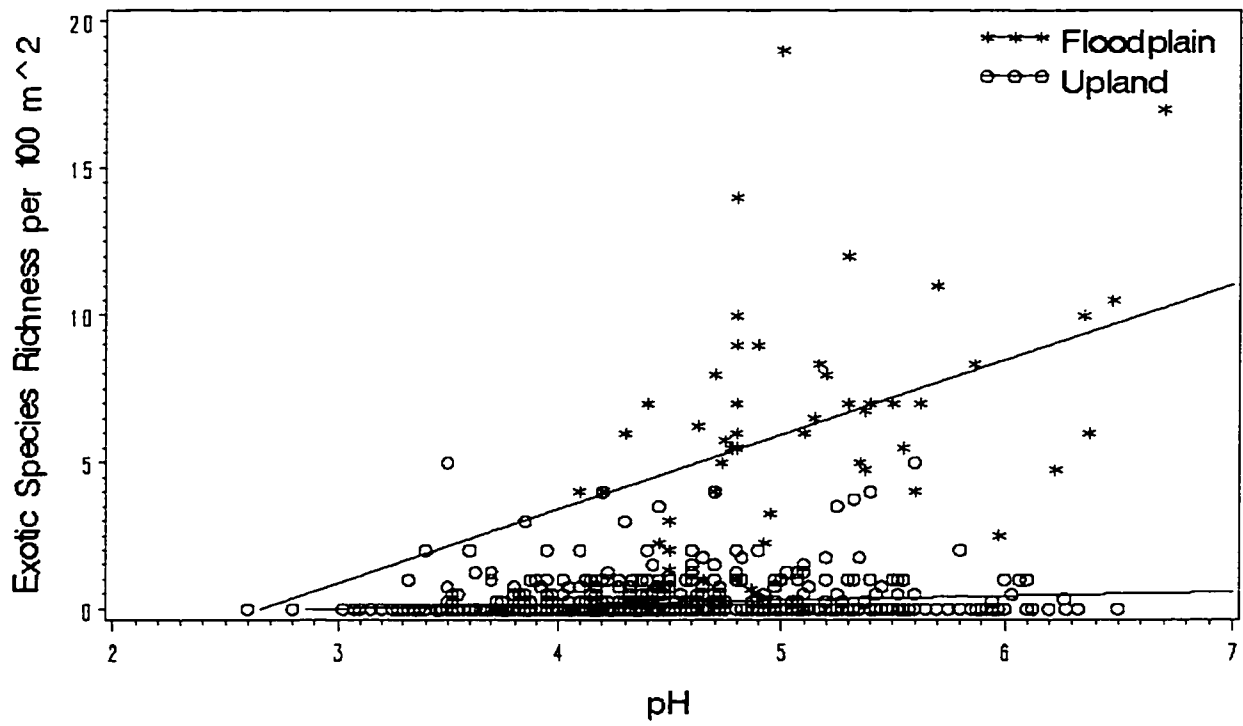
Soil pH had a positive effect on exotic species diversity in floodplains and little effect in uplands (Figure 2.3). For any given pH, exotic species richness was higher in floodplains than uplands, suggesting that differences in soil fertility between floodplain and upland plots do not explain the observed differences in exotic species richness.

## DISCUSSION

As Wardle (2001) explains, Levine's observation of a negative relationship between diversity and invasibility at small scale could be in part due to a sampling effect with the most diverse plots having the species most likely to competitively exclude invaders, though Wardle admits this is unlikely. 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 I 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. In effect, this explanation is equivalent to observing that the small plot size relative to the size of the plants physically limits the number of plants that could invade, and at this small scale a high diversity likely means a relatively high number of plants is already present.

**Figure 2.3.** The relationship between exotic species richness per 100-m<sup>2</sup> and soil pH in floodplain and upland plots.





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), although this relationship would not necessarily be seen at the median.

Upland areas had few exotic species in general (only 12 of the 1075 upland plots had more than 2 species per 100-m<sup>2</sup> with 5 species maximum, whereas riparian areas had up to 43 exotic species in a plot and a more even distribution). The low level of exotic species invasion in upland areas relative to riparian areas may well be a consequence of dispersal limitation, with upland areas having lower propagule pressure than flooded sites. Even upland sites with similar soil pH had far fewer exotic species than riparian sites, suggesting that the differences cannot be explained by fertility differences between upland and riparian habitats.

In contrast to the uplands, riparian areas had greater cover, frequency, and species richness of exotic plants. Within riparian areas native and exotic species richness were both correlated with flooding. There was a positive relationship between native and exotic species diversity in riparian areas at large scales at the upper quantile, which was much stronger than that seen in upland areas. These results are consistent with the hypothesis that flooded areas are more immigration-driven than uplands due to increased disturbance and resource availability, and greater rates of propagule influx. The differences in exotic species richness between riparian and upland areas were not explained by differences in pH or native species cover (and were pronounced even comparing closed canopy floodplain forests with uplands), suggesting that factors such as propagule inputs play a more important role than soil nutrients, native species cover, or light in driving the exotic species invasions seen in riparian areas.

Our results are consistent with an immigration-extinction gradient framework in that immigration-driven riparian areas have high rates of invasion, high species diversity, and a positive relationship between native and exotic species richness as compared to the more extinction-driven uplands. The immigration-extinction gradient framework complements the work of Davis et al. (2000) and Levine (2000) in that disturbance, water, and nutrient inputs characteristic of riparian zones allow high levels of net resource availability (*sensu* Davis et al. 2000), which when combined with high levels of propagule pressure (also characteristic of riparian systems) results in the exceptional species richness I observed. The positive relationship between native and exotic species richness in uplands suggests that resource complementarity did not observably affect the relationship between diversity and invasion in these habitats, although competitive dominance by a single species, reducing diversity of both native and exotic species (*sensu* Wardle 2001), could affect some of the relationships seen.

## CONCLUSION

Overall, the 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).

Elton's classic 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. Even at small scales, the apparent decline in invasibility with high richness is more readily explained as an artifact of the small number of individual plants that can fit in a small space. 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.

## Chapter 3

### RIPARIAN VEGETATION ANALYSIS AND CLASSIFICATION

#### ABSTRACT:

Few undisturbed riparian areas remain on large rivers in the southern Appalachians because of the concentration of land use activities such as agriculture and roads. Riparian zones can harbor high levels of species diversity and serve as corridors for the migration of species and for exotic species invasion. Despite their potential ecological importance on the landscape, there has been no comprehensive study of the riparian plant communities across a broad geographic scale in the southern Appalachians.

The objectives of this chapter are to identify how environmental and geographic factors interact to structure riparian vegetation communities of the southern Appalachians at both regional and local scales. In particular, I have explored the extent to which geomorphic position can be used as an environmental surrogate to predict and explain vegetation patterns in a riparian system. I surveyed vegetation and environmental factors in 128 vegetation plots stratified across a range of geomorphic positions along three southern Appalachian rivers: the New, the Nolichucky, and the Little Tennessee. The relationship between plot species composition and environment was explored using Nonmetric Multi-dimensional Scaling (an ordination method), and the plots were clustered using the Unweighted Pair Group Method of

cluster analysis. Finally, I compared the distance decay of similarity in species composition among a range of geomorphic positions at the scale of a single watershed, and across a range of rivers.

Overall, I found recurrent types of vegetation and environmental variables that corresponded to geomorphic position, consistent with current understanding about the relationship between geomorphic position and vegetation within rivers. However, plant species composition was also influenced by a geographic gradient reflecting variation among the three rivers, which could be attributed to both environmental differences among the three rivers and/or to the connectivity of vegetation within a river (i.e. the relatively easy dispersal of species within a watershed as compared to the greater difficulty of dispersing between watersheds creates some geographic patterns in species composition that are more related to watershed dispersal limitations than to habitat preferences). The most frequently flooded sites showed the highest amounts of compositional similarity (e.g. at a given distance, the flooded sites were more similar than uplands) and, within a watershed, a higher rate of distance decay than uplands (e.g. the amount of compositional difference increased with distance, which did not occur in uplands). This could be a consequence of flooded sites being driven more by chance immigration than upland sites. These dynamics in vegetation compositional consistency due to factors such as immigration make traditional vegetation classification by habitat difficult, and suggests that a classification approach is needed that can incorporate such processes.

## INTRODUCTION

Riparian areas are ecologically important on the landscape because they are often observed to contain unusually high plant species diversity (Naiman et al. 1993; Planty-Tabacchi et al. 1996; Brinson and Verhoeven 1999; Stohlgren et al. 1999) and because they provide corridors for plant species migrations and exotic species invasion (Bratton et al. 1994; Pysek and Prach 1994; Nilsson and Grelsson 1995; Pysek et al. 1995; Johansson et al. 1996). Because riparian plant communities play an important role in maintaining regional patterns of species composition and diversity, it is important to understand what processes structure riparian vegetation at both local and regional scales.

Riparian plant communities are characterized by recurrent river flooding, which affects the underlying substrate, provides disturbance, increases resource availability of moisture and nutrients, and affects dispersal processes (Menges and Waller 1983; Junk et al. 1989). The effects of flooding are patchy due to fine-scale spatial and temporal variations in water speed and sediment deposition (Ilhardt et al. 2000) with the consequence that riparian vegetation often appears highly heterogeneous over small spatial scales (Kalliola and Puhakka 1988; Henry et al. 1996). The variation in flood frequency and intensity with vertical distance from the river creates gradients of disturbance and environmental variables that are correlated with geomorphic surfaces and vegetation (Barnes 1978; Lyon and Sagers 1998). Within the active channel of the river where flooding is most intense, shifting bars of sand and cobble form, with the size of the persistent substrate directly related to water velocity. As flood frequency and intensity decrease with increasing elevation, finer substrates persist characteristic of floodplains and terraces in high gradient streams of the eastern United States (Hupp and Osterkamp 1996). Vegetation composition in riparian areas

is typically closely related to these geomorphic features (Wistendahl 1958; Lindsey et al. 1961; Fonda 1974; Harris 1987; Hupp 1988; Auble et al. 1994; Goebel et al. 1996; Gregory et al. 1991; Alcaraz et al. 1997; Ferreira 1997; Toner and Keddy 1997; Pabst and Spies 1998; Ilhardt et al. 2000).

In the southern Appalachian Mountains, intact riparian vegetation on rivers of stream order 3 or above has become increasingly rare because of land use patterns in the region. Hydroelectric dams operated by the Tennessee Valley Authority are heavily concentrated in the southern Appalachian region and the relatively flat, fertile floodplains of southern Appalachian rivers make them ideal for agriculture, roads, railways, campgrounds, and front yards.

Few studies of southern Appalachian riparian vegetation have been undertaken. Hedman and Van Lear (1995) studied riparian floodplain forests occurring across a range of river sizes and logging histories. They concluded that their riparian stands were representative of two Whittaker (1956) vegetation types and transitions between these types: mixed mesophytic deciduous forest (cove hardwood type), and eastern hemlock forest. However this study is limited in scope because it was focused on floodplains (excluding other geomorphic positions), most of which were dominated by a *Rhododendron maximum* understory, which is not characteristic of many southern Appalachian riparian areas on larger rivers. While they related vegetation to logging history, no attempt was made to relate vegetation to river size, geomorphology, or flood regime on the rivers selected.

Other southern Appalachian riparian studies include Baker and Van Lear (1998), who studied the effects of *Rhododendron maximum* on riparian vegetation on Wine Spring Creek in the southern Appalachians. They found that *Rhododendron* thickets have expanded in the

past 30 years following logging, and they negatively affect diversity. Vandermast and Van Lear (2002) examined the effects of *Castanea dentata* loss in four southern Appalachian riparian forest sites. Both of these studies were local in scope and did not include large rivers.

No comprehensive effort to study the riparian plant communities at local and regional scales on large rivers in the southern Appalachian region has previously been undertaken. Consequently, the objectives of this study are to identify vegetation-environment relationships and riparian plant communities that occur at both local and regional scales across a broad geographic range in the southern Appalachians. Further, riparian systems offer special problems for vegetation analysis in that they are structured not only by environmental factors and disturbance, but potentially by high levels of propagule pressure (with seed rain due to flooding). Most traditional vegetation classifications have organized communities based on the assumption that communities have consistent species composition related to environment, and have ignored dynamic processes such as the amount of immigration into the community. Frequently flooded riparian plant communities may have inconsistent species composition, structured by chance immigration events rather than just the underlying environment. To assess the degree of compositional similarity among geomorphic positions with different amounts of flooding I determined the distance decay of similarity, the relationship between the distance between two observations and their compositional similarity (Nekola and White 1999; Hubbell 2001). I expected that more frequently flooded geomorphic positions would have higher compositional similarity (because of the dispersal of species) and higher distance decay rates (because these are



structured more by immigration events than underlying environment) than unflooded geomorphic positions.

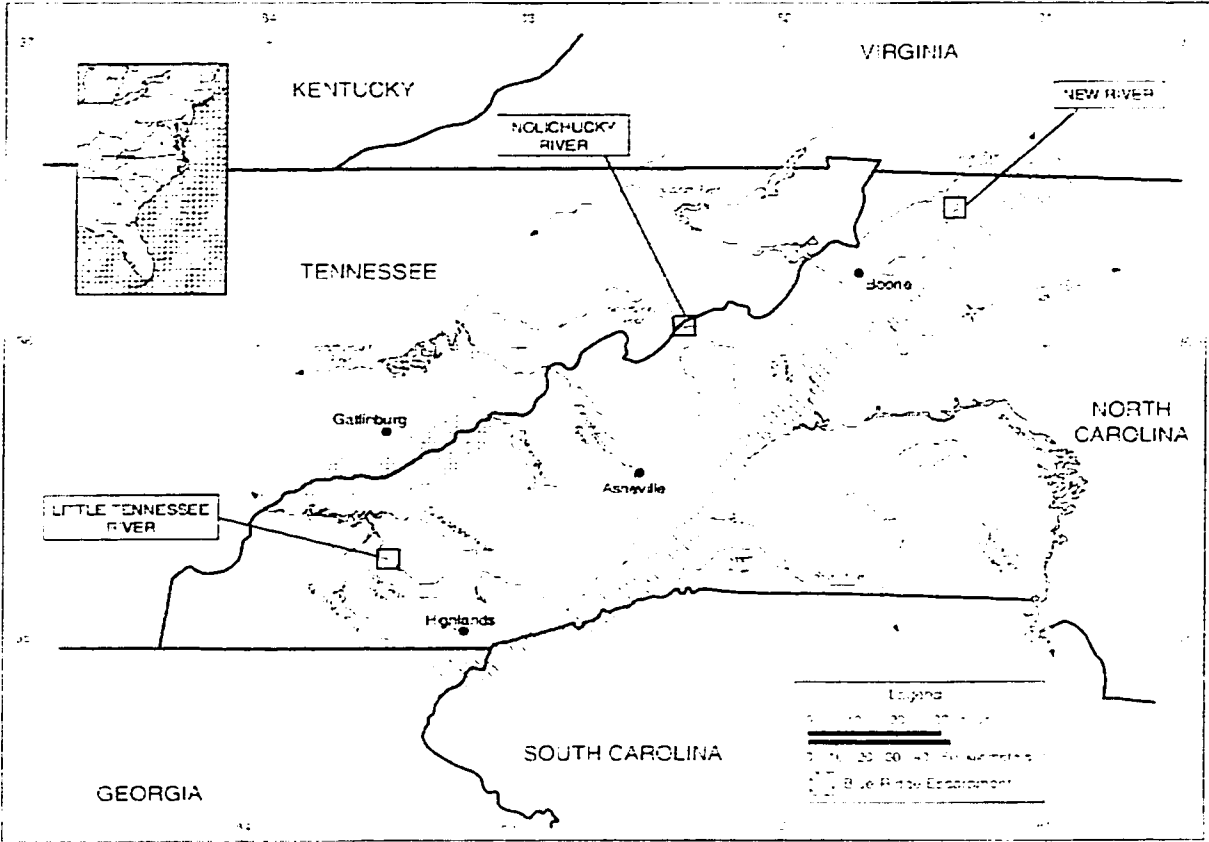
## STUDY AREA

Data were collected on sections of three rivers: the New, Nolichucky, and Little Tennessee (Figure 3.1). These were selected because they had unregulated hydrologic regimes, a USGS Gage in or near they study reach, significant amounts of natural intact riparian vegetation, and they span a broad geographic region. The river segments vary in terms of land use history and geology, and dams have not significantly altered their flow regimes. The study sections range in stream order from 4 to 5 (Strahler 1964) and have similar volumes of water flow. A comparison of the characteristics of the three river sections is shown in Table 1. In general, the sections of the New and Little Tennessee Rivers have less gradient, finer grained alluvial sediments, and wider floodplains than the Nolichucky River section, which cuts through bedrock.

The three rivers vary in terms of their levels of anthropogenic disturbance. Agricultural fields are located on many floodplains particularly on the New but also on the Little Tennessee River. There is no agricultural disturbance within the immediate study section of the Nolichucky (because it has fewer large, flat accessible floodplains), however, there are extensive agriculture fields on riparian areas upstream within the Nolichucky watershed. The most noticeable disturbance on the Nolichucky River is the Clinchfield railroad track, built at the turn of the century, which runs the length of the study reach. In places where the floodplain is narrow, boulders and concrete structures from the railroad track overflow into the river, and likely affect local riparian vegetation and hydrology. The

railroad company regularly sprays herbicide along the track, which occasionally spreads to riparian areas. In addition, the maintenance of the track (which involves grinding the rails) regularly causes forest fires in uplands and terraces adjacent to the river. On the Little Tennessee River, the dam at the Porter's Bend power plant at Lake Emory, about 20 miles upstream of the study section, causes slight diurnal water flow fluctuations but does not otherwise appear to affect the natural flood regime. Within the southern Appalachians, I found no rivers of the stream order 4 or above without anthropogenic disturbance at some place within their watershed.

**Figure 3.1.** Map of western North Carolina showing locations of the three study river sections.



**Table 3.1.** Comparison of the three southern Appalachian river sections used in this study.

	<i>Little Tennessee</i>	<i>New</i>	<i>Nolichucky</i>
Watershed area (at nearest gage station)	436 mi <sup>2</sup> Needmore, NC	205 mi <sup>2</sup> Jefferson, NC	608 mi <sup>2</sup> Poplar, NC
Stream Order	4	4 – 5	5
Length of Study Section	~10 miles	~14 miles	~8 miles
Human disturbance near river	Agriculture (natural areas > 50% land adjacent to the river)	Agriculture (natural areas < 50% land adjacent to the river)	Railroad (river left)
Gradient of Study Section	2.78 m/km	0.41 m/km	6.22 m/km
Median daily flow during period of study (May 15, 1998 – October 1, 2000)	539 cfs	240 cfs	418 cfs
5 year recurrence interval flood discharge*	9490 cfs	5060 cfs	16,000 cfs
Channel Slope*	6.48 ft/mi	10.53 ft/mi	23.71 ft/mi
Basin Slope*	408.05 ft/mi	314.07 ft/mi	452.57 ft/mi
Basin Shape* (drainage area/length)	0.16	0.05	0.11
Substrate	Cobble	Silt	Bedrock
Channel type	Semi-controlled	Semi-controlled	Bedrock
USGS Gage Station number	03503000 Needmore, NC	03161000 Jefferson, NC	03465500 Embreeville, TN Poplar, NC (no longer active)
Counties of NC	Swain, Macon	Ashe, Allegheny	Mitchell, Yancey
Predominant geologic formation (North Carolina State Geological Survey, 1991)	Clastic metasedimentary and metavolcanic rocks of the Ocoee Supergroup	Clastic metasedimentary rock and mafic and felsic metavolcanic rock of the Ashe metamorphic suite and felsic and biotite gneiss	Sedimentary rocks – sandstone, dolomite, shale, sandstone
Predominant soil formations	Evard (Fine, loamy, mesic, typic hapludults) (Thomas 1996) Heyesville – Clifton – Rabun Heyesville – Saluda (Hermann 1996)	Colvard Fine Sandy Loam (in flats), Chandler Loam (slopes) (Brewer 1984) Heyesville – Fanin Porters – Ashe (Hermann 1996)	Porters – Edneyville Ditney – Jeffrey – Brookshire (Hermann 1996)

\* Data source: (Pope et al. 2001)

## SAMPLING METHODS

### *Sampling Strategy*

Vegetation plots were established along multiple transects perpendicular to each river in order to survey across the range of geomorphic positions. Each transect spans all geomorphic landform classes present and the adjacent upland areas on each side of the river. There were 7 transects per river for a total of 21 transects on the three rivers. 128 plots were used for analyses; several plots were excluded because they lacked sufficient environmental data. Table 3.2 summarizes the number of plots and their vertical distance from the river by geomorphic position and river. Plots were located in riparian areas and adjacent uplands with natural vegetation and a minimum of human disturbance (though forested plots were often relatively mature second growth).

### *Geomorphic landform classes*

Geomorphic landform classes were in most cases distinguished by abrupt changes in vertical height above the river and by changes in substrate following Hupp and Osterkamp (1985; see Figure 3.2 and Table 3.2). The typical landforms found in southern Appalachian riparian areas included bars, floodplains, and terraces, which varied in terms of flood frequency and intensity. Bars had the highest flood frequency, with flood events occurring several times per year, followed by floodplains (1-3 year flood interval), then terraces (with greater than 3 years between flooding). Flood frequency and intensity influences the substrate found in each of these landforms. Bars with high water velocity tend to have a rocky substrate compared to those in areas with slower water. In southern Appalachian riparian areas, floods are typically of short duration due to the high gradient of the rivers.

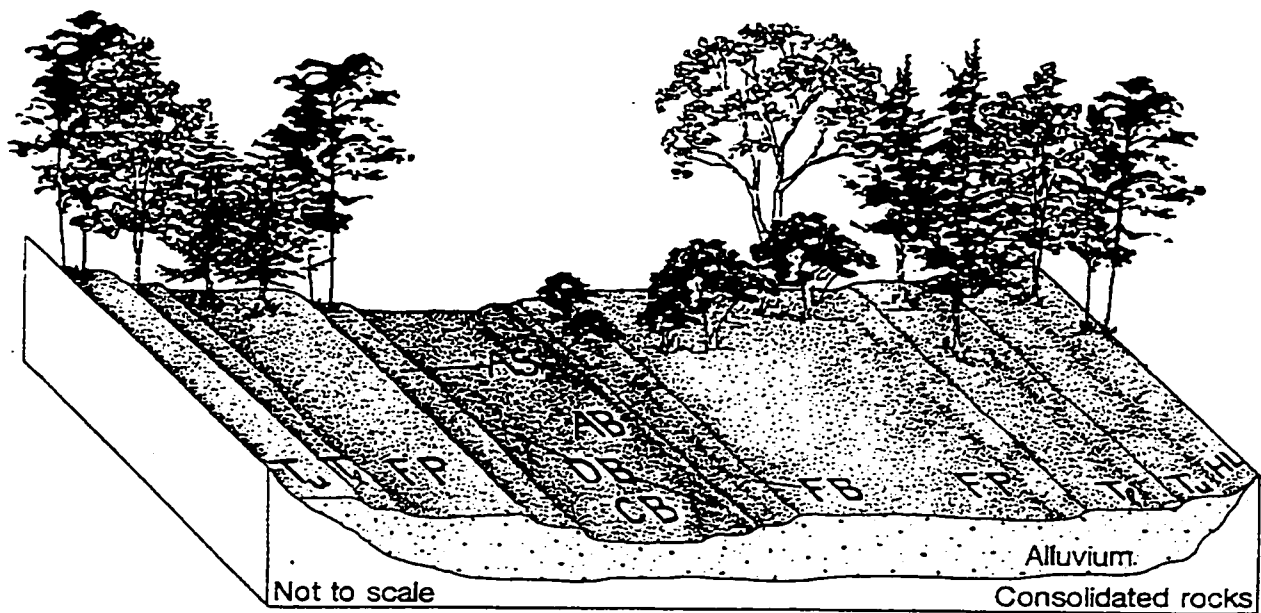
### *Vegetation Sampling*

All vascular plant species were surveyed following the plot sampling protocol of the Carolina Vegetation Survey (Peet et al. 1998). Vegetation was surveyed using a nested quadrat system with quadrat scales ranging across a log-10 scale from 0.01-m<sup>2</sup> to 1000-m<sup>2</sup> (most plots were 100-m<sup>2</sup>, Figure 3.3) in order to assess changes in species composition and diversity across multiple scales. Percent cover by species of all vascular plants was recorded at the 100-m<sup>2</sup> scale, and averaged at that scale for those plots with more than one 100-m<sup>2</sup> module. In cases where the landform was too small for a 100-m<sup>2</sup> plot, one of the smaller nest sizes was selected as the maximum plot size. Botanical nomenclature follows Weakley (2001) and otherwise (Kartesz and Meacham 1999). Before analyses, varieties and subspecies were combined into single species groups to facilitate comparison of broad species composition patterns.

**Table 3.2.** Number of plots and average vertical distance to river per landform class for each river included in this study.

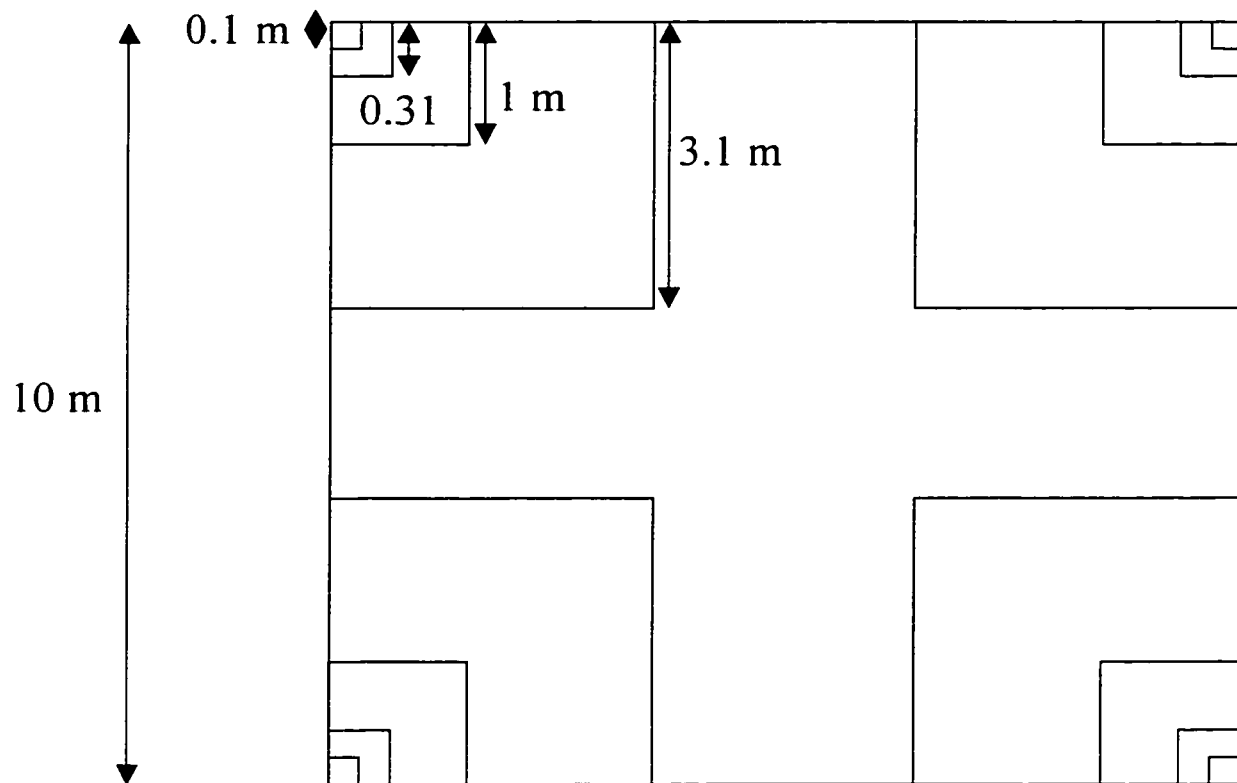
<i>River</i>	<i>Bar</i>	<i>Floodplain</i>	<i>Floodplain Bank</i>	<i>Terrace</i>	<i>Upland</i>
Little Tennessee	7 plots 0.13 m	19 1.03 m	3 0.61 m	4 2.08 m	14 5.97 m
New	6 0.61 m	18 1.87 m	2 0.83 m	4 3.29 m	11 6.75 m
Nolichucky	19 0.38 m	6 1.94 m	3 1.43 m	1 4.37 m	12 10.59 m
Total	32 0.38 m	42 1.49 m	8 0.97 m	9 3.11 m	37 7.70

**Figure 3.2.** Osterkamp and Hupp diagram illustrating geomorphic landforms including channel bed (CB), bar (DB), active channel bank (AB), channel shelf (AS), floodplain bank (FB), floodplain (FP), low terrace (T<sub>l</sub>) and upper terrace (T<sub>u</sub>). From Osterkamp and Hupp (1984) and Hupp and Osterkamp (1985), with kind permission from Cliff Hupp and the Ecological Society of America.





