DIVERSITY, INVASIBILITY, AND STABILITY OF APPALACHIAN FORESTS ACROSS AN EXPERIMENTAL DISTURBANCE GRADIENT

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Dissertation submitted to the faculty of the Virginia Polytechnic Institute and State University in partial fulfillment of the requirements for the degree of

Doctor of Philosophy
In
Biological Sciences

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September 5, 2008
Blacksburg, Virginia

Keywords: Appalachian Mountains, diversity-invasibility, diversity-stability, earthworms, forest management, introduced species, silviculture, species richness

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ABSTRACT

For this dissertation, I measured how plant communities in Appalachian forests responded to disturbances caused by forest management activities. I had two primary objectives including (1) testing theories of biological diversity and invasions by nonnative species; and (2) providing empirical data that will help guide the sustainable use of forest resources. This work is part of the Southern Appalachian Silviculture and Biodiversity (SASAB) experiment that was established in the early 1990s to investigate ecosystem responses to a gradient of timber harvesting disturbances. Ranging from undisturbed controls to silvicultural clearcuts, the disturbance gradient is replicated at sites located throughout the Appalachian mountains of Virginia and West Virginia. The plant community was sampled across a wide range of spatial scales (2 hectares to 1 m^2) using a nested sampling design and was also sampled at three times including pre-disturbance, one year post-disturbance, and ten year post-disturbance.

For one element of the study I tested modern theories of biological invasions and investigated how the forest disturbance gradient interacted with species diversity to influence invasion by nonnative species (Chapter 2). Contrary to popular ecological theories of biotic resistance, the most diverse sites tended to be more easily invaded following intense canopy disturbance. Interestingly, none of the sites in this study were dominated by invasive plants, which led me to ask whether dominant tree species in forests provided resistance to nonnative plant establishment and growth through the quality of the litter they produce. I also asked how might animals that are known to alter litter layers interact with dominant tree species to influence plant invasions. Therefore, I conducted an experiment investigating how changes in litter from

dominant tree species and invasions by nonnative earthworms might influence invasibility of forests using forest floor mesocosms (Chapter 3). I found that plant invasion was inhibited by native oak litter even when earthworms were present, suggesting that oak forests may resist plant invasions via oak tree litter. In contrast, plant invasion was greater under invasive tree litter and earthworm activity tended to facilitate invasive plant success only under invasive tree litter.

I was also interested in understanding how disturbance might alter relationships between local and regional diversity. The long-term data of the forest disturbance experiment allowed me to investigate how local species richness is mediated by regional species richness after disturbance and during forest community development (Chapter 4). Local richness depended strongly on regional richness only after disturbance via colonization of species, but this relationship changed during forest aggradation. These results suggest that regional species pools are important to maintain local diversity following disturbance, but that local interactions (through canopy closure of dominant trees) exert control over species diversity during community reorganization.

Lastly, I tested current theories on how diversity influences compositional stability after disturbance (Chapter 5). Disturbance consistently resulted in decreased compositional stability, but diversity was associated with stability in complex ways, which depended on how stability was measured and at what scale. Species-rich areas were in some instances less stable; in other instances areas with intermediate levels of diversity were more stable. These results suggest that disturbance causes shifts in species composition via colonization, but the ways in which diversity of sites influences compositional stability is complex and depends on methods used and the scales of observation.

Taken together, these results suggest that disturbance influences invasibility, species saturation, and compositional stability of ecological communities. These properties change immediately following disturbance, and during forest development and canopy closure. Data from this project were useful in testing existing theories of community ecology, and may ultimately prove useful for forest managers as they decide how to protect biodiversity while planning for other uses of forest resources. Overall, these results suggest that colonization of species is the primary process driving plant community patterns in Appalachian forests following disturbance.

GRANTING AGENCIES

ACKNOWLEDGEMENTS

My committee always was challenging and supportive, and provided guidance, advice, patience, and ideas. To them I am thankful. Dr. Bob Jones provided enthusiasm, encouragement, skepticism, and optimism to help me develop ideas and think big and broad with an anchor to nature. In the midst of all of Bob's other obligations, he always found time to meet with me and spent hours reviewing drafts manuscripts and proposals. Dr. Carola Haas' encouragement and enthusiasm for ideas helped me develop the confidence to pursue broad and interesting questions. Dr. Tom Fox provided an always appreciated management perspective, which kept me focused on the application of my research. Dr. Fox's Appalachian silviculture class was a "modern synthesis" for my thinking about natural resource management. Dr. Erik Nilsen's support through all phases of thinking and developing ideas provided me a deeper understanding of ecology, academics, and grantsmanship.

While my committee members served as my primary academic coaches, I had the opportunity to interact and consult with others who helped me develop conceptual frameworks or taught me the tools needed to think deeper about ecology. At Virginia Tech, Drs. Steve Prisley, Maury Valett, Jack Webster, Kirsten de Beurs, Carolyn Copenheaver, John Galbraith, Jim Burger, Dave Parrish, and JP Morgan all influenced my thinking and perspectives on nature and science. The diverse insights I gained from these professors across disciplines at Virginia Tech were instrumental in my development as a researcher. Drs. Fred Benfield, Dana Hawley, and Lisa Belden provided friendship that made me feel part of the academic community at Virginia Tech. Graduate students who helped intellectually and emotionally were Matt Dittler, Verl Emrick, Amanda Malueg, Philip Taylor, Amanda Lentz, Tom Gorman, Camille Harris, Lori Blanc, Eric Sokol, Chris Burcher, Damon Ely, Erika Kratzer, and Sunny Crawley. Drs. Dan

ATTRIBUTION

Several colleagues aided in the writing and research of several of the chapters in this dissertation. Brief descriptions of their contributions are included here.