**Figure 3.3.** Layout of standard 100-m<sup>2</sup> vegetation plot showing nested subplots.



### *Environmental Data*

A range of environmental information was collected for each plot location in order to relate species composition to environmental variables. The environmental data collected fall into four categories: topography, soils, ground cover, and flood data. For each plot, slope, aspect, and elevation were recorded to assess the general affects of topography on riparian vegetation. Elevation was estimated by locating the plot on a USGS topographic map. Aspect was transformed ( $\cos(45 - \text{aspect}) + 1$ ) following the method of Beers et al. (1966) to assign relatively warm, dry southwesterly slopes a value of 0 and cool, moist northeasterly slopes a value of 2. McNab Landform Index (LFI) and Terrain Shape Index (TSI) were calculated to quantify the microtopographic and regional topographic position of the plot in the landscape. LFI is assessed by measuring the slope percentage to the horizon for the plot in 8 cardinal and subcardinal directions (45 degree increments). This allows one to assess whether the plot is on a ridge or in a cove, for example. TSI is assessed by measuring the slope percentage to the ground 20 meters away using the same 8 directions (McNab 1989). Plot UTM locations were determined using a GPS.

To assess soil fertility and texture, soil samples were collected from the center of each 100-m<sup>2</sup> plot, following the methodology of the Carolina Vegetation Survey (Peet et al. 1998). Soil samples were collected from the top 10 cm of soil below the leaf litter (the A horizon). In plots with more than one subsample from the A horizon (typically 4 samples for a 1000-m<sup>2</sup> plot), the results of soil analyses were averaged over the 4 modules. Cation exchange capacity, pH, estimated nitrogen release (N), easily extractable phosphorus (P), exchangeable cations (ppm Ca, Mg, K, Na), percent base saturation (%Ca, Mg, K, Na), extractable micronutrients (ppm B, Fe, Mn, Cu, Zn, Al), soluble sulfur (S), and bulk density values

(density) were determined for each subsample. Soil textural analyses were conducted to identify percent sand, silt, and clay (sand, silt, clay). Soil nutrient and textural analyses were carried out at Brookside Laboratory, Inc., New Knoxville, Ohio, following methods described in Newell and Peet (1998). Soil depth (up to 30 cm) was measured in a standard location, 1 meter inside of 4 corners of each 100-m<sup>2</sup> plot (and 16 corners in a 1000-m<sup>2</sup> plot), using a 30 cm metal probe. The depth was averaged over the corners.

Groundcover percent allows an estimate of flood frequency since frequent flooding removes small particles such as silt, leaving cobbles and boulders. Leaf litter has also been shown to affect vegetation distribution, and is affected by flooding which removes the litter (Xiong and Nilsson 1997). Groundcover percent was estimated for each 100-m<sup>2</sup> plot module for bryophytes/lichens, decaying wood, bedrock/boulders, gravel/cobble, sand/soil, litter/organic matter, and water. The ground cover percents for all items sum to 100 except in cases where bryophytes, lichens, or decaying wood covered bedrock. In these cases percentages were given for the underlying bedrock in addition to the overlying wood, lichens, or mosses and thus the total ground cover percent exceeds 100.

The vertical distance from each plot to the river surface (height above water) was measured to provide a general index of flood frequency. The height was measured on the same day (when water flow fluctuations were minimal) for each plot on a given river to control for water flow fluctuations.

### *Exotic Plant Species*

Exotic plant species were identified using the USDA Plants Database (USDA 2001). The total percent cover of all exotic species (exotic percent cover) was calculated by summing the percent cover per 100-m<sup>2</sup> of each exotic species in a plot.

## DATA ANALYSIS

### *Ordination*

Ordination was used to determine patterns in vegetation composition and to relate these to environmental gradients. I used non-metric multidimensional scaling (NMDS), an ordination technique appropriate for non-normally distributed ecological data (Minchin 1987; McCune and Mefford 1999). NMDS iteratively ranks and places plots (or other entities) in multidimensional space based on a distance matrix, selecting the minimum number of dimensions and plot placement that minimizes the stress of the configuration. Stress is the goodness-of-fit between the original distance matrix and the ordination of plots (Legendre P. and Legendre 1998). In the ordination figure, plots that are more similar are placed closer together, while dissimilar plots are further apart. I used relative Sorensen distance for the dissimilarity matrix (Sorensen distance standardized by the number of sample units) (McCune and Mefford 1999). Ordination analyses were run using all of the data combined, and separately for the each river to identify important environmental variables at both the local (within river scale) and within the wider geographic region.

The environmental variables (slope, aspect, elevation, soil nutrients, soil texture, height above water, ground cover percent) and total cover of exotic species were correlated with each of the ordination axes to determine the relationship between the ordination derived

species composition axes and environment using Pearson and Kendall correlations. The correlation coefficients express the linear (Pearson's  $r$ ) and rank (Kendall's tau) relationships between the ordination scores and the individual variables used to construct the ordination. Joint plots with vectors representing environmental variables were created to illustrate the relationships between environmental variables and ordination axes. Only variables with Pearson's  $r^2 > 0.2$  are displayed. The angle and length of the vector represent the strength and direction of the relationships. Ordination analyses were conducted using PC-Ord version 4.0.1 (McCune and Mefford 1999).

### *Cluster Analysis*

Sample plots were clustered into groups with compositionally similar vegetation to identify community types and to quantify compositional variation. I used the unweighted arithmetic average clustering method (also called the Unweighted Pair-Group Method: UPGMA) in PC-Ord (McCune and Mefford 1999) to cluster plots. UPGMA is a distance-based, agglomerative cluster technique that identifies clusters using average dissimilarity. Average dissimilarity between each plot was computed using relative Sorensen distance. UPGMA was selected over other clustering methods for its ability to separate rare samples (Sneath et al. 1973; Newell 1997). Species were sorted into 27 groups at the 37.5 % information remaining cutoff level by comparing the results of the cluster analysis with the ordination diagrams and selecting groups that made logical sense given knowledge about site factors. To select the number of groups, clustered groups were examined on the ordination diagram with all plots. I selected the cutoff level that created groups with delineations that matched environmental gradients, landform class, and river.

### *Community Classification*

I conducted Legendre and Dufrene Indicator Species Analysis available in PC-Ord (McCune and Mefford 1999) to identify Legendre Dufrene Indicator Species Values and relative frequency of each species in each of the groups identified in the cluster analysis. I used these two values along with the average cover of each species per group to identify group names for species associations consistent with the National Vegetation Classification nomenclature (Grossman et al. 1998).

The following criteria were used in selecting species to name riparian associations:

- **Association name:** The 1-4 most common species (having top 10 average abundance) that *also* occur with high frequency (relative frequency > 90). Species separated by ‘-’ are from the same strata and by a ‘/’ are from different strata. The highest strata is listed first, and species within strata are listed in descending order of average abundance.
- **In parentheses:** those species not included in the name with high indicator values (greater than 25% or the 10 species in the group with the highest indicator values) and the 10 species with the highest abundance. Of those, only species with > 70% relative frequency and >10% average cover are listed in the parentheses. Rare species found in these groups will also be included in parentheses. Species are listed alphabetically.

- For groups with only one plot, the most common species were used in the name. These groups have been assigned provisional status.

### *Distance Decay of Similarity*

In order to determine whether there were differences in distance decay of similarity among the four geomorphic positions, I calculated the log-transformed Sorensen similarity in species composition for every possible pair of plots in the data set. I then plotted the Sorensen similarity between plots (calculated using log-transformed Sorensen similarity) against geographic distance between plots (obtained from UTM coordinates) for each geomorphic position. For this analysis, I included the riparian plots from my original study of three rivers plus 23 other plots collected on other rivers in the southern Appalachian region including Wilson Creek, the Green, and the Nantahala (sampled with the same survey protocol). Using the data for all rivers, I compared distance decay rates of four geomorphic positions: scour bar, floodplain, terrace, and upland, at two spatial scales representing distance decay within a river (less than 10,000 meters distance) and between rivers (up to 250,000 meters distance).

To determine whether overall compositional similarity (the intercept) and the rate of distance decay (slope) differed significantly among the geomorphic positions, I used a randomization procedure based on code written by Jack Weiss of the Ecology Curriculum at the University of North Carolina. The assignments of geomorphic positions were permuted to different distances, and the mean for each geomorphic position was calculated from the randomized data. This procedure was repeated 1000 times in order to generate an empirical null distribution from which the P-value was generated (Manley 1997). Then the actual

intercept and slope were compared to the randomized value to determine significance with a Bonferroni correction ( $P/6$ ) for the 6 comparisons among geomorphic positions.

## RESULTS

### *Overview*

A total of 890 vascular plant species were sampled in 128 vegetation plots, representing 122 families and 422 genera. Of these, 552 species were found in the Little Tennessee River sites, 442 were found in the New River sites, and 521 were found in the Nolichucky River sites. There were 132 exotic species (15% of the flora), with more exotic species occurring in the more frequently flooded geomorphic positions, as discussed in Chapter 2. The ordination of all plots together produced a 3-dimensional ordination. Axis 1 appears to relate to geomorphic position and flooding, with uplands on the opposite side of the ordination as bars and floodplains (Figure 3.4), while axes 2 and 3 appear to relate to geographic location, with the groups of plots differentiating by river (Figure 3.5).

### *General Environmental Factors*

The correlations between the axes and environmental factors are listed in Table 3.3. Axis 1 is most strongly positively correlated ( $r^2 > 0.2$ ) with soil density, % Ca, pH, exotic species cover, lnCu, and sand, while it is negatively correlated with N, height above water, organic matter, lnAl, silt, % K, and ln K. Axis 2 is negatively correlated with litter, soil depth, and elevation. Axis 3 is positively correlated with landform index (LFI).

### *Individual Rivers*



The ordinations of each river separately produced 2-dimensional ordinations (Figures 3.6 to 3.8). Several variables consistently had relatively high  $r^2$  values (greater than 0.20 for axis 1 or 2). Percent Ca, density, sand, lnCu, and exotic species cover are always positively correlated with the upper left corner of the ordination, and thus positively correlated with axis 2 while negatively correlated with axis 1. Conversely, height above water, lnK, organic matter, silt, lnAl, S, and N are always negatively correlated with the upper left corner of the ordination, and thus negatively correlated with axis 2 while positively correlated with axis 1.

For the Nolichucky River (Figure 3.8), there were several variables that had  $r^2 > 0.2$  which were not found on the other two rivers. LFI, % bryophytes and lichens, P, CEC, and percent litter are positively correlated with the lower right, while % Mg and % Na are positively correlated with the upper left side of the ordination. Likewise, only on the New River were lnZn, lnMg, CEC, and % water correlated with the upper left part of the ordination (Figure 3.7). On the New (Figure 3.7) and Little Tennessee (Figure 3.6), but not the Nolichucky, lnCa-Mg, lnCa, and lnCu were correlated with the upper left and elevation, slope, and %K were correlated with the lower right. Percent gravel was negatively correlated with axis 1 on the Nolichucky and Little Tennessee but not the New.

### *Groups*

The UPGMA cluster analysis and subsequent evaluation of the groups on the ordination diagram resulted in 24 groups of similar species composition being identified (Figures 3.9, 3.10, and Table 3.7). While the UPGMA initially produced 27 groups, I reassigned 3 groups into other groups based on knowledge of the local environment in the plots (thus groups 3, 58, and 16 appear in two places on the cluster dendrogram, Figure 3.9).

The groups created by UPGMA are mapped onto the dendrogram in Figure 3.10. For ease of reference I use the group number assigned by UPGMA analysis to refer to groups. Groups usually correspond to geomorphic positions, substrate, river, and plot proximity. In a few cases, plots on a transect fell into the same group, despite being in slightly different (but adjacent) geomorphic positions (e.g. floodplain-bar). Terraces and uplands overlapped significantly, with most terrace plots being classified as uplands communities. There were few terraces in the dataset because terraces are not a common geomorphic feature on these rivers (perhaps because the valleys are narrow). For the most part, however, geomorphic position and river were very important for predicting vegetation community type. A few bar, floodplain, and upland groups were common across more than one river (as shown in Table 3.7).

The groups correspond to six general classes: floodplains, floodplain banks, anthropogenically-disturbed herbaceous vegetation, deposition bars, bedrock scour bars, and uplands. The floodplains sort into six groups (shown in Table 3.7). Group 1 is a unique, old-growth floodplain plot on the Nolichucky dominated by *Quercus rubra* and *Acer rubrum*. Groups 2 and 18 are *Carpinus caroliniana* dominated floodplains on the Little Tennessee River. The two groups differ in that Group 18 plots are typically on low-lying, frequently flooded Little Tennessee islands, with shallower soil depth, less leaf litter, and they tend to be more open, with no canopy above the *Carpinus*, while group 2 plots are on large floodplains with an upper canopy (Figure 3.11.A). Group 4 comprises *Platanus occidentalis* and *Liriodendron tulipifera* dominated floodplains found on the Little Tennessee and Nolichucky (Figure 3.11.B). These floodplains have greater soil depth and soil fertility values than

Groups 2 or 18. Group 5 are *Juglans sp.* dominated floodplains from the New River, and these have the highest soil fertility and soil depth values of the floodplain plots.

There are two floodplain bank communities, both with *Acer rubrum* and *Rhododendron maximum* as dominant species. Group 17 (Figure 3.11.C) is found on the Little Tennessee and Group 59 is found on the New River. The group on the New tends to be more frequently flooded than that on the Little Tennessee, and consequently has slightly higher soil fertility values.

There were two disturbed herbaceous communities. Group 42 was a road bank on the Little Tennessee dominated by *Festuca subverticillata*, and Group 78 is found in old fields on the New River dominated by *Verbesina alternifolia* (Figure 3.11.D).

There were four bar communities. Group 10 was a *Festuca subverticillata/Scirpus expansus* community found on very frequently flooded silt bars of the Little Tennessee and New Rivers (Figure 3.12.G). The rest were generally found in rocky or sandy bars. The largest group was 61, with bars on the New and Nolichucky Rivers dominated by *Platanus occidentalis* and *Cornus amomum* (Figure 3.12.C-D). Group 3 found on the Little Tennessee and Nolichucky Rivers was similar, except with *Betula nigra* rather than *Cornus amomum* (Figure 3.12.F). Finally, group 38 represents a shaded sand bar (overhung by trees) on a back slough of the Little Tennessee with *Leersia virginiana* as a dominant species in the plot.

There were three bedrock scour communities (with bedrock as a substrate and very shallow or no soil) on the Nolichucky River. Group 91 was dominated by *Salix nigra* (Figure 3.12.B), while group 104 was dominated by *Ulmus alata* and *Platanus occidentalis* (Figure 3.12.A). These communities differed environmentally in that group 104 was more frequently flooded. Group 95, dominated by *Nyssa sylvatica* and *Fraxinus pennsylvanica*

represents a transition zone between bedrock scour communities and rocky slopes (Figure 3.12.E).

I identified 8 upland communities types in the uplands and terraces adjacent to the floodplains that were surveyed. Group 58 on the New, dominated by *Fagus grandifolia* and *Betula lenta*, was often found adjacent to the floodplain bank communities on the New (group 59) and many of the species overlap. Group 58 is found on the low soil fertility, high leaf litter end of the ordination axes. Group 109 represents a terrace dominated by *Carya pallida*, *Nyssa sylvatica*, and *Piptochaetium avense* (Figure 3.11.E). This terrace community is likely maintained by accidental fires set by the railroad when maintaining the track. Group 109 intergrades with Nolichucky group 106, dominated by *Carya pallida*, *Quercus montana*, and *Philadelphus hirsutus*. Group 106 further intergrades with another group on the Nolichucky: Group 119 dominated by *Quercus montana*, *Quercus rubra* and *Philadelphus hirsutus*. This group in turn has many overlapping species with Group 16, another *Quercus montana* - *Quercus rubra* community that was commonly found on infertile soils of all three rivers, although Group 16 had *Rhododendron maximum* rather than *Philadelphus hirsutus* in the understory. Other uplands communities are found in Table 3.7.

**Table 3.3.** Pearson and Kendall correlations with NMDS ordination axes (includes data for all three rivers). In bold are all  $r^2 > 0.20$  (which also appear in the ordination biplots).

<i>Axis:</i>	<i>1</i>	<i>1</i>	<i>1</i>	<i>2</i>	<i>2</i>	<i>2</i>	<i>3</i>	<i>3</i>	<i>3</i>
<i>Statistic:</i>	<i>r</i>	<i>r</i> <sup>2</sup>	<i>tau</i>	<i>r</i>	<i>r</i> <sup>2</sup>	<i>tau</i>	<i>r</i>	<i>r</i> <sup>2</sup>	<i>tau</i>
Aspect	0.09	0.01	0.06	-0.05	0.00	-0.04	0.06	0.00	0.05
Slope	-0.43	<b>0.18</b>	-0.31	0.01	0.00	0.03	-0.05	0.00	-0.06
Landform index	-0.13	0.02	-0.09	0.21	0.04	0.16	0.47	<b>0.22</b>	0.30
Terrain shape index	-0.04	0.00	-0.05	0.14	0.02	0.11	0.20	0.04	0.11
Exotic Species Cover	<b>0.53</b>	<b>0.28</b>	0.61	-0.30	0.09	-0.18	0.04	0.00	-0.03
Soil CEC	-0.13	0.02	-0.07	-0.41	0.17	-0.32	0.23	0.05	0.12
Soil pH	<b>0.58</b>	<b>0.33</b>	0.40	0.06	0.00	0.03	-0.01	0.00	-0.04
Soil Organic matter	-0.57	<b>0.33</b>	-0.51	0.08	0.01	-0.11	0.23	0.05	0.03
Soil N	-0.68	<b>0.46</b>	-0.52	-0.23	0.05	-0.11	0.03	0.00	0.03
Soil S	-0.50	<b>0.25</b>	-0.37	-0.09	0.01	-0.07	0.13	0.02	0.10
Soil P	-0.15	0.02	-0.03	-0.25	0.06	-0.15	0.08	0.01	0.12
Soil % Ca	<b>0.62</b>	<b>0.39</b>	0.46	-0.05	0.00	-0.06	0.08	0.01	0.04
Soil % Mg	0.31	0.10	0.19	0.34	0.12	0.25	-0.16	0.03	-0.13
Soil % K	-0.51	<b>0.26</b>	-0.36	0.19	0.04	0.17	-0.26	0.07	-0.19
Soil % Na	0.25	0.07	0.15	0.34	0.12	0.29	-0.08	0.01	-0.05
Soil density	<b>0.65</b>	<b>0.42</b>	0.46	0.16	0.03	0.12	-0.18	0.03	-0.11
Soil % Clay	-0.14	0.02	-0.09	-0.24	0.06	-0.13	-0.16	0.03	-0.04
Soil % Silt	-0.51	<b>0.26</b>	-0.37	-0.12	0.01	-0.12	0.10	0.01	0.05
Soil % Sand	0.49	<b>0.24</b>	0.36	0.16	0.03	0.13	-0.05	0.00	-0.02
Soil ln Al	-0.57	<b>0.32</b>	-0.43	-0.21	0.05	-0.13	-0.22	0.05	-0.15
Soil ln B	0.00	0.00	0.01	-0.12	0.02	-0.06	0.31	0.10	0.19
Soil lnCa-Mg	0.41	0.16	0.30	-0.34	0.12	-0.26	0.20	0.04	0.16
Soil ln Ca	0.26	0.07	0.17	-0.44	0.19	-0.32	0.18	0.03	0.10
Soil ln Cu	0.50	<b>0.25</b>	0.33	-0.39	0.15	-0.25	0.07	0.00	0.03
Soil ln Fe	0.11	0.01	0.05	0.03	0.00	0.03	0.34	0.12	0.24
Soil ln K	-0.48	<b>0.23</b>	-0.32	-0.32	0.10	-0.19	0.01	0.00	0.02
Soil ln Mg	0.05	0.00	0.04	-0.35	0.12	-0.26	0.09	0.01	0.05
Soil ln Mn	0.36	0.13	0.26	0.01	0.00	0.05	-0.02	0.00	-0.03
Soil ln Na	0.18	0.03	0.10	-0.14	0.02	-0.10	0.15	0.02	0.10
Soil ln Zn	0.32	0.10	0.24	-0.11	0.01	-0.09	0.32	0.10	0.25
Height above river	-0.66	<b>0.44</b>	-0.47	-0.15	0.02	-0.24	0.16	0.02	0.04
Soil depth	-0.01	0.00	0.05	-0.46	<b>0.21</b>	-0.32	-0.41	0.17	-0.30
Elevation	0.05	0.00	-0.12	-0.46	<b>0.21</b>	-0.14	0.44	0.19	0.31
% Cover bryophytes and lichens	-0.15	0.02	-0.24	0.15	0.02	0.13	0.05	0.00	0.13
% Cover decaying wood	-0.14	0.02	-0.16	-0.05	0.00	-0.09	0.11	0.01	-0.06
% Cover bedrock and boulder	-0.05	0.00	-0.14	0.38	0.14	0.23	0.37	0.13	0.30
% Cover gravel and cobble	0.33	0.11	0.35	0.28	0.08	0.20	0.14	0.02	0.10
% Cover sand and soil	0.39	0.15	0.34	0.04	0.00	0.01	0.07	0.01	0.11
% Cover litter and organic matter	-0.39	0.15	-0.21	-0.46	<b>0.21</b>	-0.29	-0.30	0.09	-0.23
% Cover water	0.24	0.06	0.22	0.27	0.07	0.32	0.05	0.00	0.07

**Table 3.4.** Pearson and Kendall correlations with NMDS ordination axes for the Little Tennessee River. In bold are all  $r\text{-sq} > 0.20$  (which also appear in the ordination biplots).

<i>Axis:</i>	<i>1</i>	<i>1</i>	<i>1</i>	<i>2</i>	<i>2</i>	<i>2</i>
<i>Statistic:</i>	<i>r</i>	<i>r-sq</i>	<i>tau</i>	<i>r</i>	<i>r-sq</i>	<i>tau</i>
Aspect	0.15	0.02	0.12	-0.06	0.00	-0.06
Slope	0.46	<b>0.21</b>	0.34	-0.58	<b>0.34</b>	-0.55
Landform index	0.02	0.00	0.05	-0.35	0.12	-0.21
Terrain shape index	-0.01	0.00	-0.10	-0.08	0.01	-0.10
Exotic Species Cover	-0.26	0.07	-0.48	0.45	<b>0.20</b>	0.43
Soil CEC	0.19	0.04	0.14	0.11	0.01	0.08
Soil pH	-0.48	<b>0.23</b>	-0.32	0.44	<b>0.20</b>	0.31
Soil Organic matter	0.34	0.11	0.44	-0.46	<b>0.22</b>	-0.30
Soil N	0.64	<b>0.42</b>	0.44	-0.32	0.10	-0.29
Soil S	0.47	<b>0.22</b>	0.45	-0.25	0.06	-0.21
Soil P	0.02	0.00	-0.05	-0.27	0.07	-0.06
Soil % Ca	-0.56	<b>0.31</b>	-0.40	0.58	<b>0.33</b>	0.44
Soil % Mg	-0.08	0.01	-0.05	-0.09	0.01	-0.10
Soil % K	0.43	0.19	0.27	-0.58	<b>0.34</b>	-0.48
Soil % Na	-0.26	0.07	-0.08	0.05	0.00	0.04
Soil density	-0.60	<b>0.36</b>	-0.41	0.42	0.18	0.30
Soil % Clay	0.48	<b>0.23</b>	0.34	-0.06	0.00	-0.04
Soil % Silt	0.43	0.19	0.43	-0.28	0.08	-0.27
Soil % Sand	-0.50	<b>0.25</b>	-0.43	0.25	0.06	0.23
Soil ln Al	0.61	<b>0.38</b>	0.48	-0.22	0.05	-0.29
Soil ln B	0.09	0.01	0.08	0.19	0.04	0.14
Soil lnCa-Mg	-0.41	0.17	-0.34	0.59	<b>0.34</b>	0.45
Soil ln Ca	-0.09	0.01	-0.08	0.45	<b>0.20</b>	0.29
Soil ln Cu	-0.21	0.04	-0.19	0.44	<b>0.20</b>	0.31
Soil ln Fe	-0.06	0.00	-0.03	0.12	0.02	0.07
Soil ln K	0.52	<b>0.27</b>	0.34	-0.31	0.10	-0.23
Soil ln Mg	0.24	0.06	0.18	0.11	0.01	0.06
Soil ln Mn	-0.38	0.14	-0.21	0.37	0.14	0.17
Soil ln Na	-0.01	0.00	0.03	0.26	0.07	0.15
Soil ln Zn	-0.34	0.12	-0.26	0.33	0.11	0.32
Height above river	0.62	<b>0.38</b>	0.61	-0.38	0.15	-0.26
Soil depth	0.19	0.04	0.02	0.31	0.10	0.29
Elevation	0.36	0.13	0.30	-0.66	<b>0.44</b>	-0.50
% Cover bryophytes and lichens	-0.26	0.07	-0.02	-0.21	0.05	-0.33
% Cover decaying wood	-0.01	0.00	0.23	-0.13	0.02	-0.22
% Cover bedrock and boulder	-0.05	0.00	0.15	-0.28	0.08	-0.32
% Cover gravel and cobble	-0.49	<b>0.24</b>	-0.34	0.14	0.02	-0.03
% Cover sand and soil	-0.41	0.17	-0.30	0.21	0.05	0.06
% Cover litter and organic matter	0.62	<b>0.39</b>	0.31	-0.10	0.01	0.07
% Cover water	-0.44	0.19	-0.41	0.06	0.00	-0.03

**Table 3.5.** Pearson and Kendall correlations with NMDS ordination axes for the New River. In bold are all  $r$ -sq > 0.20 (which also appear in the ordination biplots).

<i>Statistic:</i>	<i>Axis: 1</i>			<i>Axis: 2</i>		
	<i>r</i>	<i>r-sq</i>	<i>tau</i>	<i>r</i>	<i>r-sq</i>	<i>tau</i>
Aspect	-0.20	0.04	-0.13	-0.08	0.01	-0.03
Slope	-0.52	<b>0.27</b>	-0.26	-0.13	0.02	-0.07
Landform index	-0.14	0.02	-0.10	0.07	0.01	0.00
Terrain shape index	0.18	0.03	0.13	-0.04	0.00	-0.13
Exotic Species Cover	0.64	<b>0.41</b>	0.69	-0.02	0.00	0.00
Soil CEC	0.22	0.05	0.13	-0.75	<b>0.57</b>	-0.57
Soil pH	0.32	0.11	0.22	-0.04	0.00	-0.05
Soil Organic matter	-0.71	<b>0.51</b>	-0.52	-0.23	0.05	-0.25
Soil N	-0.67	<b>0.45</b>	-0.54	-0.43	0.19	-0.25
Soil S	-0.47	<b>0.22</b>	-0.33	-0.24	0.06	-0.14
Soil P	-0.06	0.00	0.14	-0.50	<b>0.25</b>	-0.42
Soil % Ca	0.41	0.17	0.28	-0.16	0.03	-0.12
Soil % Mg	-0.09	0.01	-0.06	0.30	0.09	0.18
Soil % K	-0.59	<b>0.34</b>	-0.38	0.33	0.11	0.24
Soil % Na	-0.04	0.00	-0.08	0.56	<b>0.31</b>	0.41
Soil density	0.65	<b>0.42</b>	0.47	0.30	0.09	0.16
Soil % Clay	0.08	0.01	-0.03	-0.31	0.10	-0.30
Soil % Silt	-0.50	<b>0.25</b>	-0.31	-0.20	0.04	-0.16
Soil % Sand	0.39	0.15	0.24	0.26	0.07	0.22
Soil ln Al	-0.63	<b>0.40</b>	-0.48	-0.29	0.08	-0.21
Soil ln B	-0.23	0.05	-0.09	-0.41	0.17	-0.20
Soil lnCa-Mg	0.52	<b>0.27</b>	0.25	-0.35	0.12	-0.29
Soil ln Ca	0.46	<b>0.22</b>	0.20	-0.63	<b>0.39</b>	-0.54
Soil ln Cu	0.61	<b>0.38</b>	0.40	-0.07	0.00	-0.04
Soil ln Fe	0.12	0.01	0.18	0.22	0.05	0.11
Soil ln K	-0.24	0.06	-0.19	-0.63	<b>0.40</b>	-0.44
Soil ln Mg	0.25	0.06	0.12	-0.65	<b>0.43</b>	-0.51
Soil ln Mn	0.36	0.13	0.26	-0.14	0.02	-0.11
Soil ln Na	0.19	0.04	0.12	-0.14	0.02	-0.13
Soil ln Zn	0.49	<b>0.24</b>	0.32	0.09	0.01	0.03
Height above river	-0.68	<b>0.46</b>	-0.46	-0.31	0.10	-0.30
Soil depth	0.32	0.10	0.33	-0.06	0.00	-0.01
Elevation	-0.71	<b>0.51</b>	-0.58	0.30	0.09	0.21
% Cover bryophytes and lichens	0.00	0.00	-0.17	-0.26	0.07	-0.15
% Cover decaying wood	-0.20	0.04	-0.14	0.22	0.05	0.17
% Cover bedrock and boulder	-0.27	0.07	-0.33	-0.08	0.01	-0.17
% Cover gravel and cobble	0.27	0.07	0.26	0.29	0.08	0.18
% Cover sand and soil	0.34	0.12	0.21	0.05	0.00	0.02
% Cover litter and organic matter	-0.18	0.03	-0.02	-0.11	0.01	-0.04
% Cover water	0.26	0.07	0.16	0.50	<b>0.25</b>	0.34

**Table 3.6.** Pearson and Kendall correlations with NMDS ordination axes for the Nolichucky River. In bold are all  $r$ -sq > 0.20 (which also appear in the ordination biplots).

<i>Statistic:</i>	<i>Axis: 1</i>			<i>Axis: 2</i>		
	<i>r</i>	<i>r-sq</i>	<i>tau</i>	<i>r</i>	<i>r-sq</i>	<i>tau</i>
Aspect	0.08	0.01	0.04	0.14	0.02	0.09
Slope	0.25	0.06	0.04	-0.10	0.01	0.00
Landform index	0.45	<b>0.20</b>	0.32	-0.02	0.00	-0.04
Terrain shape index	0.36	0.13	0.23	-0.03	0.00	0.02
Exotic Species Cover	-0.66	<b>0.44</b>	-0.70	0.20	0.04	0.30
Soil CEC	0.50	<b>0.25</b>	0.30	-0.60	<b>0.36</b>	-0.49
Soil pH	-0.80	<b>0.64</b>	-0.58	0.60	<b>0.36</b>	0.38
Soil Organic matter	0.68	<b>0.46</b>	0.45	-0.63	<b>0.39</b>	-0.54
Soil N	0.67	<b>0.45</b>	0.43	-0.71	<b>0.51</b>	-0.56
Soil S	0.63	<b>0.40</b>	0.40	-0.55	<b>0.30</b>	-0.38
Soil P	0.58	<b>0.33</b>	0.38	-0.48	<b>0.23</b>	-0.35
Soil % Ca	-0.78	<b>0.61</b>	-0.57	0.55	<b>0.30</b>	0.34
Soil % Mg	-0.73	<b>0.53</b>	-0.44	0.70	<b>0.49</b>	0.52
Soil % K	0.14	0.02	0.19	-0.20	0.04	-0.16
Soil % Na	-0.45	<b>0.20</b>	-0.31	0.69	<b>0.47</b>	0.52
Soil density	-0.64	<b>0.41</b>	-0.40	0.69	<b>0.47</b>	0.52
Soil % Clay	-0.10	0.01	0.07	0.21	0.05	0.19
Soil % Silt	0.52	<b>0.27</b>	0.28	-0.52	<b>0.27</b>	-0.45
Soil % Sand	-0.50	<b>0.25</b>	-0.27	0.49	<b>0.24</b>	0.45
Soil ln Al	0.57	<b>0.33</b>	0.36	-0.49	<b>0.24</b>	-0.38
Soil ln B	-0.02	0.00	0.05	-0.23	0.05	-0.12
Soil lnCa-Mg	0.03	0.00	-0.08	-0.34	0.11	-0.22
Soil ln Ca	0.01	0.00	-0.05	-0.39	0.15	-0.26
Soil ln Cu	-0.58	<b>0.33</b>	-0.47	0.40	0.16	0.29
Soil ln Fe	0.17	0.03	0.13	0.04	0.00	-0.01
Soil ln K	0.50	<b>0.25</b>	0.37	-0.68	<b>0.47</b>	-0.52
Soil ln Mg	0.00	0.00	0.02	-0.30	0.09	-0.22
Soil ln Mn	-0.30	0.09	-0.24	0.30	0.09	0.32
Soil ln Na	-0.01	0.00	0.01	-0.04	0.00	0.00
Soil ln Zn	0.03	0.00	-0.01	-0.15	0.02	-0.04
Height above river	0.65	<b>0.43</b>	0.43	-0.76	<b>0.58</b>	-0.65
Soil depth	-0.07	0.01	0.03	-0.23	0.05	-0.25
Elevation	0.43	0.19	0.32	-0.02	0.00	0.02
% Cover bryophytes and lichens	0.52	<b>0.27</b>	0.40	-0.28	0.08	-0.23
% Cover decaying wood	0.16	0.03	0.11	-0.31	0.10	-0.34
% Cover bedrock and boulder	0.30	0.09	0.26	0.14	0.02	0.05
% Cover gravel and cobble	-0.43	0.18	-0.46	0.45	<b>0.21</b>	0.36
% Cover sand and soil	-0.30	0.09	-0.35	0.31	0.09	0.34
% Cover litter and organic matter	0.28	0.08	0.19	-0.69	<b>0.47</b>	-0.47



**Table 3.7.** Community types organized according to geomorphic position.

Landform(s)	River	Grp.#	Group name (association)	#Plots
Floodplain	Nol.	1	<i>Quercus rubra</i> – <i>Acer rubrum</i> – <i>Carya alba</i> / <i>Leucothoe fontanesiana</i> ( <i>Fraxinus americana</i> , <i>Liquidambar styraciflua</i> , <i>Nyssa sylvatica</i> , <i>Quercus</i> <i>montana</i> , <i>Robinia pseudoacacia</i> , <i>Tsuga canadense</i> ) forest.	1
Floodplain (1 upland. 1 fp/sc transition)	LTN	2	<i>Carpinus caroliniana</i> – <i>Halesia tetraptera</i> / <i>Arundinaria gigantea</i> ssp. <i>gigantea</i> ( <i>Acer rubrum</i> , <i>Chasmanthium latifolium</i> , <i>Quercus imbricaria</i> ) Forest	15
Floodplain (low), bar (1 plot)	LTN, 1 on Nol.	18	<i>Carpinus caroliniana</i> – <i>Acer rubrum</i> / <i>Rhododendron</i> <i>arborea</i> ( <i>Houstonia serpyllifolia</i> , <i>Sisyrinchium</i> <i>angustifolium</i> , <i>Viola cuculata</i> ) Forest	5
Floodplain	LTN, Nol.	4	<i>Platanus occidentalis</i> – <i>Liriodendron</i> <i>tulipifera</i> / <i>Lindera benzoin</i> / <i>Microstegium vimineum</i> ( <i>Dioscorea oppositifolia</i> , <i>Laportea canadense</i> , <i>Lonicera japonica</i> , <i>Vitis cinera</i> var. <i>baileyana</i> ) Forest	11
Floodplain (plus 2 uplands)	New	5	<i>Juglans</i> sp./ <i>Lindera benzoin</i> / <i>Verbesina alternifolia</i> ( <i>Juglans cinera</i> , <i>Juglans nigra</i> ) Forest	16
Floodplain bank	LTN	17	<i>Acer rubrum</i> / <i>Rhododendron maximum</i> - <i>Kalmia</i> <i>latifolia</i> - <i>Leucothoe fontanesia</i> ( <i>Arundinaria gigantea</i> ssp. <i>gigantea</i> , <i>Galax urceola</i> , <i>Clethra alnifolia</i> , <i>Hexastylis arifolia</i> , <i>Medeola virginiana</i> , <i>Mitchella</i> <i>repens</i> , <i>Oxydendron arborea</i> , <i>Pyrularia pubera</i> ) Forest	3
Floodplain bank	New	59	<i>Acer rubrum</i> – <i>Fagus grandifolia</i> / <i>Rhododendron</i> <i>maximum</i> - <i>Clethra acuminata</i> ( <i>Agrostis hymenalis</i> , <i>Alnus serrulata</i> , <i>Cinna arundinaceas</i> , <i>Collinsonia</i> <i>canadense</i> , <i>Eupatorium maculatum</i> var. <i>maculatum</i> , <i>Hypericum perforatum</i> , <i>Lobelia cardinalis</i> , <i>Lobelia</i> <i>inflata</i> , <i>Pilea pumila</i> var. <i>pumila</i> , <i>Robinia</i> <i>pseudoacacia</i> ) Forest	2
Floodplain bank	LTN	42	<i>Festuca subverticiliata</i> – <i>Lonicera japonica</i> – <i>Toxicodendron radicans</i> ( <i>Acer rubrum</i> , <i>Dichanthelium clandestinum</i> ) Herbaceous Vegetation (disturbed roadbank)	1

**Table 3.7** continued

Floodplain	New	78	<i>Verbesina alternifolia</i> – <i>Dichanthelium clandestinum</i> ( <i>Blephara ciliata</i> , <i>Cornus amomum</i> , <i>Elymus riparian</i> , <i>Glecoma hederacea</i> , <i>Heliopsis helianthoides</i> var. <i>helianthoides</i> , <i>Stellaria media</i> , <i>Teucrium canadense</i> ) Herbaceous Vegetation (disturbed – old pasture)	2
Bar (2 plots called floodplain)	Nol., New	61	<i>Platanus occidentalis</i> / <i>Cornus amomum</i> ( <i>Acalypha rhomboidea</i> , <i>Ambrosia artemisifolia</i> , <i>Oenothera biennis</i> , <i>Robinia pseudoacacia</i> , <i>Rosa multiflora</i> , <i>Salix nigra</i> , <i>Saponaria officinalis</i> ) Shrubland	17
Bar	LTN, NOL	3	<i>Platanus occidentalis</i> – <i>Betula nigra</i> ( <i>Alnus serrulata</i> , <i>Anthoxanthum odoratum</i> , <i>Apios americanum</i> , <i>Hypericum muticum</i> , <i>Microstegium vimimeum</i> ) Woodland	2
Bar	LTN	38	<i>Leersia virginiana</i> – <i>Impatiens capensis</i> – <i>Hypericum muticum</i> – <i>Boehmeria cylindrica</i> Herbaceous Vegetation	1
Bar (silty)	LTN, New	10	<i>Festuca subverticillata</i> – <i>Sciripus expansus</i> – <i>Scheonoplectus tabermontana</i> ( <i>Carex vulpinoide</i> , <i>Eupatorium perfoliatum</i> var. <i>perfoliatum</i> , <i>Glyceria striatula</i> , <i>Hypericum muticum</i> ) Herbaceous Vegetation	3
Bedrock scour	Nol.	91	<i>Salix nigra</i> – <i>Ilex verticilata</i> – <i>Polygonum cuspidatum</i> ( <i>Andropogon virginiana</i> , <i>Ionactis linarifolius</i> , <i>Ipomea pandurata</i> , <i>Toxicodendron radicans</i> ) Sparse Vegetation	1
Bedrock scour	Nol.	104	<i>Ulmus alata</i> – <i>Platanus occidentalis</i> – <i>Rosa palustris</i> / <i>Juncus marginalis</i> – <i>Equisetum arvense</i> ( <i>Andropogon virginiana</i> , <i>Dichanthelium acuminatum</i> var. <i>fasciculatum</i> , <i>Justicia Americana</i> ) Sparse Vegetation	1
Bedrock scour/rocky slope transition	Nol.	95	<i>Nyssa sylvatica</i> – <i>Fraxinus pennsylvatica</i> / <i>Alnus serrulata</i> ( <i>Acer rubrum</i> , <i>Hypericum hypericoides</i> var. <i>hypericoides</i> , <i>Liquidambar styraciflua</i> , <i>Rhododendron arborea</i> , <i>Saxifraga careyana</i> , <i>Ulmus alata</i> ) Forest	4
Upland, Terrace	New	8	<i>Tilia americana</i> var. <i>heterophylla</i> – <i>Carya ovata</i> – <i>Aesculus flava</i> Forest	4

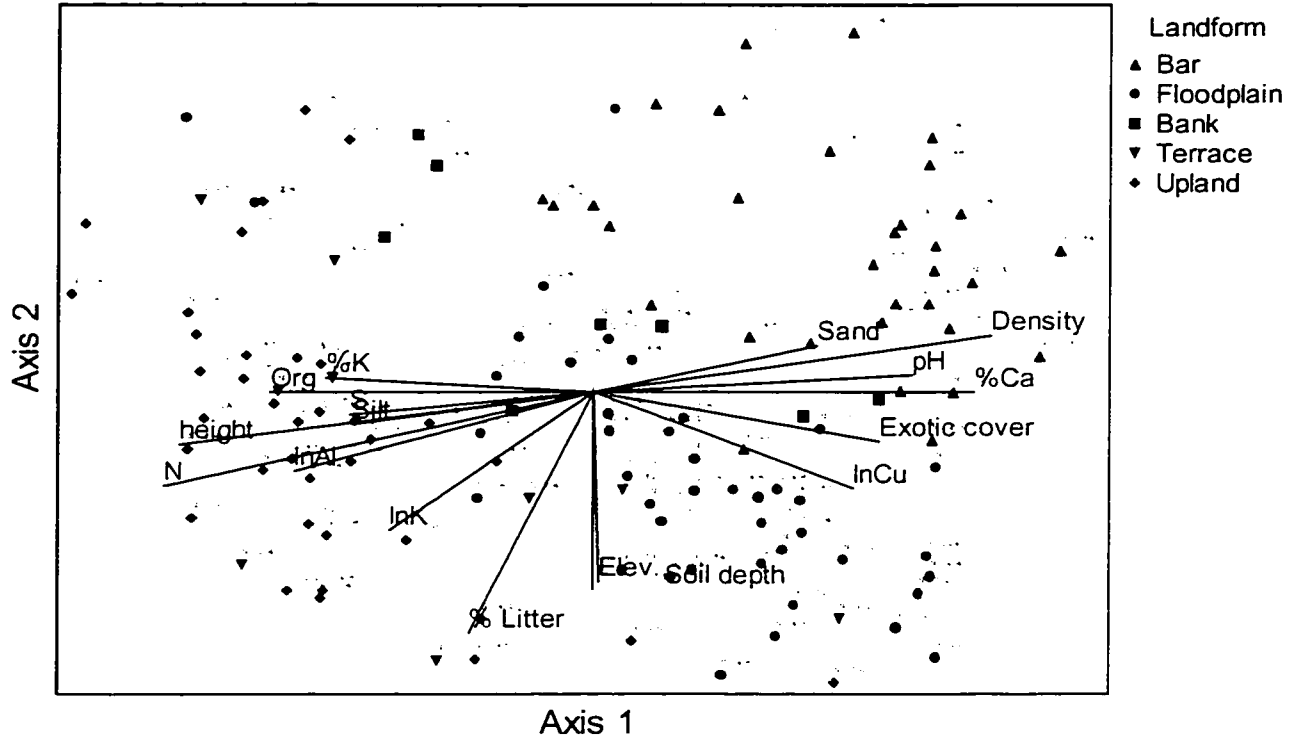
**Table 3.7** continued

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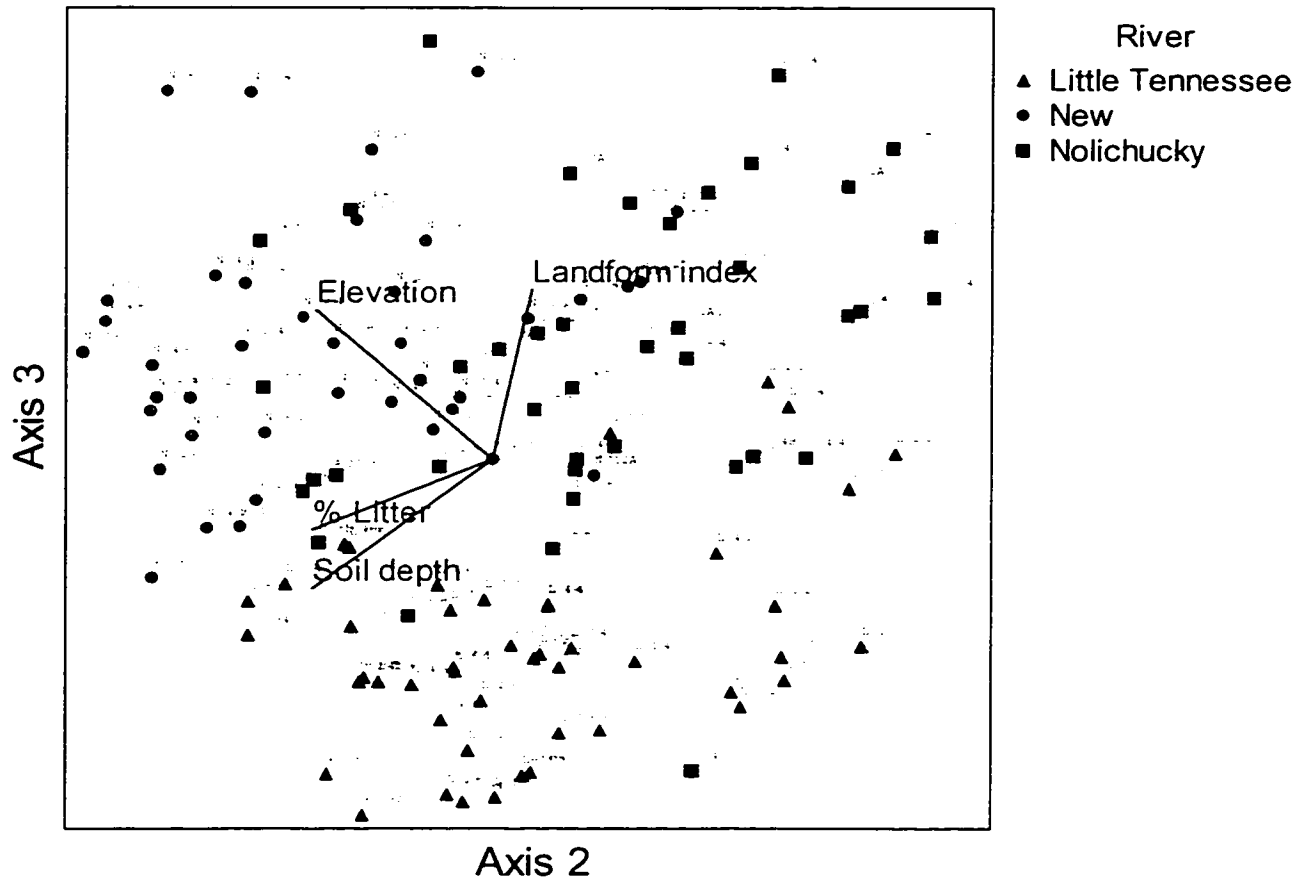
Upland, Terrace (3 terrace plots)	LTN, 2 on Nol.	21	<i>Quercus alba</i> – <i>Acer rubrum</i> / <i>Carpinus caroliniana</i> ( <i>Cornus florida</i> , <i>Euonymus americana</i> , <i>Kalmia</i> <i>latifolia</i> , <i>Liriodendron tulipifera</i> , <i>Pyrularia pubera</i> , <i>Quercus velutina</i> ) Forest	14
Upland	New, LTN (1 plot)	58	<i>Fagus grandifolia</i> – <i>Betula lenta</i> ( <i>Maianthemum</i> <i>racemosum</i> var. <i>racemosum</i> , <i>Quercus rubra</i> , <i>Rhododendron maximum</i> , <i>Stellaria pubera</i> ) Forest	6
Upland	Nol.	89	<i>Liriodendron tulipifera</i> / <i>Acer pennsylvatica</i> ( <i>Betula</i> <i>lenta</i> , <i>Dicentra eximia</i> , <i>Diervilla rivularis</i> , <i>Dryopteris</i> <i>marginalis</i> , <i>Oxydendron arborea</i> , <i>Tsuga canadense</i> ) Forest (Acid Cove Forest)	4
Upland, Terrace (2 plots)	LTN, New, Nol.	16	<i>Quercus montana</i> – <i>Quercus rubra</i> / <i>Rhododendron</i> <i>maximum</i> / <i>Galax urceolata</i> ( <i>Kalmia latifolia</i> , <i>Pinus</i> <i>virginiana</i> , <i>Tsuga caroliniana</i> ) Forest	11
Upland	Nol.	119	<i>Quercus rubra</i> – <i>Quercus montana</i> / <i>Philadelphus</i> <i>hirsuta</i> Forest	1
Upland	Nol.	106	<i>Carya pallida</i> – <i>Quercus montana</i> / <i>Philadelphus</i> <i>hirsutus</i> / <i>Carex pennsylvanica</i> ( <i>Danthonia spicata</i> , <i>Fraxinus pennsylvanica</i> , <i>Saxifraga careyana</i> , <i>Ulmus</i> <i>alata</i> ) Forest	1
Terrace	Nol.	109	<i>Carya pallida</i> – <i>Nyssa sylvatica</i> / <i>Piptochaetum</i> <i>arvense</i> ( <i>Arundinaria gigantea</i> ssp. <i>gigantea</i> , <i>Fraxinus</i> <i>pennsylvanica</i> , <i>Pinus rigida</i> , <i>Pinus virginiana</i> , <i>Pityopsis graminifolia</i> var. <i>latifolia</i> , <i>Robinia</i> <i>pseudoacacia</i> ) Forest	2

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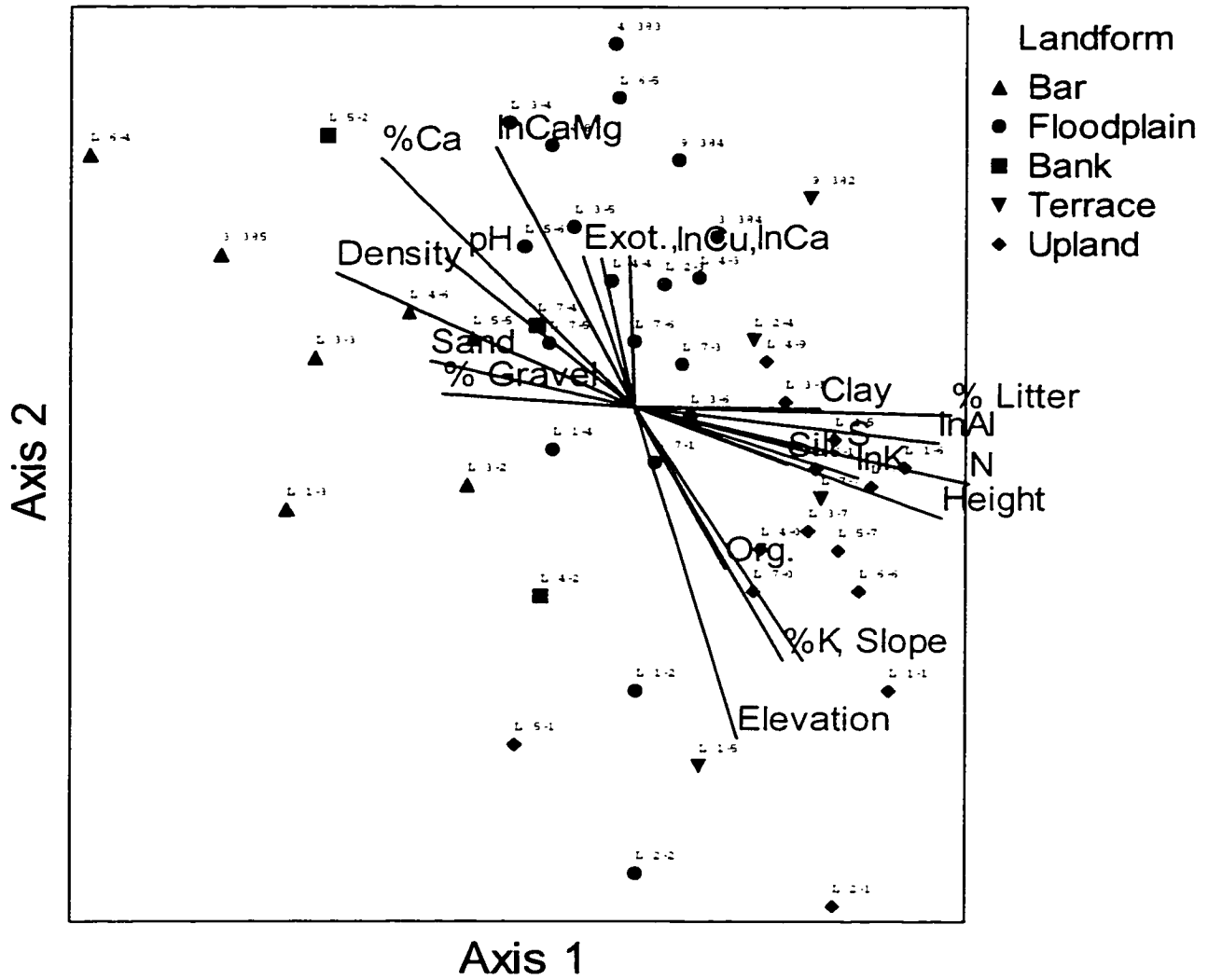
**Figure 3.4.** NMDS ordination biplot (with axes 1 and 2) of plots on all three rivers showing vectors for environmental variables correlated with axes 1 or 2 with  $r^2 > 0.20$ . Plots are grouped by landform class.