Chapter 2. Diversity-invasibility across an experimental disturbance gradient in Appalachian forests. Robert H. Jones (Department of Biological Sciences, Virginia Tech) co-refined the content of the chapter, and edited drafts of all chapters. Sharon M. Hood (Department of Forestry, Virginia Tech) currently at USDA Forest Service, Rocky Mountain Research Station Fire Science Lab, Missoula, MT collected data, conducted initial analyses on native and invasive species responses to disturbance, and edited drafts of the paper. Bryan W. Wender (Department of Forestry, Virginia Tech) current at Virginia Division of Natural Heritage, Roanoke, VA collected data, conducted initial analyses on native and invasive species responses to disturbance, and edited drafts of the paper.

Chapter 3: Tree leaf litter composition and nonnative earthworms influence plant invasion in experimental forest floor mesocosms. Robert H. Jones (Department of Biological Sciences, Virginia Tech) co-developed experimental design, co-refined the content, and edited all drafts the paper.

Chapter 4: Disturbance alters local-regional richness relationships in Appalachian forests. Nathan J. Sanders (Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville) co-developed conceptual framework, assisted in data analysis, and edited all drafts. Robert H. Jones (Department of Biological Sciences, Virginia Tech) co-refined the content, and edited all drafts the paper.

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Chapter 5: Stability and diversity of vascular plant communities following logging disturbance in Appalachian forests

CHAPTER 1: INTRODUCTION

Human populations and their use of natural resources continue to increase. At the same time, we are increasingly becoming concerned about managing our natural resources sustainably while maintaining biodiversity, compositional integrity, and functioning of ecological communities. Therefore, management objectives are complex and at times include conflicting goals. Daunting challenges exist to understand and predict consequences of management actions on ecosystems.

Many theories have been developed to understand the patterns and processes of natural ecosystems, with goals of predicting how natural systems will respond to human perturbations. In recent years, particular attention has been placed on theories pertaining to causes and consequences of biodiversity, with the specific goal of understanding how best to protect natural systems (reviewed in Quammen 1996) or to provide justification of protecting species diversity (Naeem 2002). However, many ecologists test their theories using model systems (Lawton 1995) that may not help resource managers make decisions that support conservation or sustainability of natural systems (McPherson and DeStefano 2003). To advance understanding, theories must be tested using carefully designed field studies across diverse communities and ecosystems.

In this dissertation, I test several ecological theories using data from a large-scale, long-term natural resource management experiment. The Southern Appalachian Silviculture and Biodiversity (SASAB) study was designed to study the effects of forest management alternatives on various components of Appalachian oak forest ecosystems. Forests of Appalachia are used for various reasons, and managers often must consider diverse ecological and social perspectives. In essence, SASAB was established to understand the ecological implications of alternative timber harvesting and oak regeneration methods. Past SASAB studies have investigated salamander

responses (Harpole and Haas 1999, Knapp et al. 2003), soil erosion (Hood et al. 2002), oak regeneration (Lorber 2003, Atwood 2008), and plant diversity and composition responses (Hammond et al. 1998, Wender 2000, Hood 2001) to disturbance. I had the unique opportunity to take advantage of the long-term existing dataset which includes pre-disturbance, one year post-disturbance, and ten year post-disturbance data (see Appendix A for exact years of treatments and sampling times).

In Chapter 2, I took advantage of the SASAB data and investigated how forest disturbance influenced relationships between native diversity and nonnative invasion. Modern theories of community invasibility by nonnative species developed following seminal work by Elton (1958) and suggested that species-rich areas are more resistant to invasion than species-poor areas (Shea and Chesson 2002). Lonsdale (1999) and Stohlgren et al. (1999) challenged this view with data suggesting that species-rich areas may actually be more easily invaded than species-poor areas because of environmental factors that covary with native diversity including resource availability (Davis et al. 2000) or heterogeneity (Davies et al. 2005).

Curiously, even in the most disturbed sites few of the nonnative species persisted after 10 years of forest regeneration. In fact, none of the understory communities appeared to be *dominated* by nonnative invasive plant species. I hypothesized that oak leaf litter may provide a barrier to invasion by nonnative understory species. In Chapter 3, I present results from an experiment where I investigated how litter layers from different species, including a nonnative tree, might influence nonnative plant invasion. Because nonnative earthworms have invaded some habitats and can transform organic layers of the forest floor, I crossed the litter treatments with a treatment of nonnative earthworms to investigate potential interactions, as well as test the "invasional meltdown" hypothesis (Simberloff and Von Holle 1999).