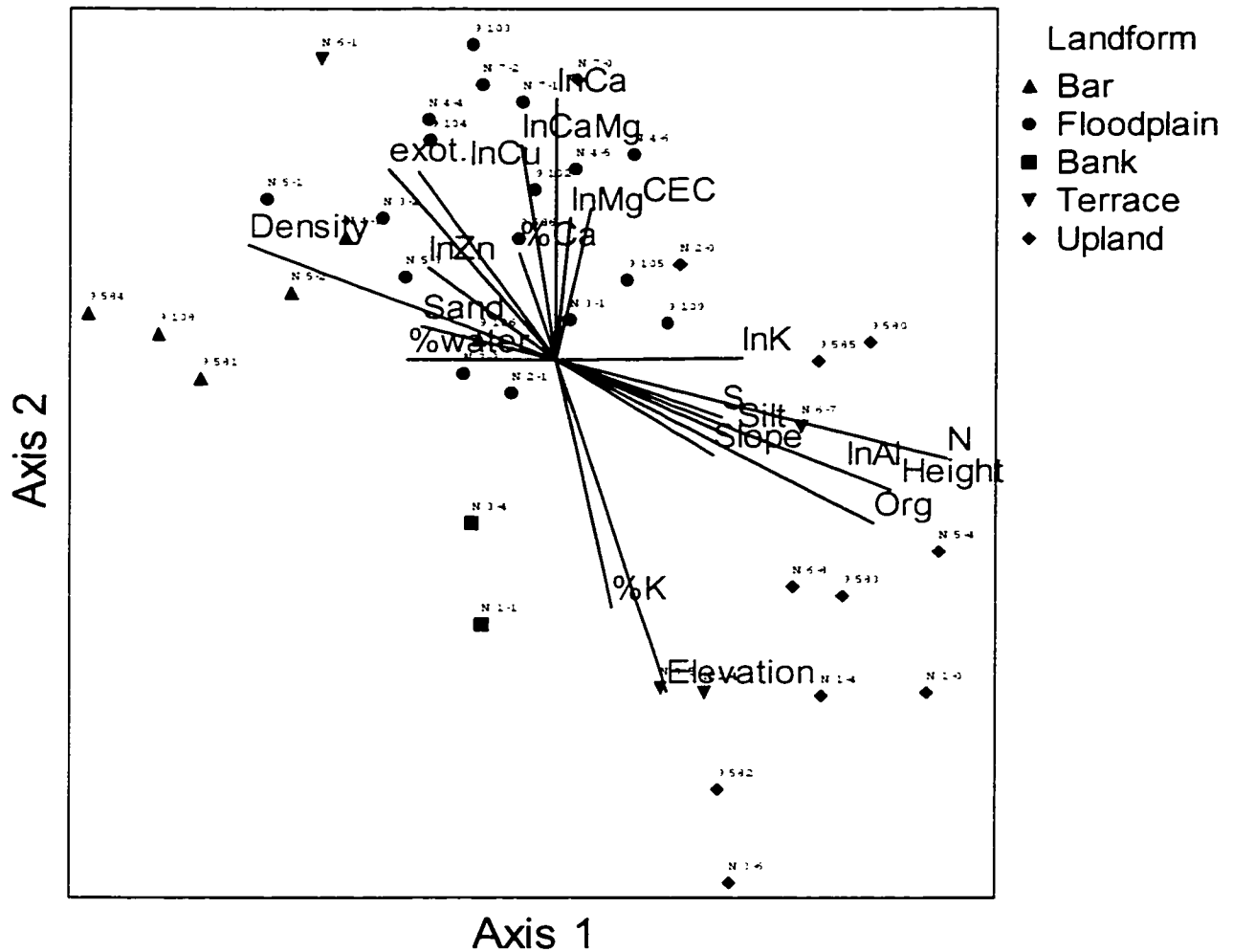
**Figure 3.5.** NMDS ordination biplot (with axes 2 and 3) of plots on all three rivers showing vectors for environmental variables correlated with axes 2 or 3 with  $r^2 > 0.20$ . Plots are grouped by river.



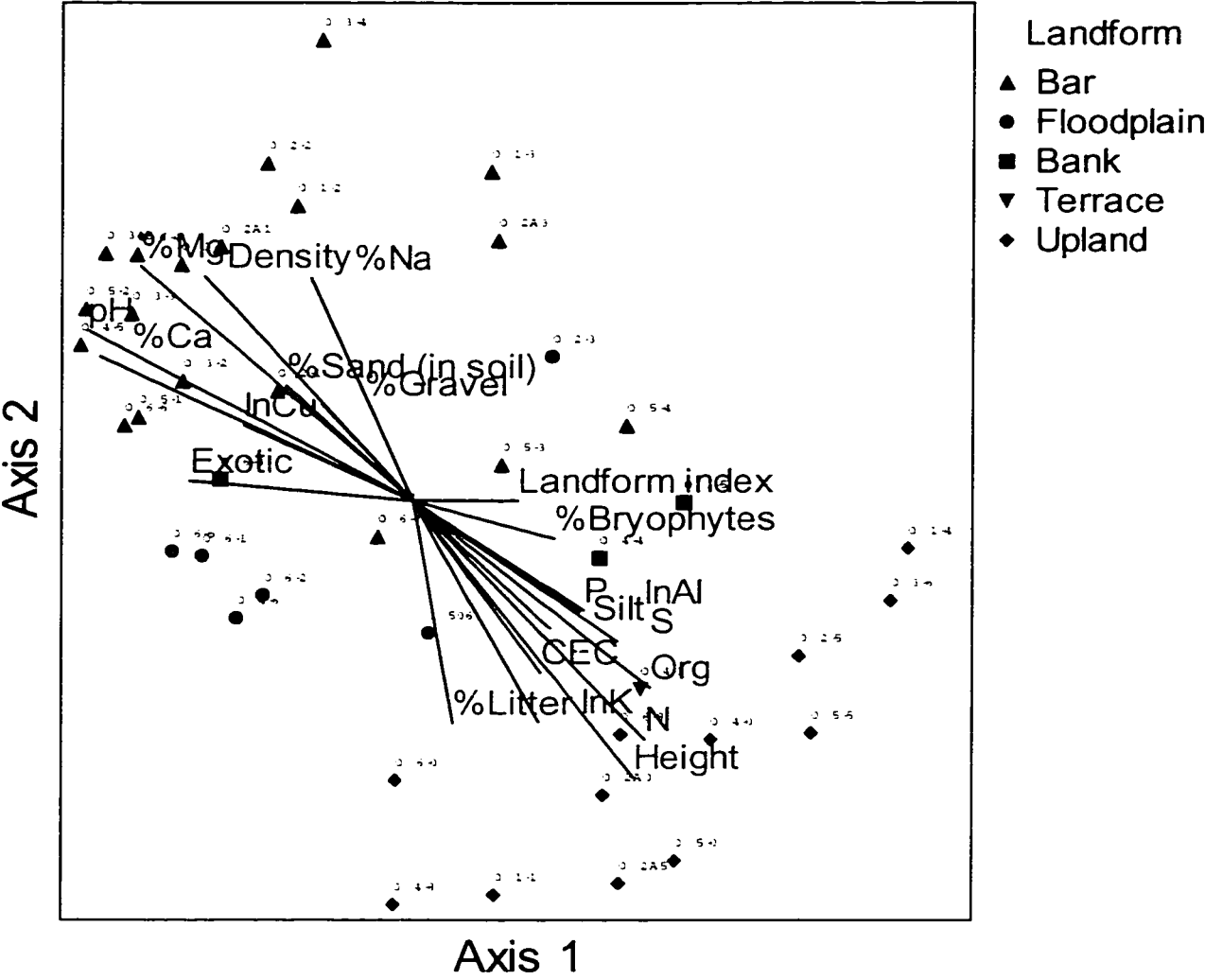
**Figure 3.6.** NMDS ordination biplot (with axes 1 and 2) of plots on the Little Tennessee River showing vectors for environmental variables correlated with axes 1 or 2 with  $r^2 > 0.20$ . Plots are grouped by landform class.



**Figure 3.7.** NMDS ordination biplot (with axes 1 and 2) of plots on the New River showing vectors for environmental variables correlated with axes 1 or 2 with  $r^2 > 0.20$ . Plots are grouped by landform class.

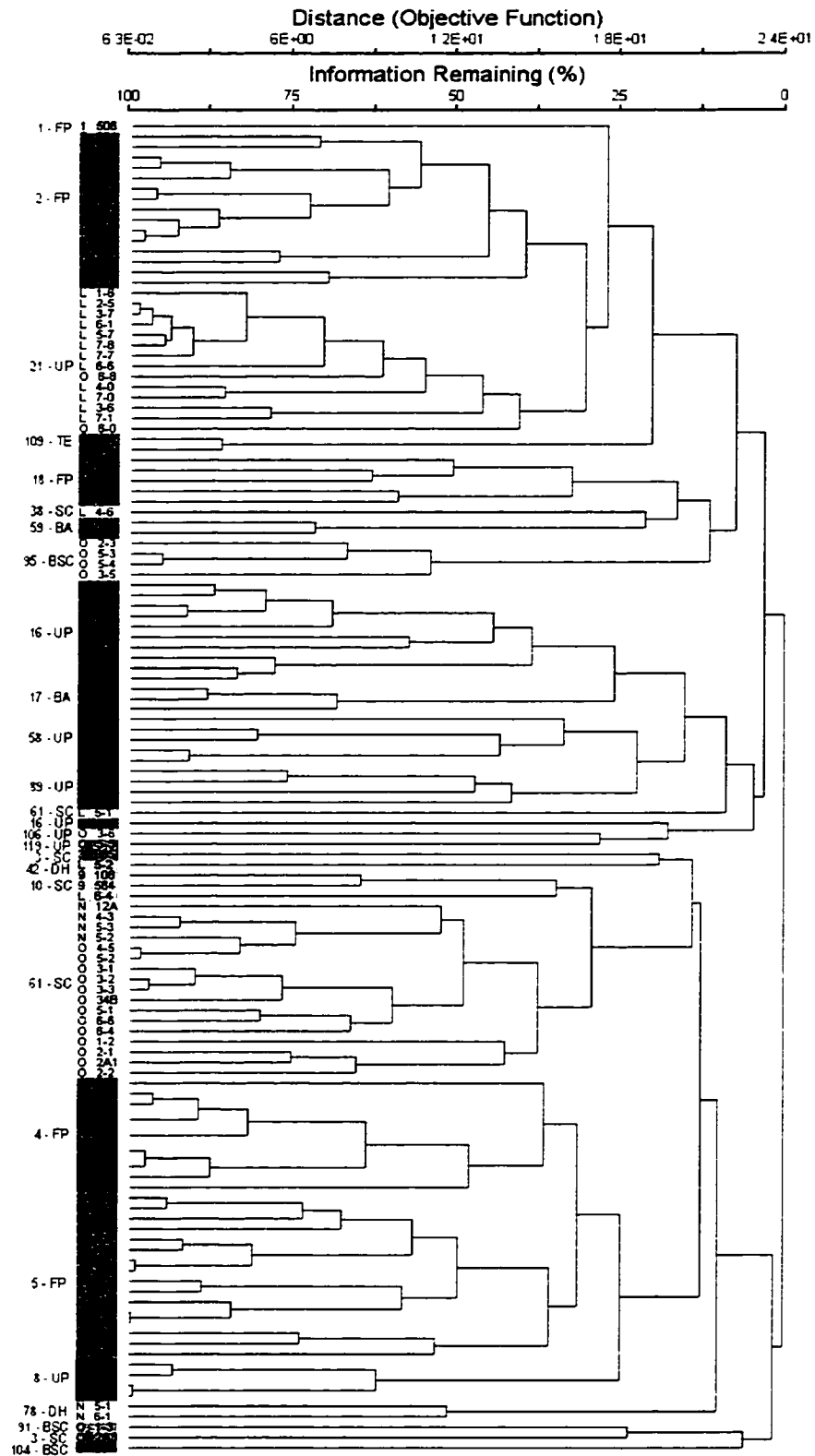


**Figure 3.8.** NMDS ordination biplot (with axes 1 and 2) of plots on the Nolichucky River showing vectors for environmental variables correlated with axes 1 or 2 with  $r^2 > 0.20$ . Plots are grouped by landform class.

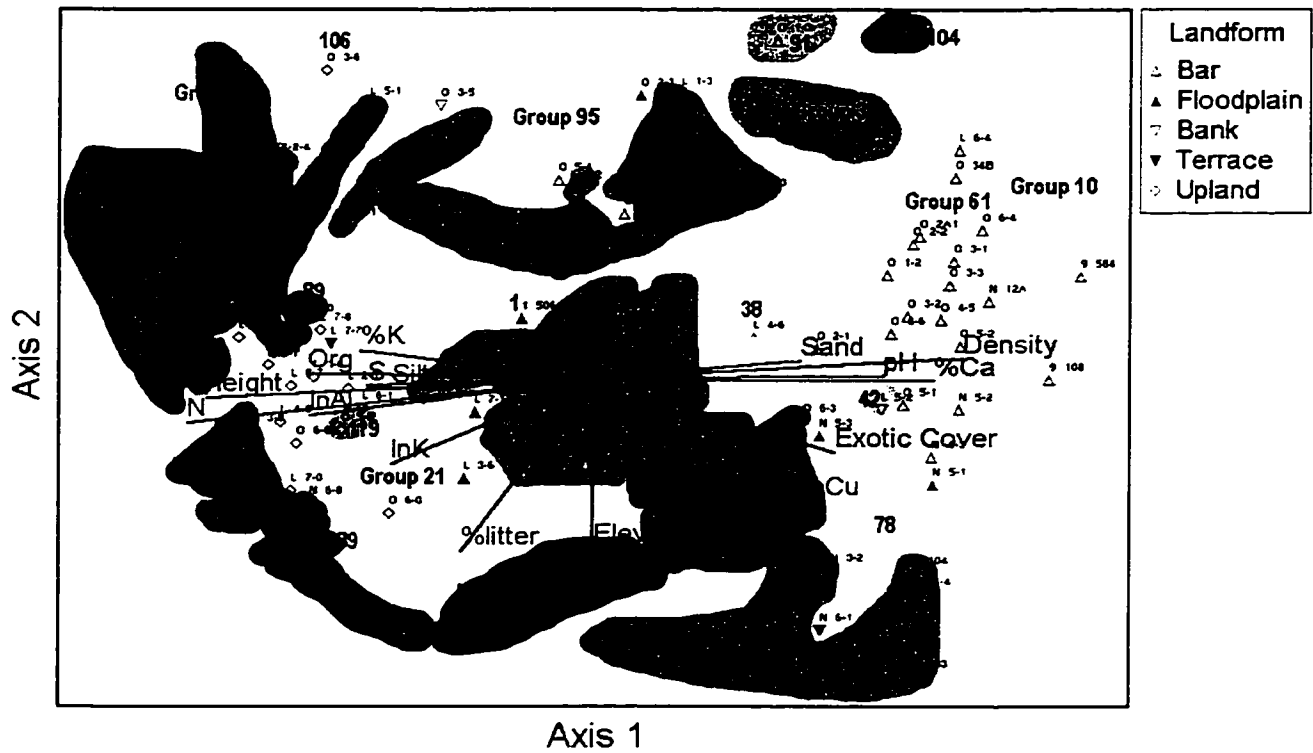




**Figure 3.9.** UPGMA Cluster dendrogram. Group numbers and geomorphic codes are in red. The geomorphic codes include FP (floodplain), UP (upland), SC (scour), BSC (bedrock scour), BA (floodplain bank), TE (terrace), and DH (anthropogenically disturbed herbaceous vegetation).



**Figure 3.10.** Positioning of clustered groups (color-shaded with group numbers as labels) on axes 1 and 2 of the ordination of plots on all rivers. Group numbers and colors correspond to numbers and colors in Figure 3.9 and numbers in Table 3.7.



**Figure 3.11.** Photographs of floodplain and terrace communities. A. *Carpinus caroliniana* dominated floodplain on the Little Tennessee River (Group 2). B. *Platanus occidentalis* - *Liriodendron tulipifera* dominated floodplain on the Little Tennessee River (Group 4). C. Floodplain bank community on the Little Tennessee River with *Rhododendrum maximum* (Group 17). D. *Verbesina alternifolia* disturbed herbaceous vegetation floodplain community on the New River (Group 78, Photo by Tom Philippi). E. Nolichucky River terrace community with *Piptochaetium avense* grassy understory (Group 109).

A.



B.



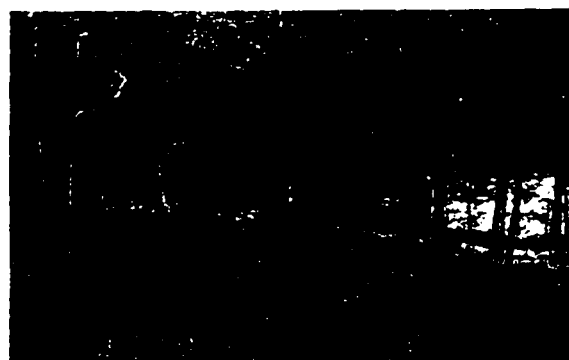
C.



D.



E.



**Figure 3.12.** Photographs of bar communities. A) *Ulmus alata* bedrock scour bar on the Nolichucky River (Group 104). B) *Salix nigra* bedrock scour bar on the Nolichucky River (Group 91, Photo by Josh Liebschutz). C) *Platanus occidentalis* rocky scour bar on the Nolichucky River (Group 61). D). Close up of the bar pictured in C. E) Rocky transition zone on the Nolichucky River (Group 95). F) Scour island on the Little Tennessee River with *Betula nigra* (Group 3, Photo by Amy Brown). G). Silt bar on the New River (Group 10).

A.



B.



C.



D.



E.



F.



G.



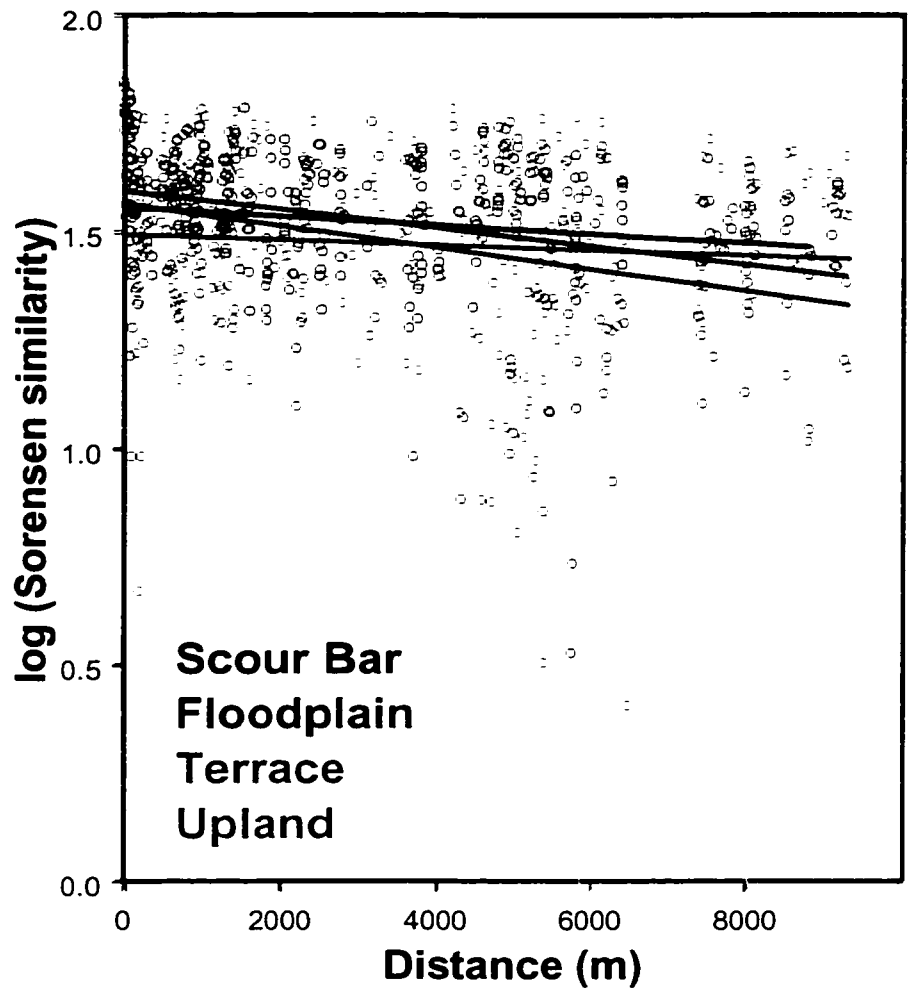
### *Distance decay of similarity*

At the small spatial scale (among rivers) floodplains had higher rates of distance decay than uplands, as reflected by their slopes. Floodplains also had higher overall similarity with a higher intercept than uplands. None of the other differences among geomorphic positions was significant (Table 3.8; Figure 3.13). At the large spatial scale (across rivers), there was no significant difference in distance decay rate among geomorphic positions. However, the overall similarity among plots was higher in scour bars and floodplains than in terraces and uplands. Uplands did not have a significantly different intercept than terraces, and neither did floodplains and scour bars (Table 3.8; Figure 3.14). The results for terraces may be insignificant because few terraces were sampled.

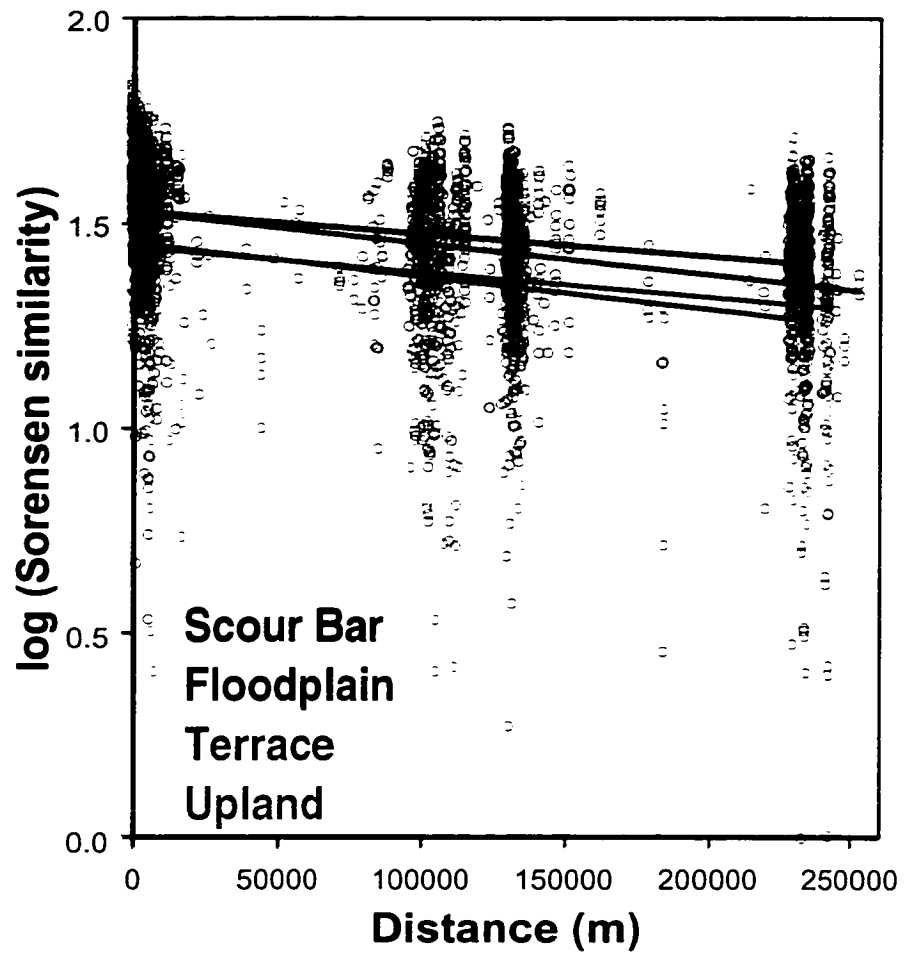
**Table 3.8.** Randomization results for comparison of distance decay of similarity among geomorphic positions. Stars indicate significance for the difference in slope or intercept between the two geomorphic positions (95%  $P=0.05/6$  with a Bonferroni adjustment).

<b>Multiple Rivers Scale – all distances up to 260,000 m</b>				
	<i>Intercept difference</i>	<i>P</i>	<i>Slope difference</i>	<i>P</i>
Upland - Scour Bar	-0.09	<b>0.002*</b>	-0.00002	0.89
Upland -Floodplain	-0.09	<b>0.002*</b>	0.00019	0.108
Upland -Terrace	0.004	0.886	0.0001	0.62
Terrace -Floodplain	-0.08	<b>0.002*</b>	0.0001	0.59
Terrace – Scour Bar	-0.09	<b>0.002*</b>	-0.0001	0.51
Floodplain - Scour Bar	0.006	0.71	0.0002	0.076
<b>Single River Scale – distances &lt; 10,000 m</b>				
	<i>Intercept difference</i>	<i>P</i>	<i>Slope difference</i>	<i>P</i>
Upland - Scour Bar	-0.07	0.026	0.004	0.61
Upland -Floodplain	-0.11	<b>0.002*</b>	0.017	<b>0.004*</b>
Upland -Terrace	0.07	0.206	-0.019	0.22
Terrace -Floodplain	-0.04	0.300	-0.002	0.88
Terrace – Scour Bar	-0.002	0.980	-0.01	0.28
Floodplain - Scour Bar	-0.04	0.055	-0.01	0.052

**Figure 3.13.** Distance decay of similarity for four geomorphic positions. Includes plots less than 10,000 meters apart (reflecting distance decay within one river).



**Figure 3.14.** Distance decay of similarity for four geomorphic positions across all rivers.





## DISCUSSION

I found recurrent types of vegetation and environmental variables that corresponded to geomorphic position, consistent with current understanding about the relationship between geomorphic position and vegetation within rivers. However, plant species composition was also influenced by a geographic gradient reflecting variation among the three rivers, which could be attributed in part to environmental differences among the three rivers and possibly to the spatial autocorrelation of vegetation within a river because of the relatively easier dispersal within a watershed than between watersheds.

The most frequently flooded sites showed the highest amounts of compositional similarity (at any distance, floodplains and scour bars were more similar than uplands) and, within a watershed, floodplains had a higher rate of distance decay than uplands. This could be a consequence of flooded sites being driven more by chance events of immigration than upland sites. Upland sites showed very little distance decay within the watersheds, perhaps because vegetation in uplands has had a longer period of time in which to become established with respect to underlying environmental patterns.

As expected, geomorphic variables related to a flood gradient had consistent, predictable effects on vegetation and environmental patterns across the three rivers (as shown in Axis 1 of the ordination in Figure 3.4), but there were also differences among the rivers which were reflected in axes 2 and 3 of the ordination (Figure 3.5). The three rivers differed in that the Nolichucky River plots had the shallowest soil depth (consistent with its bedrock channel), and the highest landform index values, consistent with the steep canyon walls, while the New River was the highest in elevation.

Several flood related variables consistently occurred across the three rivers (Figure 3.4). The upland plots on the left side of axis 1 were furthest from the river, had the finest grained soils (with the highest level of silt), and had the highest levels of nitrogen, %K, lnK, organic matter, and lnAl, which is consistent with more developed, mature soils rather than alluvial material. On the other hand, the bar and floodplain plots had higher pH, %Ca, density, and lnCu consistent with fertile alluvial soils. Bars had the highest amount of sand in the soil, which could be explained by frequent flooding that carries away finer sediments and deposits sand. Floodplains were differentiated from bars by greater soil depth and litter cover (consistent with reduced flood intensity, slower water, and increased sediment deposition).