The relative importance of local and regional patterns and processes shaping ecological communities remains a focus of ecology (Leibold et al. 2004). Recently, investigations into local-regional richness relationships have become a method to investigate whether regional versus local processes limit community diversity (Harrison and Connell 2008). Saturating relationships between local and regional richness have been interpreted to mean that strong local interactions influence local richness (Chapter 4). In contrast unsaturating relationships have been interpreted to mean that local diversity is limited only by regional species pools. However, few studies have investigated how disturbance and community reorganization after disturbance influence local-regional richness relationships. The long-term data from the SASAB project presented a unique opportunity to test theories about how small scale ("local") richness would be related to large scale ("regional") richness before disturbance, one year after disturbance, and ten years after disturbance during forest aggradation.

Theories and empirical data on how diversity influences the stability of communities in response to disturbance have a long history in ecology (see citations in Chapter 5). Are areas with more species more or less stable after disturbance? The answer usually depends on what level stability is measured. Population level stability may decrease along gradients of species diversity, whereas ecosystem-level stability is thought to increase with diversity. Questions remained as to whether increased stability is a function of diversity per se, or a result of other factors that covary with diversity (sensu Huston 1997) including site and soil factors. Nonetheless, compositional stability (i.e., the constancy of species composition) after disturbance receives less attention than ecosystem-level stability (Halpern 1988, Sankaran and McNaughton 1999, Foster et al. 2002). Again, I used SASAB vegetation data to explore how disturbance

intensity interacted with diversity of sites to influence compositional stability in terms of initial shifts (resistance) and return to pre-disturbance conditions after 10 years.

Overall, one major goal of this dissertation was to test and evaluate several key theories in ecology using data from an experiment addressing real management decisions in forest ecosystems of the Appalachian region. However, a second goal was to test the impacts of natural resource management on maintenance of biodiversity and protection of forests against invasion by nonnative plants species. Thus, this dissertation attempts to fulfill a primary challenge for ecologists and natural resource managers to develop collaborations where positive feedbacks between both parties contribute to sustainable management of our natural resources as well as our understanding of patterns and processes of natural systems (McPherson and DeStefano 2003).

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CHAPTER 2: DIVERSITY-INVASIBILITY ACROSS AN EXPERIMENTAL DISTURBANCE GRADIENT IN APPALACHIAN FORESTS

R.Travis Belote, Robert H. Jones, Sharon M. Hood, and Bryan W. Wender

ABSTRACT

Research examining the relationship between community diversity and invasions by non-native species has raised new questions about the theory and management of biological invasions. Ecological theory predicts, and small-scale experiments confirm, lower levels of non-native species invasion into species-rich compared to species-poor communities, but observational studies across a wider range of scales often report positive relationships between native and non-native species richness. This paradox has been attributed to the scale dependency of diversity-invasibility relationships and to differences between experimental and observational studies. Disturbance is widely recognized as an important factor determining invasibility of communities, but few studies have investigated the relative and interactive roles of diversity and disturbance on non-native species invasion. Here, we report how the relationship between native and non-native plant species richness responded to an experimentally applied disturbance gradient (from no disturbance up to clearcut) in oak-dominated forests. We consider whether results are consistent with various explanations of diversity-invasibility relationships including biotic resistance, resource availability and the potential effects of scale (1 m^2 to 2 ha). We found no correlation between native and non-native species richness before disturbance except at the largest spatial scale, but a positive relationship after disturbance across scales and levels of disturbance. Post-disturbance richness of both native and non-native species was positively correlated with disturbance intensity and with variability of residual basal area of trees. These

results suggest that more non-native plants may invade species-rich communities compared to species-poor communities following disturbance.

Keywords: plant invasions; diversity-invasibility relationships; disturbance; biotic resistance; biotic acceptance; deciduous forests; forest management

INTRODUCTION

Predicting which non-native species will invade particular habitats is a major focus of ecologists and natural resource managers (Parker et al. 1999, Shea and Chesson 2002). Popular ecological theory has suggested that fewer species can colonize areas with higher resident species diversity, because more species occupy more niches, and thus provide greater "biotic resistance" to invasion (Elton 1959). Small-scale experiments have corroborated this prediction (Levine 2000, Naeem et al. 2000, Kennedy et al. 2002, Fargione and Tilman 2005). However, most observational studies that span a larger range of spatial scales suggest the opposite pattern is true – areas with more native species also support more non-native species (Levine and D'Antonio 1999, Lonsdale 1999, Stohlgren et al. 1999, Levine 2000, Fridley et al. 2004).

Several hypotheses have been proposed to account for the paradox between experimental and observational studies (reviewed by Fridley et al. 2007), including the scale dependent nature of diversity-invasibility relationships (Stohlgren et al. 1999, Levine 2000, Brown and Peet 2003, Fridley et al. 2004, Knight and Reich 2005), co-varying extrinsic factors or favorable conditions that promote higher levels of both native and non-native diversity (Levine and D'Antonio 1999, Naeem et al. 2000, Shea and Chesson 2002, Figure 2.1A), and resource heterogeneity (Davies et al. 2005). For example, at small scales or within sites the number of individuals and their competitive interactions limit diversity of both native and non-native species (Levine 2000),

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whereas at large scales or across sites resource heterogeneity contributes to higher native and non-native species richness (Shea and Chesson 2002, Davies et al. 2005, Figure 2.1A). Environmental factors that promote higher native diversity within sites and at both small and large scales may also promote non-native diversity (Stachowicz and Tilman 2005) – a pattern described as "the rich get richer" (Stohlgren et al. 2003, Figure 2.1B). Ortega and Pearson (2005) recently suggested that positive relationships between native and non-native species are found only in areas where "weak invaders" (e.g., non-invasive non-native species) coexist with native species, but not where "strong invaders" (e.g., invasive non-native species) dominate habitats.

Other hypotheses of plant invasions, while not mutually exclusive from those described above focus more attention on disturbance and resource availability than on potential biotic resistance of species-rich communities (Hobbs and Huenneke 1992, Sher and Hyatt 1999, Davis et al. 2000, Huston 2004, Gross et al. 2005, Walker et al., 2005, Suding and Gross 2006). Davis et al. (2000, 2005) suggest that colonization of non-native species occurs during times of increased resource supply or decreased resource uptake by resident species. Resource supply and uptake is often altered following disturbance (Huston 2004) because individual mortality leads to decreased uptake and increased availability of resources (Sher and Hyatt 1999). Moreover, disturbance is often proposed as an extrinsic factor contributing to diversity-invasibility relationships (Stohlgren et al. 1999, Levine 2000, Naeem et al. 2000, Brown and Peet 2003, Gilbert and Lechowicz 2005, Von Holle 2005). However, to our knowledge no studies have experimentally manipulated disturbance and compared pre-disturbance with post-disturbance diversity-invasibility patterns across various spatial scales, although the need for such studies is well recognized (Stohlgren 2002, Fridley et al. 2007).

In this study, we used data from an ongoing experiment in the southern Appalachian Mountains (USA) to assess the relationship between richness of native and non-native plant species across an experimentally created, large-scale disturbance gradient. Seven silvicultural disturbance treatments, representing alternative management practices, were replicated at seven oak-dominated forested sites in West Virginia and Virginia. The experimental design allowed us to test the effects of disturbance intensity on relationships between richness of native and non-native plant species across sites and disturbance treatments, within sites and disturbance treatments, and at various spatial scales using both pre-disturbance and post-disturbance data. We could then determine if extrinsic factors caused by site differences (i.e., biotic and abiotic variability associated with geographic location) or disturbance intensity led to changes in the relationship between richness of native and non-native species across a range of spatial scales (Naeem et al. 2000, Shea and Chesson 2002, Stohlgren et al. 2006). Shea and Chesson's (2002) model predicts negative relationships between native and non-native species where extrinsic factors are similar (e.g., at small spatial scales or in areas of similar environmental conditions), but positive relationships across areas of differing extrinsic factors that may occur at larger spatial scales or across sites. This is illustrated in Figure 2.1A where each line segment represents data from a particular community type or unique set of environmental conditions. Alternatively, the "biotic acceptance" conceptual model suggests that favorable conditions that promote high native richness of a habitat will also promote high non-native richness within *and* across sites (Figure 2.1B, Stohlgren 2002, 2006).

After considering these various models, we made two general predictions, each tested by a series of correlation analyses. First, when data were analyzed *across* all sites and disturbance treatments, we predicted an overall positive relationship between native and non-native richness,

corresponding to the general positive trends in Figures 2.1A and 2.1B. Second, when data were analyzed *within* sites or disturbance treatments, we predicted negative relationships, represented by the negative trend for individual line segments in Figure 2.1A. Further, we expected to find more negative relationships between native and non-native richness at the smallest scales, where species interactions would likely be the strongest. We also investigated whether areas of higher pre-disturbance richness resisted invasions by non-native species following disturbance compared to areas of lower pre-disturbance richness. All correlations and regressions were tested separately at each of three spatial scales ($1m^2$, $576m^2$, and 2 hectares).

METHODS

Study Sites

Seven sites (experimental blocks) were chosen in the Valley and Ridge province and Appalachian Plateau region of southwest Virginia and northeastern West Virginia located on the Jefferson National Forest and the Westvaco Corporation's Wildlife and Ecosystem Research Forest, respectively (Appendix B1). Sites were selected to represent similar overstory composition and age and were dominated by *Quercus* spp. (red and white oaks), *Acer rubrum* L. (red maple), and *Carya* spp. (hickories). The understory at the sites is diverse with native species exceeding 700 species, including a variety of understory trees (e.g., *Sassafras albidum* (Nutt.) Nees, *Nyssa sylvatica* (Marsh.)), shrubs (e.g., *Rhododendron* spp., *Vaccinium* spp.), lianas (e.g., *Smilax* spp.), graminoids (e.g., *Carex* spp., *Dichanthelium* spp.), and herbaceous monocots (e.g., members of Liliaceae and Orchidaceae) and dicots (e.g., species from Asteracea and Roseacea). Sites were located on similar topographic positions with generally south-facing, moderate slopes (10-40%) and intermediate elevations (600-1200 m). Soils at all sites are rocky, well-drained,

acidic, and derived from sandstone and shale residuum and colluvium. Precipitation is generally evenly distributed throughout the year.

At each of the seven sites, seven two-hectare experimental units (EUs) were established with no buffer between units (Appendix B2). Nested within each EU, three permanent 576 m^2 (24 m × 24 m) plots were randomly arranged so that they were 23 meters from the EU edge and were separated by an azimuth of 120° from EU center. Six 1 m^2 subplots were nested within each 576 m^2 plot (subplots were located along plot perimeters). For additional information about the sites and plot designs see Wender (2000) and Hood (2001).