At the individual river scale, several patterns emerge. The vegetation of all three rivers is organized along a flood gradient, with many of the same environmental variables important for all of the rivers despite the geographic distance among them. Flooding (measured as height above water) is also related to soil fertility (with higher pH soils being more frequently flooded) and the grain size of the substrate. The ordination diagram does not reflect the importance of light differences among the communities, which also co-varies with flooding and sediment size. The most intensely flooded communities (bars) had the largest sediments and the most light (both because vegetation had been removed and/or the rocky substrate was unsuitable for many tree species). Geomorphic position incorporates many of these variables, and thus does a good job of predicting riparian vegetation patterns, as reflected on the ordination diagram and in the cluster analysis.

The rivers differed slightly in the degree to which particular variables were important. For example, in the Nolichucky and Little Tennessee Rivers, % gravel is an important

variable, while it is not important on the New. The New in general has more silt and sand (and fewer rocky cobble bars), which may be a consequence of the underlying geology being somewhat different in the New River and possibly more basic (Table 1). On the Nolichucky, LFI is important for species composition, which may be due to its being a steep gorge with high walls, or due to the fact that the uplands of the Nolichucky have different underlying geology on the south vs. north side of the river (NC Geological Survey 1991), which could co-vary with LFI. Elevation shows up as important on the New and Little Tennessee, but this is likely because all of the uplands plots on these rivers have higher elevation than the riparian plots because the rivers have such low gradient. Slope is more important on these rivers because the uplands have higher slopes than the flat floodplains. There are some slight differences in micronutrients among the three rivers, perhaps relating to underlying geology.

There are several floristic patterns that emerge from the community classification that I would like to mention briefly. Some species (*Platanus occidentalis*, *Liriodendron tulipifera*, *Lindera benzoin*, *Juglans nigra*, *Cornus amomum*, *Ilex verticillata*, *Microstegium vimineum*) were widespread in the riparian communities on all three rivers. Other species were specific to a particular river, or were only found with high abundance in one region. *Aesculus flava* was found in abundance in and around floodplains on the New River, but not the other two rivers. Of the three rivers, only on the Little Tennessee were *Carpinus caroliniana*, *Arundinaria gigantea*, and *Betula nigra* found in abundance as community dominants, and *Pyrularia pubera*, *Itea virginiana*, and *Quercus imbricaria* were not seen on the more northern rivers. Only found on the Nolichucky River were *Liquidambar styraciflua*, *Philadelphus hirsutus*, *Carya pallida*, *Diervilla rivularis*, *Dicentra eximia*, and *Saxifraga careyana*. *Fraxinus pennsylvatica* was much more abundant in the Nolichucky

than the other rivers, as was the exotic species, *Polygonum cuspidatum*. These floristic patterns likely reflect regional distribution patterns of these species, and in some cases (such as the with exotic species), migration through river corridors, although more research is needed to understand the distributions of these particular species.

Floristic patterns were also related to geomorphic position. For example, *Betula nigra*, *Justicia americana*, *Salix nigra*, and *Spiraea virginiana* are a few of the species restricted to bars; *Platanus occidentalis* and *Carpinus caroliniana* characterize both bars and floodplains; and *Quercus montana* was only found in the uplands. These patterns reflect environmental differences and species habitat requirements.

The communities classified in the cluster analysis fit into groups based on geomorphic position and river. Bars and floodplains resulted in distinct groups, but uplands and terraces overlapped both in the cluster analysis and the distance decay analysis. Terraces were formed by ancient flood processes, but are very rarely exposed to flooding. That they overlap so much with uplands suggests that without frequent flooding, riparian communities may succeed communities very similar to uplands. The Nolichucky has more bar communities than the other rivers because bars are a more prevalent feature there. Bar communities are dominated by herbaceous and shrubby species, while floodplains are forested (but with many herbaceous species).

Some of the frequently flooded communities that I classified and named should be considered in light of ongoing immigration processes. For example, the *Leersia virginiana* – *Impatiens capensis* – *Hypericum muticum* – *Boehmeria cylindrica* Herbaceous Vegetation Association (group 38) or the *Festuca subverticillata* – *Sciripus expansus* – *Scheonoplectus tabermontana* (*Carex vulpinoide*, *Eupatorium perfoliatum* var. *perfoliatum*, *Glyceria*

*striatula*, *Hypericum muticum*) Herbaceous Vegetation Association (group 10) are likely very dynamic in terms of their species composition because they flood frequently, although the species listed in their names were the most prevalent at the time the community was surveyed. Because there maybe high species turnover on these disturbed sites, these groups might be better identified in terms of flood regime than by traditional classification approaches that assume stable species composition. In addition, ongoing surveys are needed to establish whether species turnover is common on these sites.

## CONCLUSION

Riparian vegetation is affected by processes occurring across a range of spatial scales. Among rivers, underlying geology, topography, and the geographic distribution of species relate to vegetation distribution. Flooding, which provides disturbance, sediment transport and deposition (with particle size related to flood water velocity), soil nutrient enrichment, and hydrochorous seed dispersal, creates consistent, predictable environmental gradients that are apparent across a broad geographic region. These patterns are reflected in geomorphology and plant species composition. In addition to environment, riparian vegetation is also structured by immigration processes, which was reflected in the amount of spatial autocorrelation of riparian vegetation among different types of habitats. The most frequently flooded riparian habitats had greater compositional similarity for any given distance, and greater rates of distance decay within a watershed than upland habitats. Uplands had very little distance decay within a watershed, perhaps because upland communities have been established for a longer period of time and are structured relatively more by the underlying environment than by immigration processes. Dynamics in vegetation

composition due to factors such as chance immigration events make traditional vegetation classification by habitat difficult, and suggests that a classification approach is needed that can incorporate such processes.

## Chapter 4

### PROPAGULE INFLUX IN SOUTHERN APPALACHIAN RIPARIAN PLANT COMMUNITIES

#### ABSTRACT

Ecological communities can be visualized as occurring along a gradient from those structured largely by immigration processes to those structured largely by competition processes. Propagule influx is an important factor in determining the degree to which a community is immigration-driven. However, propagule influx has rarely been quantified in ecological communities and variation in propagule influx among communities is largely unknown. I predicted that riparian plant communities are more driven by immigration processes than upland communities due to increased influx of flood-borne propagules. To test this hypothesis I quantified patterns in propagule deposition (due to recent dispersal) of vascular plant species across a flood gradient by establishing propagule deposition pads along transects spanning all geomorphic positions in the riparian areas and adjacent uplands of three southern Appalachian rivers. For each site, I assessed the species richness and abundance of propagules over a period of three years by sampling deposition pads twice each year and germinating the samples in a greenhouse to identify propagule composition and abundance.

Diversity and abundance of both native and exotic species of propagules were higher in the more frequently flooded geomorphic positions and in sites that had flooded in the past three years. Specifically, propagule influx was consistently highest in scour-bar communities, high on floodplains and terraces and lowest on adjacent uplands. The increase in propagule abundance and diversity in frequently flooded sites is consistent with the hypothesis that propagule influx increases with flooding frequency.

The diversity and abundance of propagules varied among sampling dates and river systems. Variation among sampling dates may reflect recent variation in flood patterns. The New River had the highest levels of propagule diversity and abundance, probably reflecting the greater regional soil fertility derived from the adjacent amphibolite-rich mountains, and the largest percentage of exotic species, probably reflecting the greater level of human development of the adjacent landscape.

## INTRODUCTION

Riparian areas are unusual in that they are often observed to be hotspots for species richness and exotic plant invasion (Pysek and Prach 1994; Planty-Tabacchi et al. 1996; Stohlgren et al. 1999), which may be attributable to unusually high immigration rates. The composition of ecological communities can be visualized as resulting from the opposing processes of immigration and extinction, with species richness high in areas of low extinction and/or high immigration (Chapter 1, 2). In addition, high immigration systems are more likely to have high levels of exotic species and to have low compositional predictability. I suggest that riparian systems, unlike most terrestrial systems, are structured largely by



immigration processes, owing to high propagule influx, coupled with recurrent flood disturbance.

Propagule influx is the quantity and diversity of seeds or other propagules entering a plant community (Williamson and Fitter 1996), and is likely high in riparian areas due to inputs of flood-dispersed seeds. A number of studies have explored the role that rivers play in seed dispersal or as corridors for the spread of invasive species (Skoglund 1990; Thebauld and Debussche 1991; Johansson et al. 1996), although only a few studies have quantified dispersal rates and patterns of propagule dispersal in riparian plant communities. Nilssen et al. (1989) conducted an experiment where they cast small blocks of wood of different sizes into a Swedish river and observed marked differences in their dispersal. Schneider and Sharitz (1988) showed that waterborne seeds on the Savannah River in Georgia tend to be deposited in areas around logs when floodwaters settle. However, none of these studies documented patterns in the diversity of seed.

I have hypothesized that flooding provides a mechanism for high seed input into riparian communities and for the dispersal of exotic species (Chapter 1, 2). I have further hypothesized that that propagule influx is highest in the most frequently flooded areas, and that propagule influx varies with time due to seasonal patterns of seed release (Chapter 1, 2). The objective of this chapter is to document variation in patterns of seed deposition across a flood gradient as observed along three southern Appalachian rivers so as to test these expectations. For the purpose of this paper, 'seed' refers to not just true seeds, but also all other propagules including rhizomes and other vegetative structures.

## METHODS

### *Sampling Strategy*

Data collection was carried out on three rivers: the New, Nolichucky, and Little Tennessee. These three rivers were selected to represent the broad range of geologic settings and land-use histories associated with rivers of the southern Appalachians (as described in Chapter 3). Sites were stratified by geomorphic position to assure a broad range of flooding frequencies and vegetation types (Hupp and Osterkamp 1996). Specifically, I measured variation in seed deposition across a geomorphic sequence of sites from scour bars (most frequently flooded), through floodplains, floodplain banks, and terraces (which rarely or never flood), to uplands (not flooded). To capture the range of variation with geomorphic position, I sampled transects at seven locations on each river. Each transect ran perpendicular to the river and spanned all geomorphic positions present between the upland areas on each side of the river. Along these transects I sampled propagule influx by placing a 50-cm diameter propagule deposition pad on each geomorphic position along each transect associated with the vegetation plots described in Chapters 2 and 3. Geomorphic positions were distinguished by abrupt changes in vertical height above the river and by changes in substrate (see Chapter 3). Near each pad, soil nutrient data was collected as described in Chapter 3 in order to corroborate soil fertility to patterns in seed deposition among the three rivers.

One of the problems with measuring seed deposition is that it can be highly variable over small spatial scales as there are many local sources of seeds. Seed deposition also varies seasonally as different species release seeds at different times. To account for small-scale spatial variation in propagule influx, deposition pads were replicated on many of the

geomorphic positions. To account for temporal variation in seed deposition patterns, seeds were collected twice each year (June and September) over a three-year period (1998 – 2000).

I established 91 deposition pads in early May of 1998. In June of 1999 I established 40 additional upland site deposition pads (which had not been surveyed initially) and 41 additional pads in riparian sites so as to better represent variation with geomorphic position. Data were collected from these additional sites only in September of 1999 and during the two 2000 sampling events.

### *Deposition Pad Construction and Seed Collection*

Propagule deposition must be measured in such a way as to include seeds added to a site (via flood, wind, animals, or gravity) subsequent to the time the deposition pad was established or last sampled, but to exclude seeds from the local seed bank. Deposition pads were constructed as white feldspar clay pads similar to those used by hydrologists to measure sedimentation rates (Baumann et al. 1984; Hupp and Bazemore 1993). This method of collecting seeds was chosen over other methods because clay pads are more likely to endure the intense floods of mountainous rivers than other propagule collection methods owing to the fact that they conform to the soil surface and stay in place under flowing water. Another advantage of this method is that the deposition of seeds and sediment on the clay pads simulates the natural deposition of seeds on the ground, unlike traditional seed traps that strain seeds from the water or that concentrate seeds, excluding natural processes such as herbivory or flooding that would otherwise lower seed deposition rates. To collect seeds, all deposited material was scraped from a square 0.025 m<sup>2</sup> area on each clay pad. When seed collections were made, a record was kept of whether the deposition pad had experienced

flooding in order to directly compare flooded and unflooded pads and thus assess the role that flooding may play in seed dispersal. After the deposition pads had been sampled, they were replenished with fresh clay to provide a clean slate for the next sample.

### *Seed Germination*

To identify and quantify seed occurrences, samples were germinated in a greenhouse. Before germination, samples were cold stratified for three to six months to break cold dormancy (Baskin and Baskin 1998). Each sample was placed in a separate container over Pro-mix potting soil, and water was added as necessary using a misting system. Any seeds large enough to be identified by eye were identified and removed before germination. Excess leaf litter, where present, was rinsed through a 0.2 mm sieve (to collect any attached seeds) and removed. Germinating plants were removed as soon as they could be identified. Flats with multiple individuals of the same species were thinned as necessary to avoid competition among plants. Germinated seedlings were allowed to grow for up to six months, and species were identified to the finest taxonomic level possible. Plant nomenclature follows Kartesz and Meacham (1999). Species exotic to the United States were identified as such using the USDA Plants Database (USDA 2001).

### *Data Analysis*

Comparisons were made of seed species richness and abundance among locations and time periods. Seed abundance represents the total number of seeds collected on a pad, for all species. Average seed species richness and seed abundance per pad were compared using Kruskal-Wallis tests for each of the six time periods, and between September and June to

assess temporal and seasonal variation in seed abundances respectively. Where propagule deposition pads had been replicated in the same geomorphic position, the values were averaged.

To control for temporal variation when comparing deposition pad values across geomorphic positions and rivers, total species richness and total abundance of seeds per deposition pad were averaged over the last three sampling periods. I excluded the first three sampling periods for all analyses but those over time because they did not include uplands deposition pads. The average pad values (over the three time periods) were then used to compare seed richness and abundance across geomorphic positions. Seed richness and abundance were also compared for pads that had been flooded versus those that had not been flooded (which is much like comparing scour bars with all of the other plots), because some of the pads expected to flood in scour bar geomorphic positions did not due to microsite elevation variations (see Table 1).

Comparisons across the four geomorphic positions and in flooded versus unflooded pads were made using Kruskal-Wallis tests and plotted as boxplots. Kruskal-Wallis tests were conducted using the PROC NPAR1WAY procedure with SAS version 8 (SAS Institute 1999). The boxplots have added notches, the endpoints of which are located at the median plus and minus  $1.58(IQR/\sqrt{n})$ , where IQR is the interquartile range and  $n$  is the group sample size. The medians (central lines) of two box-and-whisker plots are significantly different at approximately the 0.05 level if the corresponding notches do not overlap. Whiskers of the boxplots represent maximum and minimum values or a standard quartile span of the median plus and minus  $1.5 * IQR$  if values exceed the standard span. All points outside of the span

were plotted separately and are considered extreme values (Mathsoft 2000). Boxplots were created using S-Plus (S-Plus 2000)

I also compared the richness and abundance of exotic seeds across geomorphic positions, in flooded and unflooded pads, and among rivers. As was done for total species richness and abundance, exotic seed species richness and abundance values were averaged across the last three sampling periods. In addition to comparing species richness and abundance of exotic seed, I compared the percentages of all seeds that were exotic, and the percentages of all species that were exotic across geomorphic positions, flooded and unflooded pads, and rivers. Finally, I compared soil nutrient levels in floodplains and scour bars of the New River versus the other two rivers to test the hypothesis that the New River has higher soil nutrient levels than the other two rivers due to high levels of amphibolite in the region, which could relate to seed richness and abundance levels seen on the New. Comparisons were made using Kruskal-Wallis tests as described above.

## RESULTS

A total of 173 propagule deposition pads were established, 62 on the Little Tennessee River, 55 on the New River, and 56 on the Nolichucky. After replicated deposition pads were averaged, there were 131 geomorphic positions where data were collected. The number of samples (with replicates on one position averaged to one value) per geomorphic position is shown in Table 4.1. I observed 4559 individual plants from seed pads representing 373 species (including 50 exotic species) over three years. Seed species richness varied from 0 to 41 species on a deposition pad, while seed abundance varied from 0 to 154 individuals. The differences in distribution of seed species richness and seed abundance among the 6

collection periods are shown in Figures 4.1 and 4.2, respectively. There were usually fewer than 3 seeds per deposition pad, and fewer than 2 species. In June 1999 and June 2000 the distribution of species was slightly more spread out, with more plots having more species (Figure 4.1). In general, the patterns of seed species richness matched the patterns in seed abundance (Figures 4.3 to 4.6).

#### *Variation among the sampling times*

For each location sampled there was significant variation between the six sampling periods in seed species richness and seed abundance (averaged over replicate deposition pads) as shown in Figure 4.3 (Kruskal-Wallis Test for seed abundance: Chi-square = 43.57,  $P < 0.0001$ ,  $df = 5$ ; for species richness: Chi-square = 143.73,  $P < 0.0001$ ,  $df = 5$ ). Comparisons of species richness and abundance among the 2 months during which samples were collected were significant (Kruskal-Wallis test for seed abundance: Chi-square = 12.26,  $P = 0.0005$ ,  $df = 1$ ; for species richness: Chi-square = 16.54,  $P < 0.0001$ ,  $df = 1$ ), as were comparisons among the three years (Kruskal-Wallis test for seed abundance: Chi-square = 13.38,  $P = 0.001$ ,  $df = 2$ ; for species richness: Chi-square = 99.74,  $P < 0.0001$ ,  $df = 2$ ).

#### *Variation among geomorphic positions*

There was significant variation in seed species richness and seed abundance among the four geomorphic positions, with a general increase in richness and abundance from unflooded upland plots to frequently flooded scour bar plots (Figure 4.4; Kruskal-Wallis test for seed species richness: Chi-square = 35.85,  $P < 0.0001$ ,  $df = 4$ ; for seed abundance: Chi-square = 30.10,  $P < 0.0001$ ,  $df = 4$ ).

**Table 4.1.** Number of propagule deposition pads (replicates averaged) per geomorphic position. In parentheses is the number of pad sites that flooded during the 3-year period of the study.

<i>Landform</i>	<i>Little Tennessee</i>	<i>New</i>	<i>Nolichucky</i>	<i>Total</i>
<b>Scour</b>	4 (4 flooded)	5 (4 flooded)	14 (12 flooded)	23 (20 flooded)
<b>Floodplain</b>	20	14	8 (1 flooded)	42 (1 flooded)
<b>Floodplain bank</b>	5 (1 flooded)	3 (1 flooded)	5 (2 flooded)	13 (4 flooded)
<b>Terrace</b>	4	6	3	13
<b>Upland</b>	15	12	13	40
<b>Total</b>	48	40	43	131

**Table 4.2.** Kruskal-Wallis test for comparison of average nutrient levels (for nutrients with a significant difference in one of the geomorphic positions) in floodplains and scour bars of the New River versus other rivers. Nutrients for which the New River had a significantly lower value are in parentheses; for the rest the New River had a higher value. Bold indicates significance at the 95% level.

<b>Nutrient</b>	<b>Floodplains</b> n = 16 (New), 36 other rivers			<b>Scour Bars</b> n = 6 (New), 26 (other rivers)		
	<i>Chi-square</i>	<i>d.f.</i>	<i>P</i>	<i>Chi-square</i>	<i>d.f.</i>	<i>P</i>
<b>(%Mg)</b>	7.06	1	<b>&lt;0.01</b>	5.59	1	<b>0.02</b>
<b>(%Na)</b>	4.50	1	<b>0.03</b>	0.63	1	0.43
<b>CEC</b>	9.08	1	<b>0.02</b>	0.84	1	0.36
<b>(Ln B)</b>	<0.01	1	0.98	4.22	1	<b>0.04</b>
<b>Ln Ca</b>	5.38	1	<b>0.02</b>	0.42	1	0.52
<b>Ln CaMg</b>	9.57	1	<b>&lt;0.01</b>	8.11	1	<b>&lt;0.01</b>
<b>Ln Cu</b>	14.42	1	<b>&lt;0.01</b>	7.05	1	<b>&lt;0.01</b>
<b>Ln Fe</b>	4.93	1	<b>0.03</b>	0.52	1	0.47
<b>Ln K</b>	7.93	1	<b>&lt;0.01</b>	1.23	1	0.27
<b>Ln Mg</b>	4.67	1	<b>0.03</b>	0.04	1	0.85
<b>Ln Zn</b>	12.39	1	<b>&lt;0.01</b>	2.70	1	0.10



As shown in Figure 4.5, there were fewer seeds of exotic species in upland and terrace pads than in floodplains (Kruskal-Wallis test Chi-square = 10.51,  $P = 0.0327$ ,  $df = 4$ ) despite few floodplain and terrace plots actually flooding. Uplands had the fewest exotic species per pad, whereas floodplains and banks had the most exotic species (Kruskal-Wallis test: Chi-square = 10.15,  $P = 0.0379$ ,  $df = 4$ ). The percentages of seeds and species that were exotic followed similar patterns to the actual numbers of exotic seeds and species, with uplands and terraces having a lower percentage of exotic seeds and species than floodplains, scour bars, or banks (Kruskal-Wallis test for percent of species: Chi-square = 10.53,  $P < 0.0324$ ,  $df = 4$ ; for percent of seeds: Chi-square = 14.80,  $P < 0.0051$ ,  $df = 4$ ). One notable difference between the percentages and raw values is that floodplains had a higher percent of exotic seeds relative to the other geomorphic positions, and this comparison was more pronounced when looking at percentage of seeds (Figure 4.8).

#### *Variation among flooded and unflooded seedpads*

Seed species richness and abundance were greater in flooded plots than in unflooded plots (Figure 4.6; Kruskal-Wallis test for species richness: Chi-square = 4.45,  $P = 0.0350$ ,  $df = 1$ ; for seed abundance: Chi-square = 7.0,  $P = 0.0081$ ,  $df = 1$ ). These results should be viewed with the understanding that most of the flooded plots are scour bars (geomorphic position and flooding covary), with the consequence that there is some overlap between this result and the result from comparing geomorphic position.

There was no significant difference in the abundance or species richness of exotic seed between flooded and unflooded pads (Kruskal-Wallis test for exotic species richness Chi-square = 0.44,  $P=0.5064$ ,  $df=1$ ; for exotic seed abundance Chi-square = 1.99,  $P=0.1582$ ,

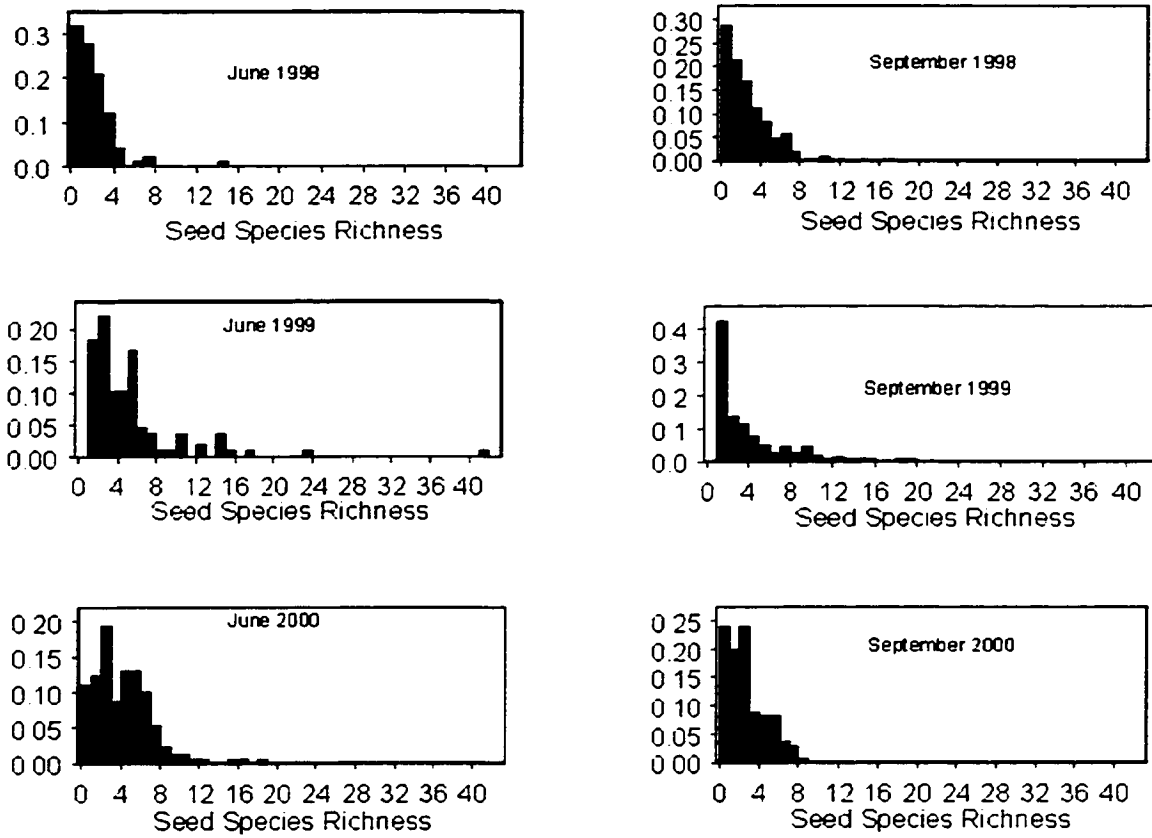
df=1). However, there were higher percentages of exotic seeds and species in flooded sites (Kruskal-Wallis test for percent exotic species: Chi-square = 5.97, P = 0.0146, df = 1; for percent exotic of all seed: Chi-square = 10.61, P = 0.0011, df = 1).

#### *Variation among rivers*

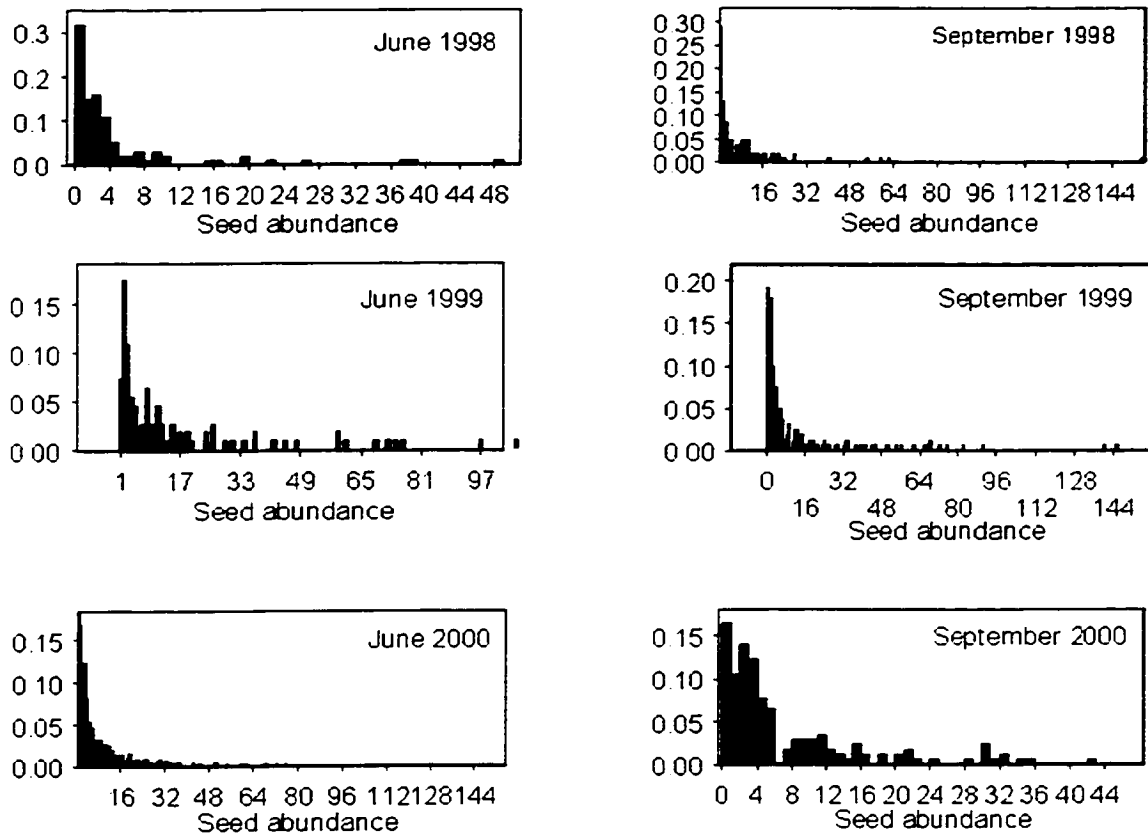
Propagule deposition pads from the New River data set had more species of seeds than the other two rivers (Figure 4.7; Kruskal-Wallis test: Chi-square = 8.07, P = 0.0177, df = 2, however the difference in seed abundance among the three rivers was not significant (Kruskal-Wallis test: Chi-square = 4.02, P = 0.1342, df = 2). The New River also had significantly higher levels of soil nutrients relative to the other rivers (Table 4.2).

The New River also had the highest number of exotic seeds and species, probably due to it having more seeds and species overall (Kruskal-Wallis test for exotic species richness: Chi-square = 6.06, P = 0.0483, df = 2; for exotic seed abundance: Chi-square = 9.01, P = 0.0110, df = 2. More importantly, the New River had a higher percentage of exotic seeds and species than did the other two rivers (Kruskal-Wallis test: for percent exotic species: Chi-square = 4.69, P = 0.0957, df = 2, for percent exotic seeds: Chi-square = 6.06, P = 0.0483, df = 2).

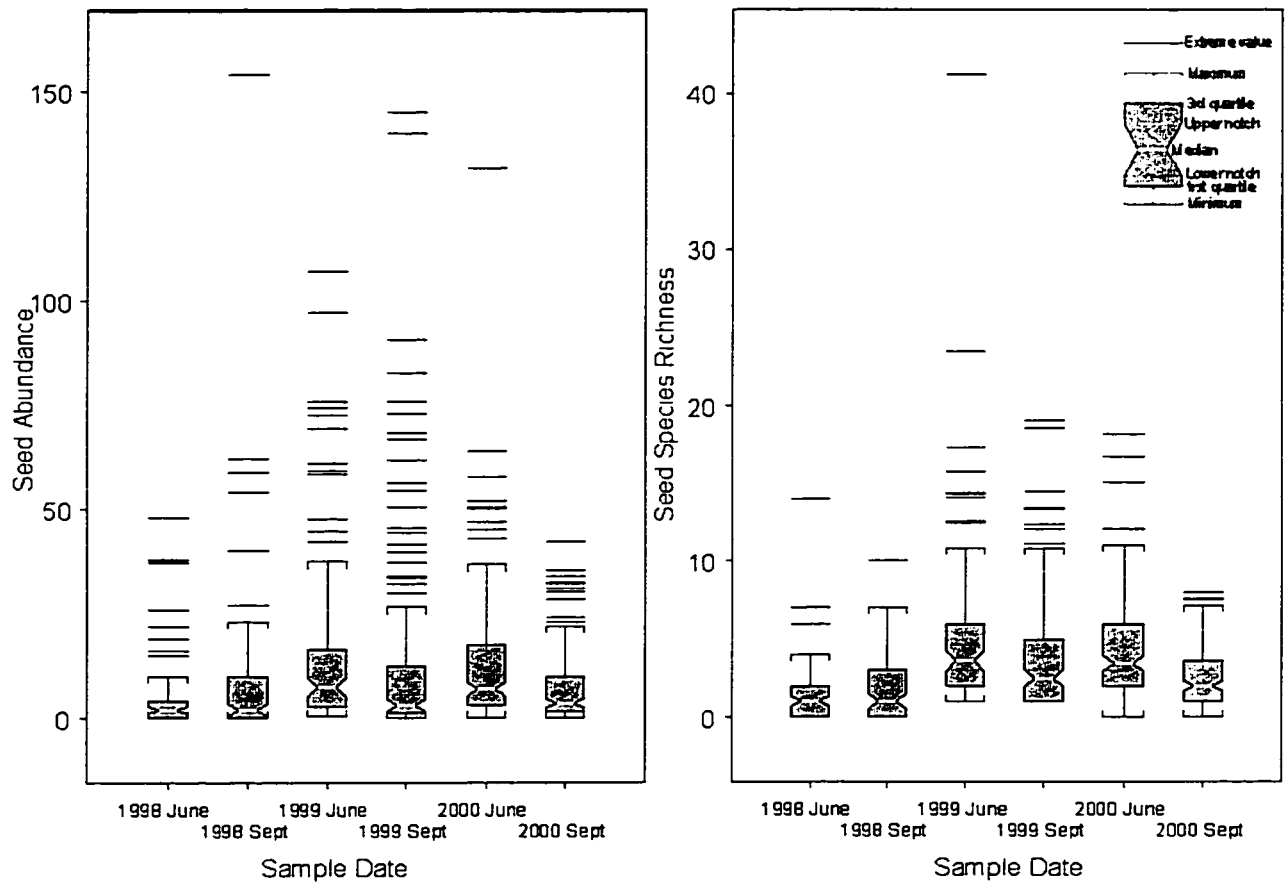
**Figure 4.1.** Histograms of seed species richness in the six sampling time periods. Bar interval is 1 species.



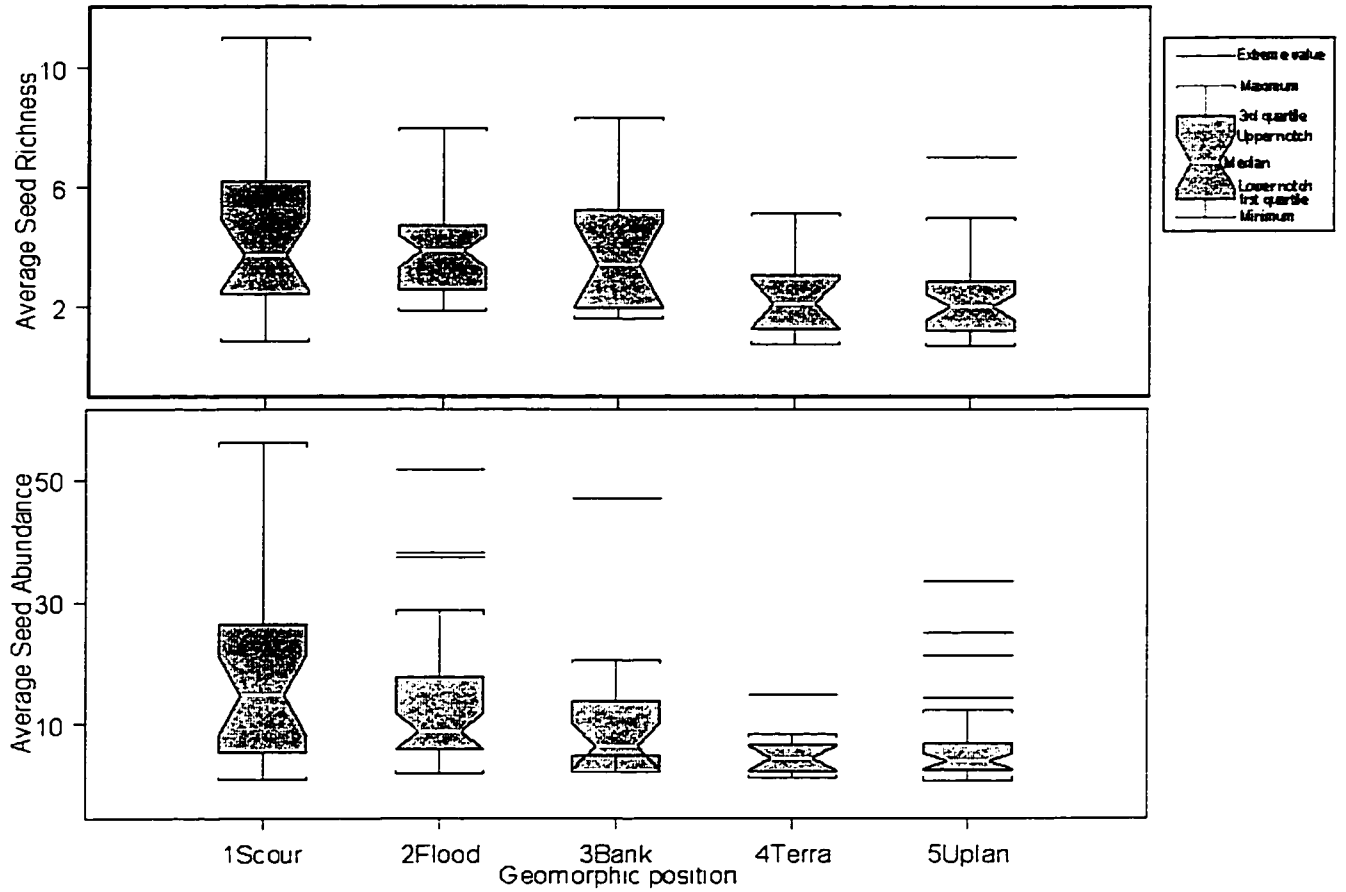
**Figure 4.2.** Histograms of seed abundances in the six time periods. Bar interval is 1 seed.



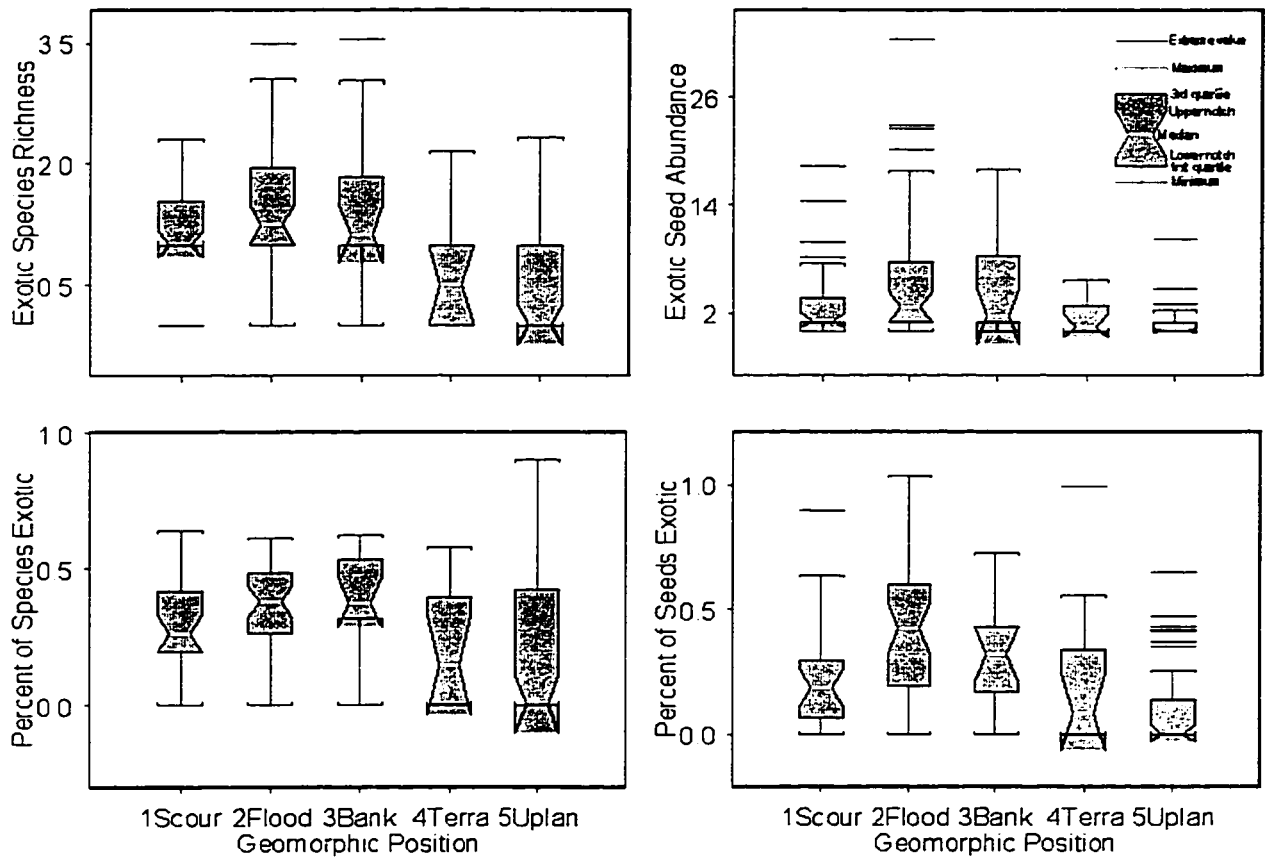
**Figure 4.3.** Variation in seed pad richness and abundance over 6 sample periods.



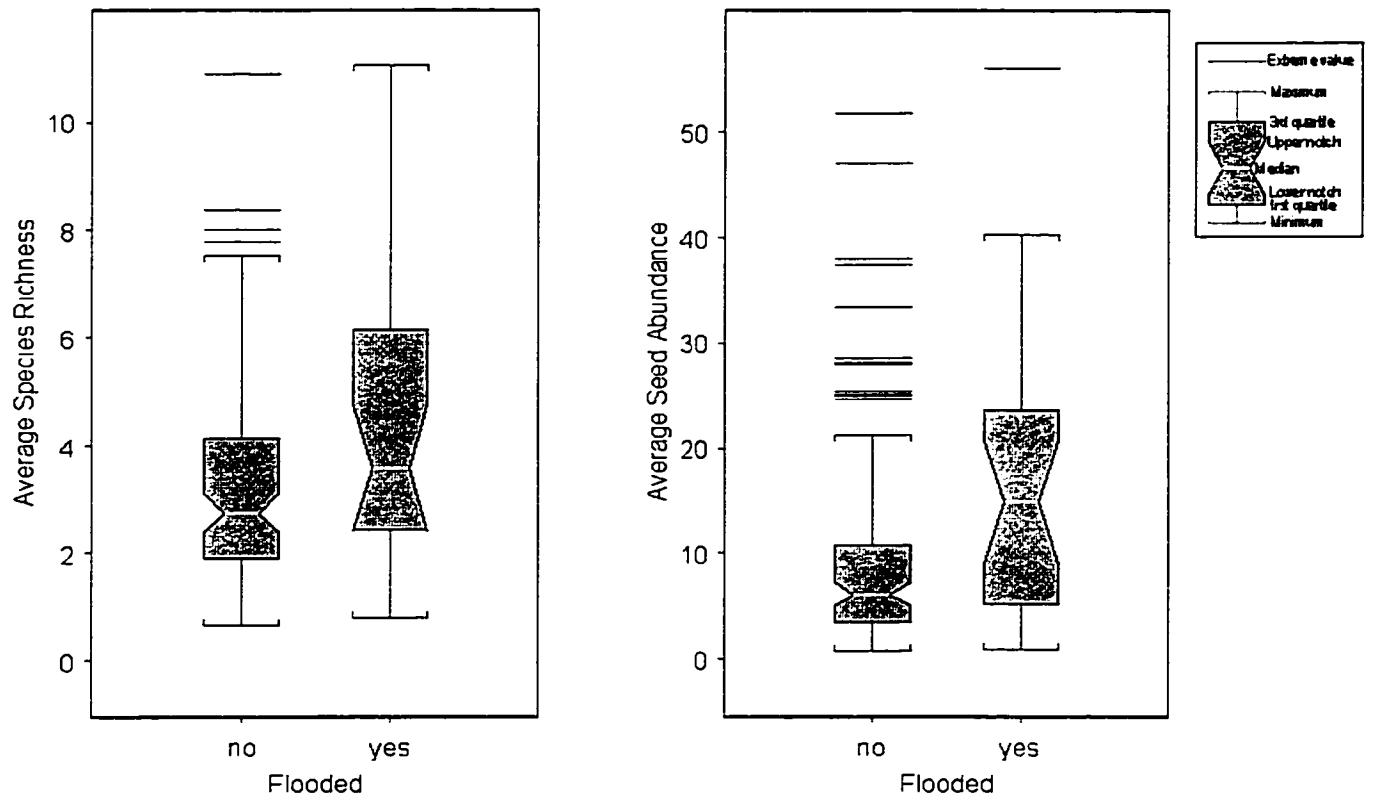
**Figure 4.4.** Standard box and whisker plots showing seed species richness and seed abundance (total number of seeds over all species) for 5 geomorphic positions averaged over three sampling periods (September 1999 – September 2000).



**Figure 4.5.** Variation in exotic species richness, exotic seed abundance, percent of species exotic, and percent of seeds exotic across geomorphic positions.

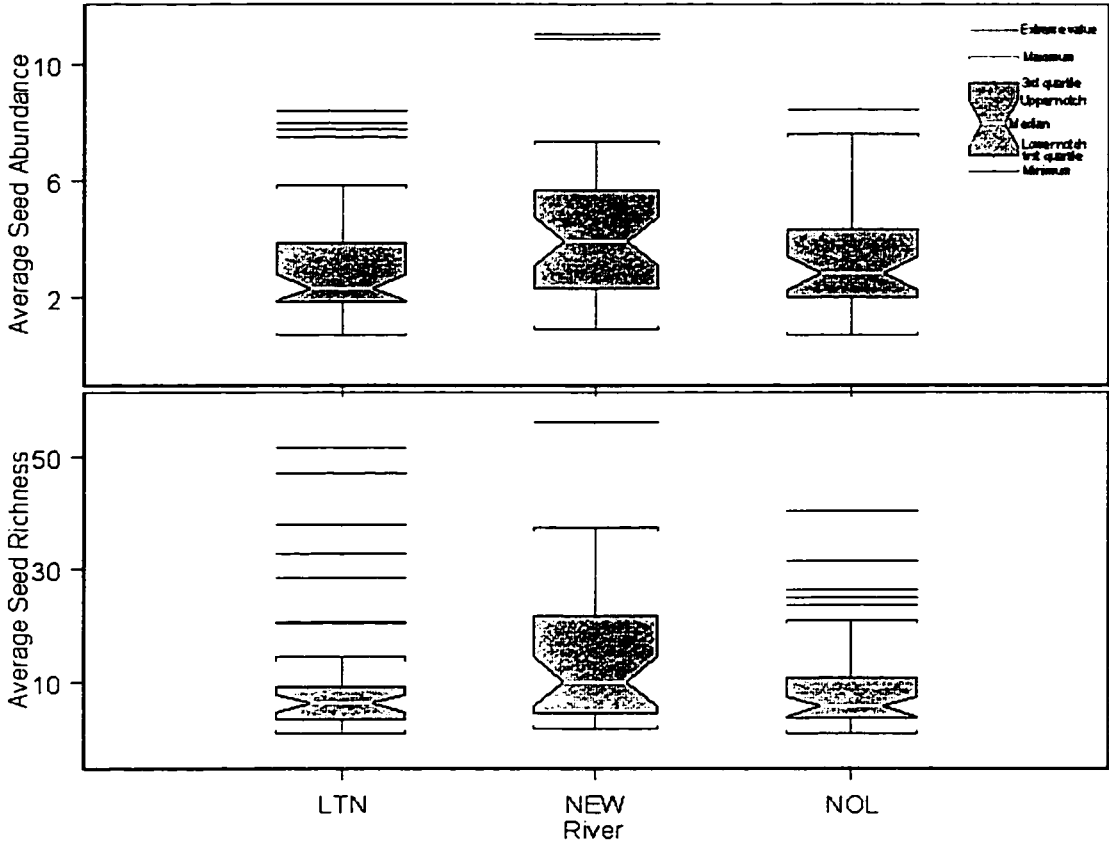


**Figure 4.6.** Standard box and whisker plots showing seed species richness and seed abundance for flooded and unflooded sites averaged over three sampling periods.





**Figure 4.7.** Variation in propagule deposition pad species richness and abundance across the three rivers averaged over three sampling periods.



## DISCUSSION

There was significant variation in seed deposition patterns across geomorphic positions, with the more frequently flooded sites having higher seed richness and abundance. There are several potential explanations for these differences. One possibility, which was supported in part by the increase in seed diversity and abundance on sites that had flooded in the past two years, is that flooding increases propagule influx. The 4 pads with the highest diversity and richness levels (greater than 140 seeds and/or greater than 20 species) were those that were completely buried with litter and sediment by flooding, or those that otherwise flooded with the highest frequency (> 5 times per year).

Other potential explanations for variation in diversity and abundance of propagules across geomorphic positions relate to the local vegetation found on those geomorphic positions. I have documented the changes in vegetation diversity of both native and exotic species across geomorphic positions (Chapter 3), and the diversity in the local vicinity of the propagule deposition pads would likely affect the contents of the pad. In the most frequently flooded sites, disturbance is high, and one finds a large number of species with a ruderal life-history strategy. One of the characteristics associated with a ruderal life-history strategy is large numbers of small seeds that can easily disperse and take advantage of ephemeral, disturbed habitats (Fenner 1985; Grime 1988). Many of the species in floodplains and scour bars are ruderals with large numbers of small seeds, whereas uplands have species with smaller numbers of larger seeds, a pattern that one might expect to be reflected in deposition pad composition. This result is consistent with my observation that the most abundant species in the pads were ruderals.

Diversity patterns in propagule rain varied with season and year. Some of this variation could have been due to differences in greenhouse conditions or to duration of propagule deposition pad observation. However, I accounted for the temporal variation by averaging richness and abundance values across the three sampling periods that had data for upland plots.

The variation in the percentages and numbers of exotic species seeds across geomorphic positions could reflect variations in exotic species numbers in extant vegetation (with more exotic species on the most flooded positions as discussed in Chapter 3), or it could reflect deposition exotic species seeds by floodwater. The plots with the highest numbers of exotic species and seeds (greater than 40 seeds and/or greater than 5 species) in this case were not those that had flooded most frequently, but rather bank or floodplain plots that had many exotic species in the local vegetation.

The New River had higher levels of seed richness and abundance, and a higher percentage of exotic species. This pattern may be the consequence of high levels of agricultural disturbance in the New River watershed relative to the other two rivers, which would lead to a prevalence of small-seeded ruderal species (as discussed in Chapter 3), combined with the generally more fertile soils of this area of amphibolite-rich rocks (Table 4.2).

Ultimately, any assessment of seed distribution pattern, cause, and effect depends on scale of observation, both temporal and spatial. Flow of river water is a mechanism by which seed dispersal occurs, though documentation of this phenomenon over a short timescale is difficult because there are many other factors affecting seed supply at the local scale.

This study is unusual because a large number of propagule deposition pads stratified across geomorphic positions were sampled repeatedly (which helps to account for small scale spatial and temporal variation in seed deposition). I was not able to differentiate propagule influx (or allochthonous seed inputs) from seeds that came from within the community, nor could I differentiate flood-dispersed seeds from those dispersed by other mechanisms such as wind or animals. Nevertheless, the patterns were consistent with the hypothesis that riparian areas have high propagule influx due to flooding, and that immigration processes drive the high diversity levels seen in riparian systems.

## CONCLUSIONS

Diversity and abundance of seed was highest in the most frequently flooded geomorphic positions, and the percentage of exotic species was higher in flooded sites. While the precise cause of these patterns is unclear, they nevertheless are consistent with the hypotheses that rivers serve as corridors for the movement of seeds and exotic species and that immigration processes such as high propagule influx drive the high diversity seen in riparian plant communities.

## Chapter 5

### CONTROL OF PLANT SPECIES DIVERSITY AND COMMUNITY INVASIBILITY BY SPECIES IMMIGRATION: SEED RICHNESS VERSUS SEED DENSITY

#### ABSTRACT

Immigration rates of species into communities are widely understood to influence community diversity, which in turn is widely expected to influence the susceptibility of ecosystems to species invasion. For a given community, however, immigration processes may impact diversity by means of two separable components: the number of species represented in seed inputs and the density of seed per species. The independent effects of these components on plant species diversity and consequent rates of invasion are poorly understood. I constructed experimental plant communities through repeated seed additions to independently measure the effects of seed richness and seed density on the trajectory of species diversity during the development of annual plant communities. Because I sowed species not found in the immediate study area, I was able to assess the invasibility of the resulting communities by recording the rate of establishment of species from adjacent vegetation. Early in community development when species only weakly interacted, seed richness had a strong effect on community diversity whereas seed density had little effect. After the plants became established, the effect of seed richness on measured diversity strongly depended on seed density, and disappeared at the highest level of seed density. The

ability of surrounding vegetation to invade the experimental communities was decreased by seed density but not by seed richness, primarily because the individual effects of a few sown species could explain the observed invasion rates. These results suggest that seed density is just as important as seed richness in the control of species diversity, and perhaps a more important determinant of community invasibility than seed richness in dynamic plant assemblages.

## INTRODUCTION

A major goal of ecologists has been to understand the factors that influence the structure and diversity of ecological communities. While much emphasis has been placed on understanding the factors that restrict communities to certain subsets of species, such as competition and disturbance (MacArthur and Levins 1967; MacArthur 1972; Connell 1978; Huston 1979; Tilman 1982), the role of species immigration in community assembly dynamics remains poorly understood (Tilman 1993; Loreau and Mouquet 1999; Hubbell 2001). This is in part due to confusion over what “immigration” actually means in relation to species diversity. For example, in MacArthur and Wilson’s (1967) classic theory of island biogeography, species diversity is in part determined by rates of immigration of new species, where, given a constant extinction rate, species diversity is increased by the *richness* of immigrants (Simberloff and Wilson 1970; Tilman et al. 1997b). On the other hand, species diversity may also be promoted by the *density* of arriving propagules, wherein certain species persist in sites where they would not otherwise be self-maintaining, a phenomenon called “mass effect” (Shmida and Wilson 1985) or “rescue effect” (Brown and Kodric-Brown 1977; Smith 1980; Loreau and Mouquet 1999). The density of propagule influx is also important

from the standpoint of recruitment limitation, where the inability of a particular species to be present in all favorable sites influences community structure (Grime 1973; Tilman 1993; Burke and Grime 1996; Tilman et al. 1997b).

The relationship between immigration and species diversity is further complicated by the possibility that propagule richness and propagule density interact to control diversity in natural communities; these interactions have generally been ignored in immigration-driven diversity models and experiments. For example, propagule density may control the intensity and timing of interspecific interactions, which in turn control the sensitivity of species diversity to propagule richness. In experiments where seeded communities are assembled by random draws from a common species pool, propagule richness increases the probability of including particularly dominant species that may themselves decrease resident species diversity, a so-called "sampling effect" (Aarssen 1997; Huston 1997; Tilman et al. 1997a; Tilman 1997; Fridley 2001; Wardle 2001). The ability of such a species to establish, however, should depend in part on its sown density (Shmida and Ellner 1984; Kunin 1998). Thus, low or high levels of seed density may decrease species diversity for a given level of seed richness. To my knowledge, however, the interactive effects of seed richness and seed density on species diversity have not previously been investigated.