Disturbance Treatments

Disturbance treatments were applied to the 2-hectare experimental units between 1993 and 1998, during the non-growing season. Treatments were randomly assigned to EUs within each site, and included a range of overstory removal, from clearcut (95% basal area removed), low-leave shelterwood (83% basal area removed, leaving un-merchantable trees), leave-tree harvest (74% of basal area removed leaving a few dominants), high-leave shelterwood (56% of basal area removed to "thin" the stand), group selection (47% basal area removed in approximately 0.10 ha patches), understory herbicide (14% of basal area removed from suppressed trees), to uncut control. During tree harvest, limbs and branches were removed from main stems and typically left on site. Control treatments were intended to represent areas that experience no disturbance related to timber harvesting. However, during treatment application of nearby sites, some minor disturbance associated with skid trails and diffuse light from adjacent treatments occurred within some uncut control EUs; however, these disturbances were mostly restricted to the edges of the EUs. The seven treatments were applied to examine the influences

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of alternative management strategies on multiple system components including plant and animal diversity, oak regeneration, and soil ecosystem processes. One West Virginia site did not include the low-leave shelterwood or the understory herbicide treatments; thus the experimental set-up is an unbalanced randomized block design consisting of 47 EUs.

Data collection

All data were collected one year prior to and one or two years following disturbance treatment application with the exception of one site where pre-disturbance data were collected two years prior to harvesting disturbance (Hammond et al. 1998, Wender 2000, Hood 2001). Presence of all herbaceous and woody plant species was recorded at each of the three scales (EU, plot, and subplot). Using number of species present, we generated estimates of species richness for native and non-native species at each scale. Basal area of the EUs was estimated using individual tree diameter data, which were collected by measuring diameters at 1.4 m of all species greater than 5 meters tall within each plot; these data were collected at the same time as the species richness data.

Statistical Analysis

We used Pearson's correlation to investigate the relationship between native and non-native species richness at each of the three spatial scales of sampling (2-hectare EUs, 576 m^2 plots, and 1 m^2 subplots) prior to disturbance and after disturbance separately. For the two smaller scales, we averaged the richness values within experimental unit to meet the assumption of independence (i.e., they were treated as subsamples within an experimental unit). First, we used the entire data set for these analyses, resulting in six correlations (pre- and post-disturbance

by three scales). However, to differentiate between the alternatives illustrated in Figure 2.1, we ran separate analyses by site (7 sites, each with the same 6 correlations for a total of 42 correlations) and by treatment (7 treatments, each with 6 correlations for another 42 analyses). Because of the large numbers of correlations (90 in all), several significant correlations were expected by chance alone, and thus, we examined results for large changes in the number of significant correlations, and for differences in negative versus positive correlations (the latter is especially useful to examine hypotheses in Figure 2.1). .

To test the prediction that greater species richness leads to greater resistance to invasion following disturbance, we regressed the change in native, non-native, and total richness (i.e., difference between pre-disturbance and post-disturbance richness) on total pre-disturbance richness at the three spatial scales; thus, we performed 9 separate analyses. Because disturbance intensity (% basal area removed) strongly influenced native and non-native post-disturbance richness, we investigated both main and interactive effects of total pre-disturbance richness and % basal area removed in the regression model (PROC GLM in SAS 9.1):

$$\Delta \text{ richness} = \mu + \text{pre-richness} + \text{disturbance} + \text{pre-richness} \times \text{disturbance} + \varepsilon$$

Where Δ richness is either the change in total, native, or non-native richness at each scale (using a separate model for each category and scale); μ is the overall mean change in richness; pre-richness is the total (native and non-native species combined) richness before disturbance treatments were applied; disturbance is % basal area removed; and ε is the residual variation.

To test whether results were consistent with hypothesized influences of resource availability and resource heterogeneity, we conducted two sets of simple linear regressions. First, we regressed experimental unit species richness on disturbance intensity (% basal area removed) for native and non-native species separately, at all three scales (six regressions where

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N = 47 for each regression). These regressions provide a test of the favorable-conditions

hypothesis (Levine and D'Antonio 1999), because resources made available by canopy

disturbance would allow both native and non-native species to colonize areas similarly. We also

regressed richness of native and non-native species at each spatial scale on the coefficient of

variation (CV) of post-disturbance basal area to investigate the potential importance of resource

heterogeneity (patchiness of residual trees left following disturbance) in determining diversity-

invasibility relationships (Davies et al. 2005). Residuals of all data were analyzed for

homogeneity of variance; those not meeting this assumption were log or arc-sine square root

transformed prior to analysis as appropriate.

RESULTS

No relationship between native and non-native plant species richness was detected prior

to disturbance across sites and disturbance treatments except at the largest spatial scale where a

positive relationship was observed (Figure 2.2). After the disturbance gradient was applied

strong positive correlations developed between native and non-native richness across sites and

disturbance treatments at all scales. When we examined data within sites (with disturbance

treatments pooled within site), few significant relationships between native and non-native

species richness were observed before disturbance, except at the two West Virginia sites at the

largest spatial scale where the relationship was negative at one site and positive at the other

(Table 2.1). Post-disturbance relationships between native and non-native species within site

were either positive or non-significant depending on scale and site. When we examined data

within disturbance treatments (sites pooled within treatment), again pre-disturbance relationships

were weak; only one negative correlation between native and non-native species richness was

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detected (Table 2.2). However, after disturbance positive correlations between native and non-native richness were commonly found at the largest spatial scale, and in the most disturbed treatments even at the smallest spatial scale. In sum, whether we examined the full data set or analyzed within sites or within treatments, pre-disturbance relationships between native and non-native richness were weak and post-disturbance relationships tended to be strongly positive.