Species diversity itself may place further limits on immigration in the form of decreasing the success of subsequent invaders (Elton 1958; MacArthur 1970; Levine and D'Antonio 1999), an observation supported by recent experimental studies (Crawley et al. 1999; Knops et al. 1999; Levine 2000; Naeem et al. 2000; Prieur-Richard et al. 2000; Symstad 2000). Diversity may decrease invasion by means of complementary resource use, where more diverse assemblages use more total available resources and thus preclude the

establishment of new species (MacArthur 1970). When diversity is manipulated as seeded richness, however, as it has been in several experiments (Knops et al. 1999; Naeem et al. 2000; Levine 2000), the negative diversity-invasibility relationship may simply be the result of a sampling effect for a particularly invasion-resistant species (Wardle 2001). Because sampling effects should also depend on the ability of a dominant species to establish, the influence of seeded richness on invasibility should depend on seed density, whatever the mechanism of invasion resistance.

I created experimental plant communities of common herbs to explicitly test the different effects of seed richness and seed density on community properties and thus clarify the role that the primary components of immigration play in structuring plant communities. By following community development through a growing season, I documented the changing interactions of seed richness and density through time. I also allowed surrounding vegetation to invade my experimental communities to test whether seed richness and density had interactive effects on rates of species invasion.

## METHODS

### *Experimental Design*

I constructed 100 75 x 75 cm experimental plots in an old field at Mason Farm Biological Preserve, Chapel Hill, North Carolina, USA. In these plots I constructed plant communities from seed with different levels of seeded richness and density of seed per species. I used three levels each of seed richness (3, 10, and 30 species) and density of seed per species (10, 100, and 1000 seeds), crossed in a fully factorial design. Each of these 9 treatments and a bare plot treatment (no sown seed) was replicated 10 times and randomly



assigned to a plot in a 10 x 10 plot grid separated by 1 m walkways. Species composition for each seeded treatment was randomly selected from a pool of 30 grass and herb species (Table 1) that had been tested for seed viability and were not already present in the surrounding vegetation. Replicates were not compositional replicates; that is, no specific assemblage was grown more than once.

I established experimental communities on bare soil that had been plowed and disked five weeks prior to seeding. To minimize species growing into plots from the local seed bank, I allowed seed bank species to germinate in the open soil for 3 weeks after plowing, and then applied the short-lived, systemic herbicide Roundup (Monsanto Corp., St. Louis, MO, USA). Seeds were added to plots in four applications at three-week intervals, from June 1 to August 3, 1999, broadcasted into plots by hand while taking care to keep all broadcast seed within the target plot. Each reapplication of seeds had the same treatment number of species and seeds per species as the original application, but the species composition was randomly varied for each reapplication of seed. After the first sowing, ambient species from the surrounding vegetation were allowed to invade the experimental plots by purely natural means, including vegetative spread from plot edges and walkways (which were not cleared of vegetation), seed dispersal, and any late-emerging species from the soil seed bank. All recorded invading species are listed in Table 2. For each plot I recorded the percent cover of each species at 3, 6, 9, and 12 weeks after first sowing. Maximum cover per species was 100%; thus, total cover and total richness were partly correlated.

**Table 5.1.** Experimental species.

<i>Agastache foeniculum</i>	<i>Nicotiana glauca</i>
<i>Amaranthus tricolor</i>	<i>Nicotiana glauca</i>
<i>Anethum graveolens</i>	<i>Oenothera biennis</i>
<i>Artemisia absinthium</i>	<i>Panicum virgatum</i>
<i>Artemisia vulgaris</i>	<i>Papaver rhoeas</i>
<i>Avena sativa</i>	<i>Papaver somniferum</i>
<i>Chenopodium ambrosioides</i>	<i>Rudbeckia hirta</i>
<i>Chrysanthemum coronarium</i>	<i>Rumex acetosa</i>
<i>Fagopyrum esculentum</i>	<i>Trifolium incarnatum</i>
<i>Festuca ovina</i>	<i>Trifolium pratense</i>
<i>Hypericum perforatum</i>	<i>Trifolium repens</i>
<i>Lolium multiflorum</i>	<i>Urtica dioica</i>
<i>Matricaria recutita</i>	<i>Verbascum thapsus</i>
<i>Medicago sativa</i>	<i>Verbena hastata</i>
<i>Nepeta cataria</i>	<i>Vicia villosa</i>

**Table 5.2.** Invasive species. Botanical nomenclature follows Kartesz and Meacham (1999).

<i>Acalypha rhomboides</i>	<i>Lespedeza cuneata</i>
<i>Acer rubrum</i>	<i>Ligustrum sinense</i>
<i>Allium vineale</i>	<i>Microstegium vimineum</i>
<i>Amaranthus hybridus</i>	<i>Mollugo verticillata</i>
<i>Ambrosia artemisiifolia</i>	<i>Oxalis stricta</i>
<i>Barbarea vulgaris</i>	<i>Paulownia tomentosa</i>
<i>Boehmeria cylindrica</i>	<i>Phyllanthus amarus</i>
<i>Campsis radicans</i>	<i>Physalis virginiana</i>
<i>Chenopodium album</i>	<i>Phytolacca americana</i>
<i>Commelina communis</i>	<i>Poa pratensis</i>
<i>Cynodon dactylon</i>	<i>Polygonum punctatum</i>
<i>Cyperus sp.</i>	<i>Portulaca oleracea</i>
<i>Datura stramonium</i>	<i>Rhus glabra</i>
<i>Digitaria ischaemum</i>	<i>Robinia pseudoacacia</i>
<i>Echinachloa crusgalli</i>	<i>Rosa multiflora</i>
<i>Festuca sp.</i>	<i>Rubus sp.</i>
<i>Galinsoga ciliata</i>	<i>Rumex crispus</i>
<i>Geranium carolinianum</i>	<i>Sida rhombifolia</i>
<i>Geum canadense</i>	<i>Solanum americanum</i>
<i>Helenium flexuosum</i>	<i>Solanum carolinense</i>
<i>Hieraceum gronovii</i>	<i>Sorghastrum nutans</i>
<i>Ipomoea sp.</i>	<i>Stellaria media</i>
<i>Juncus tenuis</i>	<i>Trifolium campestre</i>
<i>Lactuca biennis</i>	<i>Verbena urticifolia</i>
	<i>Viola sp.</i>

### *Data Analyses*

To test the effect of seed richness and density on realized diversity and invasibility over time, I performed a repeated measures analysis using the MIXED procedure of SAS version 8.0 (SAS Institute 1999). The repeated measures analysis used a mixed-model approach with unstructured covariance (in other words, no model for how data should covary with time). Denominator degrees of freedom were calculated using the general Satterthwaite approximation, which allows an accurate F approximation (Littell et al. 1996). Separate analyses were performed for two dependent variables: total cover of invasive species (representing “invasibility”) and realized plot richness (representing “community diversity”). Realized plot richness included sown species and any invading species. These two statistical models initially included quadratic terms for seed richness and seed density and all possible two-way interaction terms (and 3-way for quadratic variables), which were subsequently evaluated using backward elimination. Sown seed richness and seed density were analyzed as quantitative (rather than class) variables in order to test for polynomial effects of seed richness and density on diversity and invasibility. An overall estimation of the effects of experimental treatments on invasibility was performed with an ANOVA using total cover of invaders at the final time period.

An important and uncontrolled covariate in my study was total seed density per plot, as I independently manipulated seed richness and density per species in an additive design. For example, treatments of 30 species and 10 seeds per species were sown with 300 total seeds per time period, whereas for 3 species/10 seed treatments only 30 seeds were sown. To control for this covariate “post-hoc”, I partitioned the data into those 40 plots where overall seed density was either 300 or 3000 seeds per plot (i.e., plots of seeded richness of 3 or 30

combined with appropriate values of density per species (10, 100, or 1000). I then used total seed density as a predictor variable alongside seed richness to predict total invasive cover in ANOVA.

The potential for “sampling effects” (Wardle 2001) as the cause of a diversity-invasibility relationship in this experiment was high because seed richness treatments of 30 species were identical in species composition. If one species formed highly invasion-resistant stands, for example, this effect would be present in all 30-species treatments but only a small, random fraction of 3- and 10-species treatments. To determine whether this occurred for particular species, I examined the individual effects of each species on total final cover of invasives (measured in the last time period) in single factor ANOVAs conducted separately for each species (using all 90 plots). I then included a dummy variable for presence or absence of one species that proved particularly important in this analysis (*Fagopyrum esculentum*) in the full ANOVA model predicting invasibility (in which total density was controlled), and varied the order of listed terms in Type I SS to assess whether seeded richness could significantly predict invasibility after the effects of *F. esculentum* had been accounted for, or vice-versa. For this analysis I noted the sums of squares of invasibility accounted for by each variable, also called a factor’s magnitude of effect (Weldon and Slauson 1986).

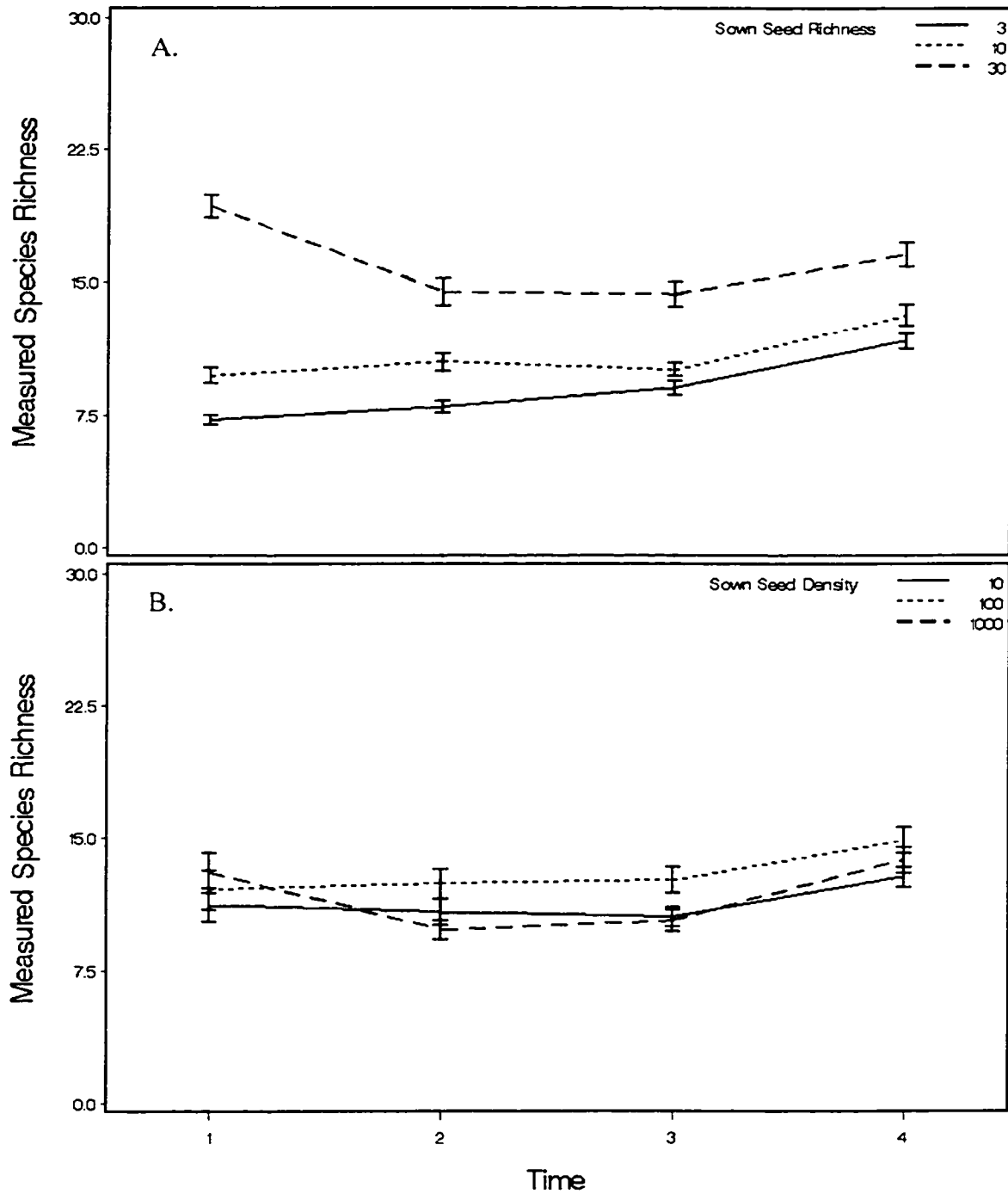
I assessed the relationship between the total cover of invasives and the realized diversity of experimental species, and the realized abundance of experimental species. (while controlling for total seed density per plot) in the final time period using a linear regression model. Analyses (other than the repeated measures tests described above) were conducted using the PROC GLM procedure in SAS (SAS Institute 1999).

## RESULTS

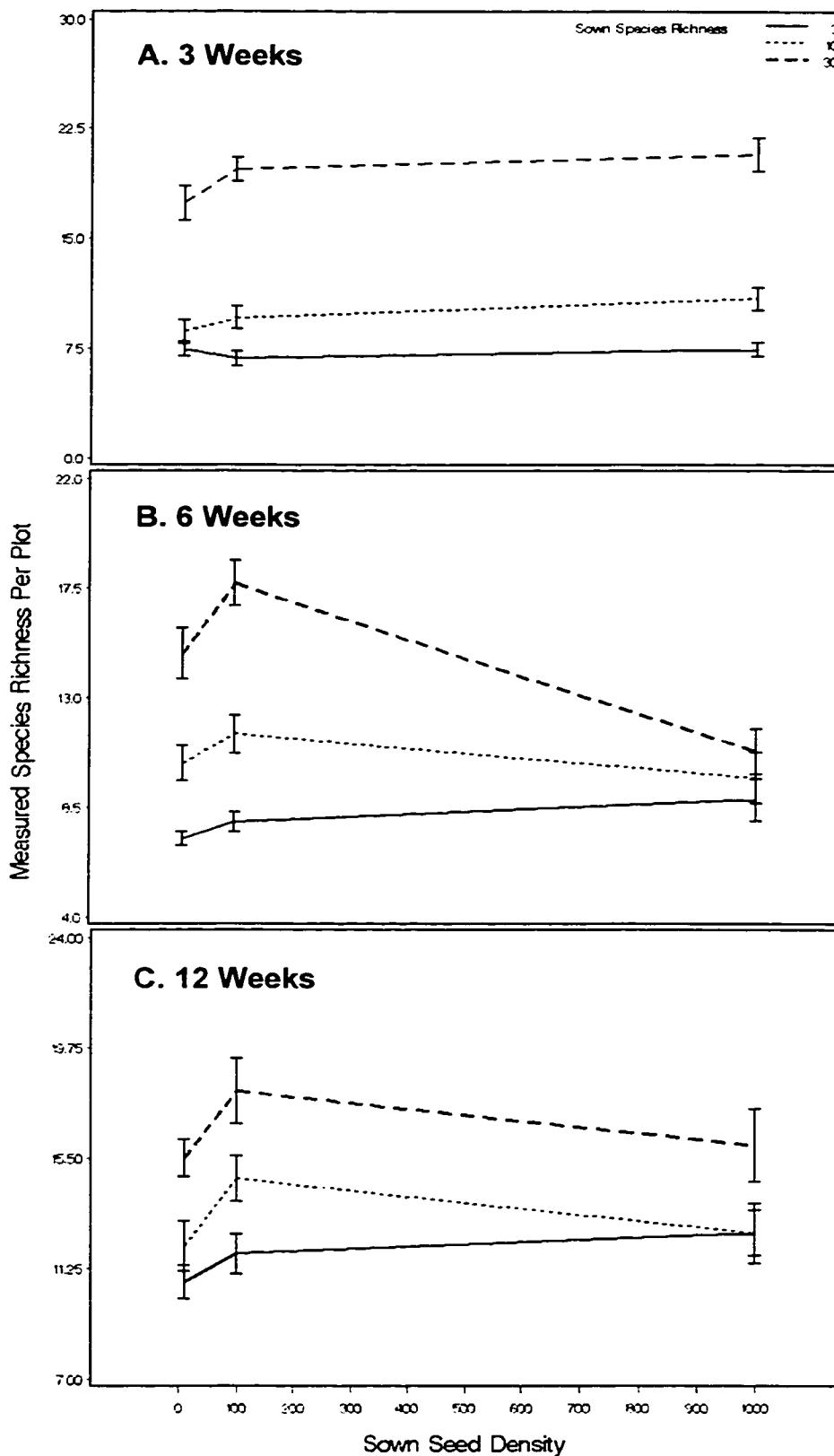
### *Effects of seed richness and seed density per species on overall community diversity*

Total community richness (seeded plus volunteer species) generally increased with time and with each level of seeded richness (Figure 1A). A major exception was the decrease in diversity in plots of 30 sown species between 3 and 6 weeks after initial sowing, probably due to a filtering process of seedlings of species that successfully germinated but could not fully establish. The isolated effects of seed density per species were less apparent over time (Figure 1B), but in general diversity was highest at the intermediate seed density. Repeated measures ANOVA revealed significant interactions between seed richness and density in the control of diversity, and of those variables over time (Table 3). Figure 2 demonstrates this interaction and the unimodal nature of the seed density effect on diversity, and how this unimodal relationship was affected by seed richness (last term in model in Table 3). Seed density per species had little effect on diversity in the first time period when plants were small: as the communities developed, the effect of density depended on seed richness, where intermediate seed densities promoted diversity at all but the lowest richness level.

**Figure 5.1.** Effects of seed richness (top) and seed density (bottom) on realized plot species richness over time. Bars represent means  $\pm$  1 SE.



**Figure 5.2.** Effect of seed richness and seed density on realized plot species richness over time. Bars represent means  $\pm$  1 SE.



**Table 5.3.** Repeated measures results for the effects of seed density and richness on realized plot species richness over time based on a mixed model approach with unstructured covariance. Degrees of Freedom are calculated using the general Satterthwaite approximation (Littell et al. 1996). Type 3 tests of fixed effects shown.

<b>Effect</b>	<b>Num. DF</b>	<b>Den. DF</b>	<b>F</b>	<b>Pr &gt; F</b>
Seed density	1	84	0.11	0.7403
Seed richness	1	86	57.14	<0.0001
Time	3	87	35.63	<0.0001
Seed density*Seed richness	1	84	5.35	0.0231
Seed richness*Time	3	87	35.99	<0.0001
Seed density*Time	3	87	6.11	0.0008
Seed density <sup>2</sup>	1	84	0.04	0.8403
Seed richness * Seed density <sup>2</sup>	1	84	6.42	0.0131

**Table 5.4.** Repeated measures analysis showing the effect of seed richness and density on the total cover of invasive species based in a mixed model approach with unstructured covariance. Degrees of Freedom are calculated using the general Satterthwaite approximation (Littell et al. 1996). Type 3 tests of fixed effects shown.

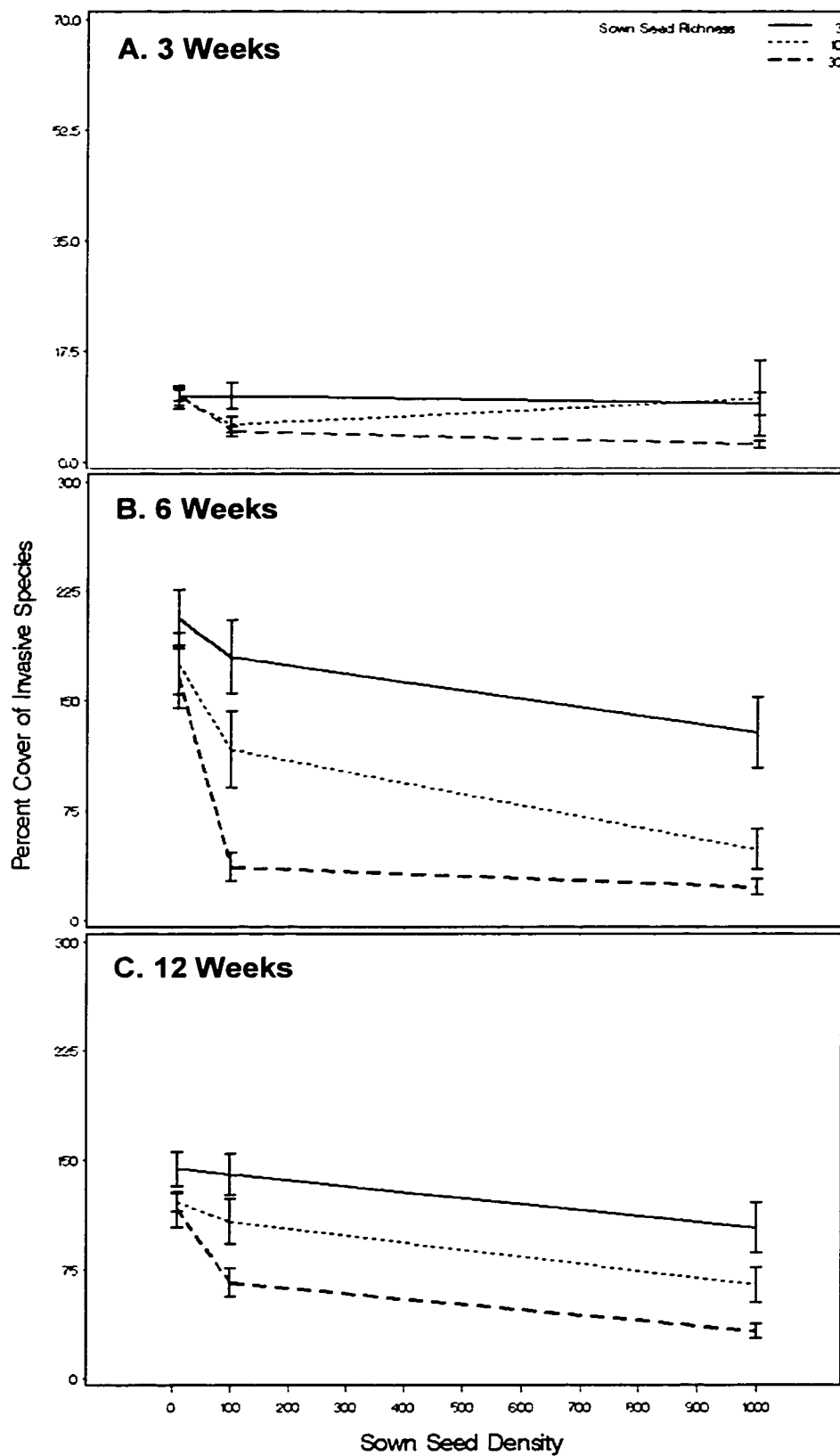
<b>Effect</b>	<b>Num. DF</b>	<b>Den. DF</b>	<b>F</b>	<b>Pr &gt; F</b>
Seed density	1	86	20.61	<0.0001
Seed richness	1	86	39.45	<0.0001
Time	3	86	119.25	<0.0001
Seed richness * Time	3	86	14.17	<0.0001
Seed density * Time	3	86	8.21	<0.0001
Seed density <sup>2</sup>	1	86	3.03	0.0851
Seed density <sup>2</sup> * Time	3	86	6.93	0.0003



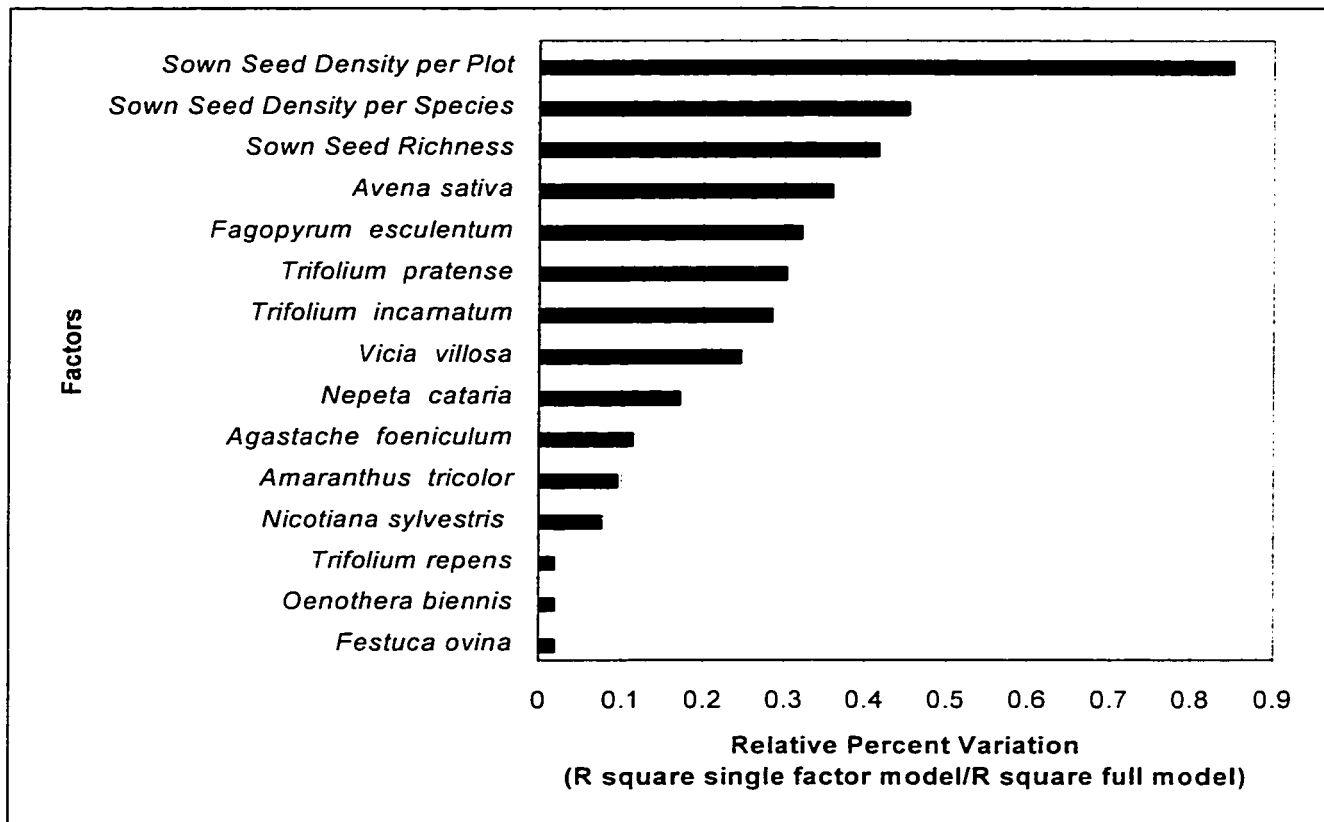
### *Effects of seed richness and seed density on invasibility*

Seed richness and seed density both negatively affected total cover of invasive species, and largely in additive fashion, but only after enough time had passed to allow species from the surrounding vegetation to invade (Figure 3, Table 4). The highest cover of invaders occurred in the least species-rich plots where species were planted with only 10 seeds; the lowest cover of invaders occurred with maximum levels of seed richness (30) and seed density (1000 seeds per species). Neither factor was a very strong predictor of invasion, however; by the final time period, seed richness alone could account for 22% of the variance in invasive cover among plots, and seed density could account for 24%. As a more conservative estimate using the 40-plot data subset where the effects of total seed density per plot could be accounted for, seed richness could explain only 10% of the variation in invasive cover (although still significant,  $p=0.026$ ), whereas that for total seed density was 20% ( $P=0.002$ ).

**Figure 5.3.** Effect of seed richness and seed density on cover of invaders over time. Bars represent means  $\pm$  1 SE.



**Figure 5.4.** An assessment of sampling effect. Percent variation in total abundance of invasive species during the final time period explained by factors when alone in the model divided by SS for the full model. Factors with a significant effect ( $P < 0.05$ ) on invasibility when alone in the model are shown.



The presence or absence of several species explained a large proportion of the variance of total invasive cover that could otherwise be attributed to seed richness (Figure 4), particularly that of *Avena sativa*, *F. esculentum*, *Trifolium pratense*, *T. incarnatum*, and *Vicia villosa*. The last three species are, notably, nitrogen-fixers. The effect of *A. sativa* is somewhat enigmatic because it never occurred at high relative abundance. The effect of *F. esculentum* was expected because of its large relative abundance in the plots in which it occurred and it had the largest effect on invasibility. I therefore chose to compare the importance of seed richness as a predictor of total invasive cover before and after accounting for the presence or absence of *F. esculentum* in experimental communities (note that p-value estimates are unwarranted here because of the reduction of statistical power associated with the factor listed last in the model, as richness and presence of any particular species were highly correlated). The 10% SS accounted for by seed richness (after total seed density) was reduced (6%) after accounting for *F. esculentum* (Table 5), suggesting that, even when only one species was included in this analysis, richness appeared to influence invasibility largely by sampling effects.

The regression of realized richness of experimental species on cover of invasive species (while controlling for total seed density) in the final time period provided further evidence that species richness did not have a significant effect on invasion. The realized richness of experimental species only explained 4.6 % of the variation in invasive cover and was not a significant effect ( $P=0.14$ ; Table 6).

**Table 5.5.** ANOVA results (Type 1 SS) showing the effect of total seed density per plot (rather than seed density per species), seed richness, and presence of *Fagopyrum esculentum* on invasibility (total cover of invasives) at time 4. Order 1 shows the results when *Fagopyrum esculentum* is placed last in the model, while order 2 shows the results when seed richness is placed last in the model. The overall model error and R<sup>2</sup> are the same for both orders.

<b>R<sup>2</sup></b>	<b>Coeff Var</b>	<b>Root MSE</b>	<b>Mean cover invasives (%)</b>	
0.32	39.61	42.10	106.30	
<b>Source</b>		<b>DF</b>	<b>SS</b>	<b>Mean Square</b>
Model		3	29557.03	9852.34
Error		36	63809.37	1772.48
Corrected Total		39	93366.40	
<b>Order 1</b>		<b>DF</b>	<b>Type I SS</b>	<b>Mean Square</b>
Total seed density		1	18922.50	18922.50
Seed richness		1	9486.40	9486.40
<i>Fagopyrum esculentum</i>		1	1148.13	1148.13
<b>Order 2</b>		<b>DF</b>	<b>Type I SS</b>	<b>Mean Square</b>
Total seed density		1	18922.50	18922.50
<i>Fagopyrum esculentum</i>		1	4605.78	4605.78
Seed richness		1	6028.75	6028.75

**Table 5.6.** Regression results for the relationship between invasibility and the realized richness of experimental species (while controlling for total seed density) in the final time period.

<b>Parameter</b>	<b>Estimate</b>	<b>Error</b>	<b>t</b>	<b>Pr &gt;  t </b>
Intercept	146.89	14.30	10.27	<.0001
Total seed density (dummy variable)	-0.01	0.006	-2.25	0.03
Plot species richness of seeded species	-3.31	2.19	-1.51	0.14

## DISCUSSION

Propagule density and richness should interact to influence diversity in two main ways. First, for any level of seed richness, a minimum threshold density of seed per species is required for each species to successfully establish with a high likelihood (given appropriate adaptations for a particular site). Some species may even be able to persist at a site with a high seed influx density even if they cannot be self-maintaining within the site (i.e., mass effect sensu Shmida and Ellner 1984). At these density levels, community diversity increases with seed richness.

Second, there is an upper threshold for seed density above which certain species dominate the assemblage and thus reduce diversity, similar to what is seen with plant assemblages in the hump-backed relationship between density and diversity described by Grime (1973; 1979). This explains the change in seed richness effect on diversity from linear to unimodal with increasing seed density (Figure 2B). When I considered the effect of seed density alone on realized richness, ignoring the interaction between seed richness and density, its influence on diversity is not immediately apparent (Figure 1B). Only by examining the interaction between seed richness and seed density could I observe the full range of effects.

Therefore, my results strongly suggest that a full mechanistic analysis of how “immigration” processes affect species diversity in natural communities must include both richness and density components.

Because I allowed the surrounding vegetation to invade my experimental plots over the course of the growing season, I was also able to measure the indirect effects of seed richness and density on community invasibility as the total cover of invasive species at the

conclusion of the experiment. Here the effects of seed richness and density appeared to operate in additive fashion to reduce invasion. If the diversity of communities is related to their ability to repel species invasion, an increase in the density at which the species grow should increase this effect, whether by intensifying the degree to which species complement each other in resource use (MacArthur 1970) or by enhancing the probability of a highly invasion-resistant species dominating (Wardle 2001). My results appear more consistent with the latter, sampling-effect explanation, for two major reasons. First, after the effect of the presence or absence of a single species (*F. esculentum*) on invasibility was accounted for, seed richness could explain very little of the variance in invasion success among plots (and indeed could only explain 10% of the variance even without accounting for *F. esculentum*). Second, there was no significant correlation between realized community diversity and invasion success after accounting for total seed density. Because such a "sampling" type process could occur in natural systems when diversity is initially maintained by seed influx to a particular community (with a particularly successful competitor more likely to arrive in more diverse seed influx), this may be a legitimate means by which natural diversity could limit species invasion, at least for annual or highly unstable systems (Fridley 2001; Wardle 2001). Although seed density had a substantially stronger effect on invasibility than seed richness, the possibility of resource complementarity in more diverse mixtures having an independent effect on invasibility cannot be ruled out without controlling for sampling effects.

## CONCLUSION

The immigration of species into communities should affect community diversity and consequent rates of species invasion, but in ways that depend both on the number of species represented by propagules and by the density of propagules for each particular species. In a field experiment where these two components were independently manipulated in factorial design, I found that seed richness and seed density interact to influence both community diversity and the ability of surrounding vegetation to invade communities. Further, I found that propagule density and richness per species had an additive effect in reducing invasibility. Although I cannot rule out the effect of increased resource utilization in the more diverse assemblages reducing invasibility, the effect of richness on invasibility independent of density appears to be due in part to sampling effects (Wardle 2001)



## GENERAL CONCLUSIONS

The patterns that I observed in southern Appalachian riparian areas included 1) a positive relationship between diversity and exotic species invasion, 2) increasing diversity and invasion with flooding, and 3) higher compositional predictability in flooded areas. These patterns are all consistent with the hypothesis that these habitats are driven more by immigration processes rather than extinction processes. As the propagule pressure experiment demonstrates, immigration processes such as propagule pressure can play an important role in structuring communities.

The ideas embodied in the immigration-extinction gradient are not limited to plant communities, but could be applied to a range of different organisms. Additional examples of communities structured by immigration and extinction processes are needed to further substantiate the generality and usefulness of the immigration-extinction gradient as an organizing framework for community ecology. One direction that might be explored is to observe how the relationship between invasibility and diversity changes across a gradient of anthropogenic disturbance within a community that is otherwise extinction-driven, which could provide insights as to how anthropogenic disturbance affects community resistance to invasion. For example, one might compare the relationship between native and exotic species diversity with distance to a road or some other disturbed zone.

Recognition of the need to merge the equilibrium, niche-assembled community perspective with the non-equilibrium perspective has been gaining ground, and more ecologists are starting to incorporate both perspectives into their research (e.g. Hubbell 2001). Ultimately, these efforts should help to increase the applicability of ecological theories. In particular, the immigration-extinction gradient helps to clarify the roles of other ecological theories because it can be used to relate theories to patterns observed in natural plant communities, and it provides a framework for understanding why many competition-based theories, such as the hypothesized negative relationship between native and exotic species diversity, are often not observed in real communities.

## REFERENCES

- Aarssen, L. W. 1997. High productivity in grassland ecosystems: effected by species diversity or productive species? *Oikos* 80: 183-4.
- Alcaraz, F., S. Rios, C. Inocencio, and A. Robledo. 1997. Variation in the riparian landscape of the Segura River Basin, SE Spain. *Journal of Vegetation Science* 8: 597-600.
- Auble, G. T., J. M. Friedman, and J. L. Scott. 1994. Relating riparian vegetation to present and future stream flows. *Ecological Applications* 4: 544-54.
- Baker, T. T. and D. H. Van Lear. 1998. Relations between density of rhododendron thickets and diversity of riparian forests. *Forest Ecology and Management* 109: 21-32.
- Barnes, W. J. 1978. The distribution of floodplain herbs as influenced by annual flood elevation. *Trans. Wis. Acad. Sci. Arts. Lett.* 66: 254-66.
- Baskin, C. C. and J. M. Baskin. 1998. *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. United States: Academic Press.
- Baumann, R. H., Jr. J. W. Day, and C. A. Miller. 1984. Mississippi deltaic wetland survival: Sedimentation versus coastal submergence. *Science* 224: 1093-5.
- Beers, T. W., P. E. Dress, and L. C. Wensel. 1966. Aspect transformation in site productivity research. *Journal of Forestry* 64: 691-2.
- Bratton, S. P., J. R. Haperman, and A. R. Mast. 1994. The lower Susquehanna River gorge and floodplain (USA) as a riparian refugia for vernal forest-floor herbs. *Conservation Biology* 8: 1069-77.
- Brewer, E. O. *Soil Survey of Ashe County, North Carolina*. 1984. Raleigh, NC: USDA Soil Conservation Service.
- Brinson, M. M. and J. Verhoeven. 1999. Riparian forests. In: Hunter, M. L. Jr., ed. *Maintaining Biodiversity in Forest Ecosystems*. Cambridge, UK: Cambridge University Press. Pages 265-99.
- Brown, J. H. and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58: 445-9.
- Burke, M. J. W. and J. P. Grime. 1996. An experimental study of plant community invasibility. *Ecology* 77: 776-90.
- Carlquist, S. 1967. The biota of long distance dispersal. V. Plant dispersal to Pacific Islands. *Bull. Torrey Bot. Club* 94: 129-62.
- Chesson, P. L. and T. J. Case. 1986. Overview: nonequilibrium community theories: Chance, variability, history, and coexistence. Diamond, J. and T. J. Case, eds. *Community*

Ecology. United States: Harper & Row.

Clark, J. S., E. Macklin, and L. Wood. 1998. Stages and spatial scales of recruitment limitation in Southern Appalachian Forests. *Ecological Monographs* 68: 213-35.

Clements, F. E. 1916. *Plant Succession*. Washington: Carnegie Inst. Wash. Publ.

Connell, J. H. 1978. Diversity in tropical rainforests and coral reefs. *Science* 199: 1302-10.

Crawley, M. J., S. L. Brown, M. S. Heard, and G. R. Edwards. 1999. Invasion-resistance in experimental grassland communities: species richness or species identity? *Ecology Letters* 2: 140-8.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88: 528-34.

Elton, C. S. 1958. *The Ecology of Invasions by Plants and Animals*. London: Methuen.

Fenner, M. 1985. *Seed Ecology*. New York: Chapman and Hall.

Ferreira, L. V. 1997. Effects of the duration of flooding on species richness and floristic composition in the Jau National Park in floodplain forests in central Amazonia. *Biodiversity and Conservation* 6: 1353-63.

Fonda, R. W. 1974. Forest succession in relation to river terrace development in Olympic National Park, Washington. *Ecology* 55: 927-42.

Fridley, J. D. 2001. The influence of species diversity on ecosystem productivity: how, where, and why? *Oikos* 93: 514-26.

Gaines, S. and J. Roughgarden. 1985. Larval settlement rate: A leading determinant of structure in an ecological community of the marine intertidal zone. *Proc. Nat. Acad. Sci. USA* 82: 3707-11.

Gleason, H. 1926. The individualistic concept of the plant association. *Bull. Torrey Bot. Club* 53: 1-20.

Goebel, P. C., B. J. Palik, L. K. Kirkman, and L. West. 1996. Geomorphic influences on riparian forest composition and structure in a karst landscape of southwestern Georgia. In: Flynn, K. M., ed. *Proceedings of the Southern Forested Wetlands Ecology and Management Conference*. Clemson, SC: Clemson University. Pages 110-6.

Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. *BioScience* 41: 540-51.

Grime, J. P. 1973. Control of species density in herbaceous vegetation. *Journal of Environmental Management* 1: 151-67.

- Grime, J. P. 1979. *Plant Strategies and Vegetation Processes*. Chinchester, UK: John Wiley & Sons.
- Grime, J. P. 1988. The C-S-R model of primary plant strategies -- origins, implications, and tests. In Gottlieb, L. B. and S. K. Jain, eds. *Plant Evolutionary Biology*. Cambridge, G.B.: Chapman and Hall Ltd. Pages 371-93.
- Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter, and founder effects. *Journal of Ecology* 86: 902-10.
- Grossman, D. H., D. Faber-Langendoen, A. S. Weakley, M. B. P. Anderson, R. Crawford, K. Goodin, S. Landaal, K. Metzler, K. D. Patterson, M. Pyne et al. 1998. *International classification of ecological communities: terrestrial vegetation of the United States. Volume II. The National Vegetation Classification System: Development, Status, and Applications*. Arlington, VA: The Nature Conservancy.
- Harris, R. R. 1987. Occurrence of vegetation on geomorphic surfaces in the active floodplain of a California alluvial stream. *American Midland Naturalist* 104: 209-23.
- Harvey, C. A. 2000. Windbreaks enhance seed dispersal into agricultural landscapes in Monteverde, Costa Rica. *Ecological Applications* 10: 155-73.
- Hector, A., B. Schmid, C. Beierkuhnlein, M. C. Caldeira, M. Diemer, P. G. Dimitrakopoulos, J. Finn, H. Freitas, P. S. Giller, J. Good et al. 1999. Plant diversity and productivity experiments in European grasslands. *Science* 286: 1123-7.
- Hedman, C. W. and D. H. Van Lear. 1995. Vegetative structure and composition of southern Appalachian riparian forests. *Bull. Torr. Bot. Club* 122: 134-44.
- Henry, C. P., Amoros C., and G. Bornette. 1996. Species traits and recolonization processes after flood disturbances in riverine macrophytes. *Vegetatio* 122: 13-27.
- Hermann, K. A., Ed. 1996. *Southern Appalachian Assessment GIS Data Base CD ROM Set*. Norris, TN: Southern Appalachian Man and the Biosphere Program.
- Howe, H. A. and J. Smallwood. 1982. Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* 13: 201-28.
- Hubbell, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton, NJ: Princeton University Press.
- Hubbell, S. P., R. B. Foster, S. T. O'Brien, K. E. Harms, R. Condit, B. Wechsler, S. J. Wright, and S. Loo de Lao. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283: 554-7.
- Hupp, C.R. 1988. Plant ecological aspects of flood geomorphology and paleoflood history. Baker, V. R., R. C. Kochel, and P. C. Patton, eds. *Flood Geomorphology*. New York: Wiley Interscience. Pages 335-56.

- Hupp, C. R. and W. R. Osterkamp. 1985. Bottomland vegetation distribution along Passage Creek, Virginia, in relation to fluvial landforms. *Ecology* 66: 670-81.
- Hupp, C. R. and D. E. Bazemore. 1993. Temporal and spatial patterns of wetland sedimentation, West Tennessee. *Journal of Hydrology* 141: 179-96.
- Hupp, C. R. and W. R. Osterkamp. 1996. Riparian vegetation and fluvial geomorphic processes. *Geomorphology* 14: 277-95.
- Huston, M. A. 1979. A General Hypothesis of Species Diversity. *American Naturalist* 113: 81-101.
- Huston, M. A. 1994. *Biological Diversity: The Coexistence of Species on Changing Landscapes*. Cambridge: Cambridge University Press.
- Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110: 449-60.
- Ilhardt, B. L., E. S. Verry, and B. J. Palik. 2000. Defining riparian areas. In: Verry, E. S., J. W. Hornbeck, and C. A. Dolloff, eds. *Riparian Management in Forests of the Continental Eastern United States*. New York: Lewis Publishers. Pages 23-42.
- Johansson, M. E., C. Nilsson, and E. Nilsson. 1996. Do rivers function as corridors for plant dispersal? *Journal of Vegetation Science* 7: 593-8.
- Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. in: Dodge, D. P., ed. *Proceedings of the International Large River Symposium*. Can. Spec. Publ. Fish. Aquat. Sci. Volume 106. Pages 110-27.
- 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.
- Kalliola, R. and M. Puhakka. 1988. River dynamics and vegetation mosaicism: a case study of the River Kamajohka, northernmost Finland. *Journal of Biogeography* 15: 703-19.
- Kartesz, J. T. and C. A. Meacham. 1999. *Synthesis of the North American Flora CD-Rom Version 1*. Chapel Hill, NC: North Carolina Botanical Garden, University of North Carolina.
- Kinzig, A. P., S. W. Pacala, D. Tilman. 2001. *The Function Consequences of Biodiversity, Empirical Progress and Theoretical Extensions*. Princeton, NJ: Princeton University Press.
- Knops, J. M. H., D. Tilman, N. M. Haddad, et al. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances, and diversity. *Ecology Letters* 2: 286-93.

- Kunin, W. E. 1998. Biodiversity at the Edge: A test of the importance of spatial "mass effects" in the Rothamsted Park grass experiments. *Proc. Nat. Acad. Sci. USA* 95: 207-12.
- Legendre P. and L. Legendre. 1998. *Numerical Ecology*. second ed. New York: Elsevier.
- Levine, J. 2000. Species diversity and biological invasions: relating local process to community pattern. *Science* 288: 852-4.
- Levine, J. M. and C. M. D'Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87: 15-26.
- Lindsey, A. A., R. O. Petty, D. K. Sterling, and W. VanAsdall. 1961. Vegetation and environment along the Wabash and Tippecanoe Rivers. *Ecological Monographs* 31: 105-56.
- Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. *SAS System for Mixed Models*. Cary, NC: SAS Institute.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* 80: 1522-36.
- Lord, L. A. and T. D. Lee. 2001. Interactions of local and regional processes: species richness in tussock sedge communities. *Ecology* 82: 313-8.
- Loreau, M. and N. Mouquet. 1999. Immigration and maintenance of local species diversity. *American Naturalist* 154: 427-40.
- Lyon, J. and C. L. Sagers. 1998. Structure of herbaceous plant assemblages in a forested riparian landscape. *Plant Ecology* 138: 1-16.
- MacArthur, R. H. 1970. Species-packing and competitive equilibrium for many species. *Theoretical Population Biology* 1: 1-11.
- MacArthur, R. H. 1972. Coexistence of species. Behnke, J., ed. *Challenging Biological Problems*. New York: Oxford University Press. Pages 253-9.
- MacArthur, R. H. and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 101: 377-85.
- MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.
- Magalef, R. 1963. On certain unifying principles in ecology. *American Naturalist* 97: 357-74.
- Manley, B. F. J. 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*. Second ed. New York: Chapman and Hall.

- Margalef, R. 1968. *Perspectives in Ecological Theory*. Chicago, IL: Univ. of Chicago Press.
- Mathsoft. 2000. *S-Plus 2000 Guide to Statistics*. Volume 2. Seattle, WA: Data Analysis Products Division, Mathsoft.
- McCune, B. and M. J. Mefford. 1999. *Multivariate Analysis of Ecological Data [PC-Ord for Windows]*. Version 4.0. Glenden Beach, Oregon, USA: MjM Software.
- McNab, W. H. 1989. Terrain Shape Index: quantifying effect of minor landforms on tree height. *Forest Science* 35: 91-104.
- Menges, E. S. and D. M. Waller. 1983. Plant strategies in relation to elevation and light in floodplain herbs. *The American Naturalist*. 122: 454-73.
- Minchin, P. R. 1987. An evaluation of the robustness of techniques for ecological ordination. *Vegetatio* 69: 89-107.
- Naeem, S., J. M. H. Knops, D. Tilman, et al. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* 91: 97-108.
- Naiman, R. J., H. Decamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* 3: 209-12.
- Nekola, J. C. and P. S. White. 1999. The distance decay of similarity in biogeography and ecology. *Journal of Biogeography* 26: 867-78.
- Newell, C. L. 1997. *Local and Regional Variation in the Vegetation of the Southern Appalachian Mountains [Dissertation]*. Chapel Hill, NC: University of North Carolina.
- Nicolson, M. and R. P. McIntosh. 2002. H. A. Gleason and the Individualistic Hypothesis revisited. *Bulletin of the Ecological Society of America* 83: 133-42.
- Nilsson, C. and G. Grelsson. 1995. The fragility of ecosystems: a review. *Journal of Applied Ecology* 32: 677-92.
- Nilsson, C., G. Grelsson, M. Johansson, and U. Sperens. 1989. Patterns of plant species richness along riverbanks. *Ecology* 70: 77-84.
- North Carolina Geological Survey. 1991. *Generalized Geologic Map of North Carolina*.
- Osterkamp, W. R. and C. R. Hupp. 1984. Geomorphic and vegetative characteristics along three northern Virginia streams. *Geol. Soc. Am. Bull.* 95: 1093-101.
- Pabst, R. J. and T. A. Spies. 1998. Distribution of herbs and shrubs in relation to landform and canopy cover in riparian forests of coastal Oregon. *Canadian Journal of Botany* 76.



- Peet, R. K. 1992. Community structure and ecosystem function. In Glenn-Lewin, D. C., R. K. Peet, and T. T. Veblen, eds. *Plant Succession: Theory and Prediction*. Volume 1. Cambridge, G.B.: Chapman & Hall. Pages 103-51.
- Peet, R. K., T. R. Wentworth, and P. S. White. 1998. A flexible, multipurpose method for recording vegetation composition and structure. *Castanea* 63: 262-74.
- Planty-Tabacchi, A., Tabacchi E., Naiman R.J., Deferrari C., and H. DeCamps. 1996. Invasibility of species rich communities in riparian zones. *Conservation Biology* 10: 598-607.
- Pope, B. F., Tasker, G. D., Robbins, J. C. 2001. Estimating the magnitude and frequency of floods in rural basins of North Carolina - revised. U.S. Geological Survey Water Resources Investigations Report 01-4207 Raleigh, NC: U.S. Geological Survey and N.C. Department of Transportation.
- 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 *Conyza bonariensis* and *Conyza canadensis*. *Ecology Letters* 2: 412-22.
- Proulx, M., Mazumder, and A. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* 79: 2581-92.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *The American Naturalist* 132: 652-61.
- Pysek, P. and K. Prach. 1994. How important are rivers for supporting plant invasions? In de Waals, L. C., L. E. Child, P. M. Wade, and J. H. Brock, eds. *Ecology and Management of Invasive Riverside Plants*. New York: John Wiley & Sons. Pages 19-26.
- Pysek, P., K. Prach, M. Rejmanek, and M. Wade, eds. 1995. *Plant Invasions - General Aspects and Special Problems*. Amsterdam: SPB Academic Publishing.
- SAS Institute. 1999. SAS. Version 8.00. Cary, NC, USA: SAS Institute, Inc.
- Scharf, F. S., F. Juanes, and M. Sutherland. 1998. Inferring ecological relationships from the edges of scatter diagrams: comparison of regression techniques. *Ecology* 79: 448-60.
- Schneider, R. L. and R. R. Sharitz. 1988. Hydrochory and regeneration in a bald cypress-water tupelo swamp forest. *Ecology* 69: 1055-63.
- Shmida, A. and M. V. Wilson. 1985. Biological determinants of species diversity. *Journal of Biogeography* 12: 1-20.

- Shmida, A. and S. P. Ellner. 1984. Coexistence of plant species with similar niches. *Vegetatio* 58: 29-55.
- Simberloff, D. S. and E. O. Wilson. 1970. Experimental Zoogeography of Islands: a two-year record of colonization. *Ecology* 51: 934-7.
- Skoglund, S. J. 1990. Seed dispersing agents in two regularly flooded river sites. *Canadian Journal of Botany*. 68: 754-60.
- Smith, A. T. 1980. Temporal changes in insular populations of the pika (*Ochtona princeps*). *Ecology* 55: 1112-9.
- Sneath, P.H.A., and R. R. Sokal. 1973. Numerical Taxonomy: The Principles and Practice of Numerical Classification. San Francisco, CA: W.H. Freeman and Company.
- S-Plus. 2000. S-Plus 2000 Professional Release 2. Seattle, Washington: Mathsoft.
- StataCorp. 2001. Stata Statistical Software: Release 7.0. College Station, TX: Stata Corporation.
- 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(1):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: 113-25.
- Strahler, A. N. 1964. Quantitative geomorphology of drainage basins and channel networks. Chow, V. T., ed. *Handbook of Applied Hydrology*. New York: McGraw-Hill.
- Symstad, A. 2000. A test of the effects of functional group richness and composition on grassland invasibility. *Ecology* 81: 99-109.
- Thebauld, C. and M. Debussche. 1991. Rapid invasion of *Fraxinus ornus* along the Herault River system in southern France: the importance of seed dispersal by water. *Journal of Biogeography* 18: 7-12.
- Thomas, D. J. 1996. Soil Survey of Macon County, North Carolina. Raleigh, NC: USDA Soil Conservation Service.
- Tilman, D. 1982. Resource Competition and Community Structure. Princeton, New Jersey: Princeton University Press.
- Tilman, D. 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton, NJ: Princeton University Press.
- Tilman, D. 1993. Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology* 74: 2179-91.

- Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78: 81-92.
- Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379: 718-20.
- Tilman, D., J. Knops, D. Wedin, et al. 1997a. The influence of functional diversity and composition on ecosystem processes. *Science* 277: 1300-2.
- Tilman, D., C. L. Lehman, and K. T. Thomas. 1997b. Plant diversity and ecosystem productivity: theoretical considerations. *Proc. Nat. Acad. Sci. USA* 94: 1857-61.
- Toner, M. and P. Keddy. 1997. River hydrology and riparian wetlands: a predictive model for ecological assembly. *Ecological Applications* 7: 236-46.
- Trenbath, B. R. 1974. Biomass productivity of mixtures. *Adv. Agron.* 26: 177-210.
- USDA. 2001. The PLANTS Database, Version 3.1 [Web Page]. Located at: <http://plants.usda.gov>. Accessed 2001.
- Vandermast, D. B. and D. H. Van Lear. 2002. Riparian vegetation in the southern Appalachian mountains (USA) following chestnut blight. *Forest Ecology and Management* 155: 97-106.
- Wardle, D. A. 2001. Experimental demonstration that plant diversity reduces invasibility - evidence of a biological mechanism or a consequence of sampling effect. *Oikos* 95: 161-70.
- Weakley, A. S. 2001 [manuscript]. Guide to the Flora of the Carolinas and Virginia. Durham, NC: The Nature Conservancy, Southern Conservation Science Department, Southern Regional Office.
- Weldon, C. W. and W. L. Slauson. 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. *The Quarterly Review of Biology* 61: 23-44.
- Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. *Ecological Monographs* 26: 1-80.
- Williamson, M. H. and A. Fitter. 1996. The characters of successful invaders. *Biological Conservation* 78: 163-70.
- Wilson, J. B. and A. J. Watkins. 1994. Guilds and assembly rules in lawn communities. *Journal of Vegetation Science* 5: 590-600.
- 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: 729-40.

- 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: 2071-81.
- Wistendahl, W. A. 1958. The floodplain of the Raritan River, New Jersey. *Ecological Monographs* 28: 129-53.
- Xiong, S. and C. Nilsson. 1997. Dynamics of leaf litter accumulation and its effects on riparian vegetation: a review. *The Botanical Review* 63: 240-64.