Change in total and native species richness did not depend on pre-disturbance species richness at any scale (Table 2.3), but % basal area removed did explain the increase in total, native, and non-native species richness at all scales. However, change in non-native species was marginally dependent ($p = 0.06$) on an interaction between pre-disturbance total richness (native and non-natives) and % basal area removed at the intermediate scale (576 m^2 plot) (Table 2.3). Specifically, at this intermediate spatial scale more non-native species colonized areas where pre-disturbance species richness was high and disturbance was most intense than areas where pre-disturbance richness and disturbance intensity were lower (Figure 2.3).

Disturbance intensity (% basal area removed) and resulting habitat heterogeneity (CV of residual basal area) were related to the patterns of increased richness. Richness of both native and non-native species was positively related to percent basal area removed at all scales (Figure 2.4, Table 2.4). Both were also positively correlated with coefficient of variation (i.e., habitat heterogeneity) of basal area following disturbance (Figure 2.4). Non-native species richness increased more dramatically (i.e., had a steeper slope) than native species with increasing disturbance intensity and variability of remaining basal area at all scales. Total basal area removed and variability of residual basal area, however, were positively correlated ($r = 0.54$; $p <$ 0.0001), and so, it is difficult to determine the independent influence that each these two factors may have on the post-harvest increase in species richness.

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DISCUSSION

Consistent with our first prediction and other observational studies (Stohlgren 2002), our study suggests that the relationship between native and non-native species richness was generally positive within oak-dominated forest systems when data were combined across sites and disturbance treatments. However, the presence and strength of the positive relationships depended on disturbance intensity and scale. More intense tree harvesting disturbance increased richness of both native and non-native species, which explains the positive correlation between native and non-native species following harvesting disturbance. As recognized by Fridley et al. (2004, 2007) and Stachowicz and Tilman (2005), the relationship between native and non-native species richness is not necessarily causal but results from each group responding similarly to extrinsic environmental factors (Naeem et al. 2000), in this case a disturbance gradient.

Our second prediction that relationships between native and non-native richness would be negative within sites or treatments was not supported. Theory suggests that negative relationships between native and non-native richness are more likely observed within sites or within treatments where intrinsic factors such as competition for resources by existing vegetation would limit invasibility but where extrinsic factors are relatively constant throughout the community (Figure 2.1A, Shea and Chesson 2002). However, even when examining data within sites and disturbance treatments, few negative relationships were detected. We also predicted that the relationship between native and non-native species would be negative at small scales where intrinsic factors are more likely to control diversity and invasibility than at larger scales where extrinsic factors more likely produce positive diversity-invasibility relationships (Fridley et al. 2004). However, we found no relationships between native and non-native richness at the $1m^2$ scale before disturbance and a positive relationship across sites and disturbance treatments and

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within the clearcut treatments following disturbance. This pattern suggests that while resident species may resist colonization of non-native species in some systems on small spatial scales (Levine 2000, Dukes 2001, Kennedy et al. 2002), co-existence mechanisms between native and non-native species may operate at least temporarily following disturbance even at the smallest spatial scale in areas of intense disturbance.

Biological resistance to colonization by both native and non-native species may have occurred in this system prior to disturbance, and this may explain the relatively low number of non-natives observed before forests were harvested. However, it appears that any biological resistance that may occur before disturbance is overwhelmed by canopy removal disturbance and the introductions or emergence of propagules following disturbance. Von Holle and Simberloff (2006) investigated non-native plant establishment in experimental plant communities located near the sites described in this study and suggested that propagule pressure of invaders can overcome biological resistance of recipient communities as well as the environmental resistance of stressful abiotic conditions. In our study, changes in total, native, or non-native species depended on disturbance intensity and not on total pre-disturbance richness at the largest and smallest spatial scales. However, at intermediate spatial scales, sites with higher pre-disturbance richness tended to be colonized by more non-native species especially in areas where disturbance was most intense. The results of this study support the "biotic acceptance" (i.e., the rich get richer, Stohlgren et al. 2003, Figure 2.1B) rather than "biotic resistance" model of species invasions (Levine et al. 2004, Von Holle 2005); i.e., areas that support more natives are also more easily invaded by non-native species, especially following disturbance.

While we have no direct environmental measures for resource-based mechanisms, tree harvesting likely increased light and nutrient availability, soil temperature, and soil moisture by

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reduced evapotranspiration (Johnson et al. 2002). Harvesting disturbance thus allowed for either more native and non-native propagules to enter sites, existing propagules to germinate, or both. Brown and Peet (2003) observed similar positive relationships between native and non-native species richness in riparian areas of the southern Appalachians with higher flooding frequency, a pattern attributed to propagule pressure from both native and non-natives species.

The disturbance treatments also resulted in patchiness of residual tree basal area (our measure of habitat heterogeneity). Davies et al. (2005) recently presented a positive relationship between variance of soil depth and native and exotic diversity and showed that the spatial heterogeneity, but not favorable conditions hypothesis, explains the positive relationship between native and non-native plants. Our results show that the favorable conditions hypothesis (Levine and D'Antonio 1999) and resource heterogeneity hypothesis (Davies et al. 2005) may not be mutually exclusive. Treatments with greater variability in residual basal area supported more native and non-native species, but more intense disturbance also resulted in more native and non-native species.

Non-native species had greater rates of colonization (proportional to richness prior to disturbance) following canopy disturbance, which may be attributed to the introduction of non-native species from nearby species pools or through deliberate or accidental introduction of propagules for management purposes. Skid trails (paths used by logging machinery) were seeded with a non-native species (*Festuca arundinacea* Schreb.) to reduce soil erosion, and it is unknown if other species were accidentally or intentionally included during seeding. However, most plots and subplots were located outside of these skid trails.

The lack of notoriously "strong" invading species (i.e., non-native species that can dominate habitats) may also explain why we found positive relationships between native and

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non-native species invasion. Ortega and Pearson (2005) suggested that in cases where negative

relationships are observed, the pattern is not driven by biotic resistance, but by strong invaders

excluding native species in some systems. The increase in both native and non-native richness

following disturbance was primarily the result of the establishment of herbaceous species, most

of which are "weak" invaders (See Appendix C for list of non-native species found at each site).

However, some non-natives that invaded the sites following disturbance are considered "strong"

invaders, but the duration of time since arrival in this study limits our ability to investigate their

spread and impact. We will continue to monitor these sites to determine the persistence and

potential effects of the strong invasive species on native diversity and composition.

Conclusions

The importance of disturbance in plant invasions has been widely recognized (Hobbs

and Huenneke 1992, Davis et al. 2000, Huston 2004), and disturbance appears to be a significant

extrinsic factor that results in positive relationships between native and non-native diversity, at

least at large scales of observation (Fridley et al. 2007). Even at smaller spatial scales, where

biotic resistance related to species richness is predicted to have the strongest influence on the

relationship between native and non-native species richness, we found little or no evidence to

support resistance by native species richness on non-native species invasion. Overall, therefore,

hypotheses based on resource availability and disturbance (Fig 1B) appear to better fit our results

than those based on biological resistance (Fig 1A). Our results show that both native and non-

native species colonize disturbed areas leading to positive correlations between native richness

and non-native richness. Future monitoring will investigate: (1) which non-native species persist

and spread and (2) how patterns of native and non-native richness relationships change during forest aggradation and development.

ACKNOWLEDGEMENTS

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Table 2.1. Relationship between native and non-native species richness (Pearson's correlation coefficient and associated p-value) at seven sites (disturbance treatments pooled within site) in oak dominated forests within the Southern Appalachian Mountains before silvicultural disturbance and post-disturbance at three spatial scales. BB1=Blacksburg District site 1; BB2=Blacksburg District site 2; CL1=Clinch District site 1; CL2=Clinch District site 2; NC=New Castle District site; WV1=Westvaco Corporation site 1; WV2=Westvaco Corporation site 2. ($N = 7$ for all correlations, except WV1 where $N = 5$ for each correlation).

| | Pre-disturbance | | | | | | Post-disturbance | | | | | |
| | 2 hectare | | 576 m^2 | | 1 m^2 | | 2 hectare | | 576 m^2 | | 1 m^2 | |
Site	r	p	r	p	r	p	r	p	r	p	r	p
BB1	0.44	0.32	-0.003	0.99	0.011	0.98	**0.85**	**0.01**	**0.91**	**0.005**	**0.91**	**0.004**
BB2	-0.04	0.93	0.46	0.29	0.39	0.38	**0.77**	**0.04**	**0.88**	**0.009**	**0.77**	**0.04**
CL1	no non-natives		-0.11	0.82	no non-natives		**0.95**	**0.001**	0.61	0.15	-0.25	0.58
CL2	0.16	0.74	0.32	0.47	no non-natives		**0.99**	**<0.0001**	**0.77**	**0.04**	0.37	0.41
NC	0.33	0.47	0.39	0.39	-0.62	0.14	**0.95**	**0.001**	**0.85**	**0.01**	0.36	0.43
WV1	**-0.95**	**0.01**	0.13	0.83	0.25	0.68	0.85	0.06	0.48	0.41	0.52	0.36
WV2	**0.96**	**0.0005**	0.69	0.08	no non-natives		**0.91**	**0.004**	**0.80**	**0.03**	0.72	0.06

Table 2.2. Relationship between native and non-native species richness (Pearson's correlation coefficient and associated p-value) within plots receiving seven silvicultural disturbance treatments in oak dominated forests within the Southern Appalachian Mountains before silvicultural disturbance and post-disturbance at three spatial scales (sites pooled within disturbance treatments). CON=uncut control; HB=understory herbicide; GR=group selection; SW50/60=high leave shelterwood; LV=leave tree harvest; SW20/30=low leave shelterwood; CC=clearcut. See Methods for description of treatments ($N = 7$ for all correlations, except SW20/30 and HB, where $N = 6$ for each correlation).

| | Pre-disturbance | | | | | | Post-disturbance | | | | | |
| | 2 hectare | | 576 m^2 | | 1 m^2 | | 2 hectare | | 576 m^2 | | 1 m^2 | |
Treatment	r	p	r	p	r	p	r	p	r	p	r	p
CON	0.31	0.49	0.17	0.71	no non-natives		0.44	0.32	-0.15	0.74	no non-natives	
HB	**0.92**	**0.003**	**-0.82**	**0.05**	-0.32	0.53	0.28	0.53	0.32	0.53	no non-natives	
GR	**0.78**	**0.04**	0.34	0.44	-0.14	0.76	**0.75**	**0.05**	**0.86**	**0.012**	0.45	0.31
SW50/60	**0.76**	**0.04**	no non-natives		no non-natives		**0.84**	**0.017**	0.72	0.066	0.43	0.34
LV	0.51	0.30	-0.29	0.54	-0.04	0.93	**0.91**	**0.01**	0.48	0.27	0.47	0.28
SW20/30	**0.14**	**0.79**	-0.19	0.72	0.37	0.47	**0.95**	**0.004**	**0.89**	**0.018**	**0.12**	**0.81**
CC	**0.75**	**0.05**	0.23	0.63	-0.14	0.76	**0.91**	**0.004**	0.64	0.12	**0.76**	**0.047**

Table 2.3. *P*-values from general linear model investigating the effects of total species richness before disturbance, % basal area removed, and their interaction on the change (difference between pre-disturbance richness and post-disturbance richness) in total, native, and non-native species richness at three spatial scales. ($N = 47$ for each model).

Scale	Change in richness	Pre-disturbance total richness	% Basal are removed	Interaction
2 hectare	Total	0.35	**0.002**	0.94
	Native	0.24	**0.008**	0.99
	Non-native	0.72	**<0.0001**	0.69
	Total	0.13	**<0.0001**	0.44
576 m²	Native	0.14	**<0.0001**	0.63
	Non-native	0.15	**0.0016**	**0.06**
	Total	0.53	**<0.0001**	0.28
1 m²	Native	0.48	**<0.0001**	0.29
	Non-native	0.65	**0.006**	0.47

Table 2.4. Slope, R^2, and p-value from regression analysis relating native and non-native richness to % basal area removed and coefficient of variation of remaining basal area at three spatial scales and across sites and disturbance treatments ($N = 47$ for each model). Figure 2.3 shows data from the 576m^2 scale.

| | % Basal area removed | | | | | | CV of remaining basal area | | | | | |
| | Native | | | Non-native | | | Native | | | Non-native | | |
Scale	slope	R^2	p	slope	R^2	p	slope	R^2	p	slope	R^2	p
2 hectare	0.37	0.11	0.02	2.8	0.32	<0.0001	0.33	0.14	0.01	2.1	0.27	0.0002
576 m^2	0.93	0.17	0.004	6.8	0.25	0.0003	0.83	0.21	0.001	5.8	0.19	0.017
1 m^2	5.36	0.18	0.003	81.85	0.16	0.006	3.07	0.09	0.04	69.45	0.18	0.003
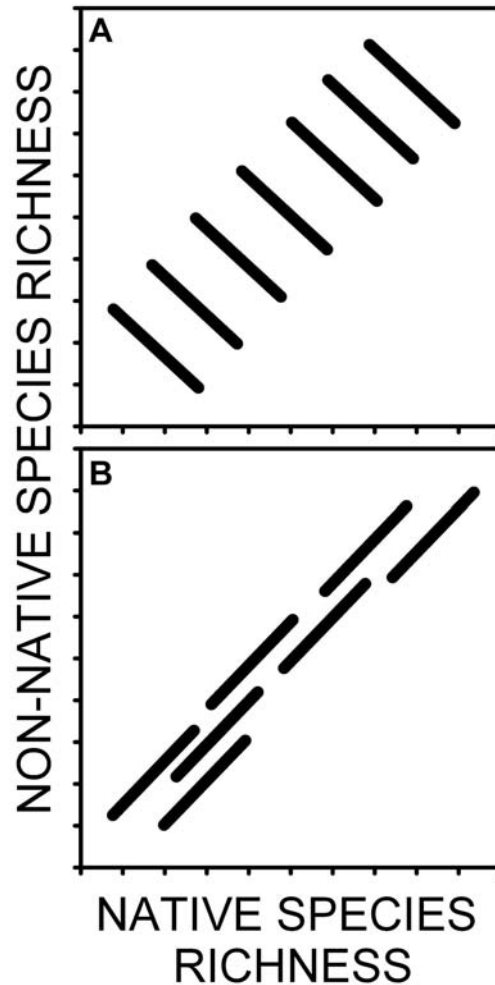
Figure 2.1. Two conceptual models describing diversity-invasibility relationships proposed by

Shea and Chesson (2002; Figure 2.1A) and inspired by Stohlgren et al. (2006; Figure 2.1B).

Each separate line represents diversity-invasibility relationships at similar scales, within sites, or

where environmental factors are similar. The top figure (A) predicts that "biotic resistance" to

invasive species (i.e., leading to a negative slope) operates where biological and environmental

factors (i.e., extrinsic factors) are similar, but relationships become positive when examined

across sites or spatial scales. The bottom figure (B) predicts that "biotic acceptance" (i.e., the

rich get richer) occurs within sites and at all spatial scales because resource availability or other

extrinsic factors (e.g., disturbance) support both more native and non-native species.
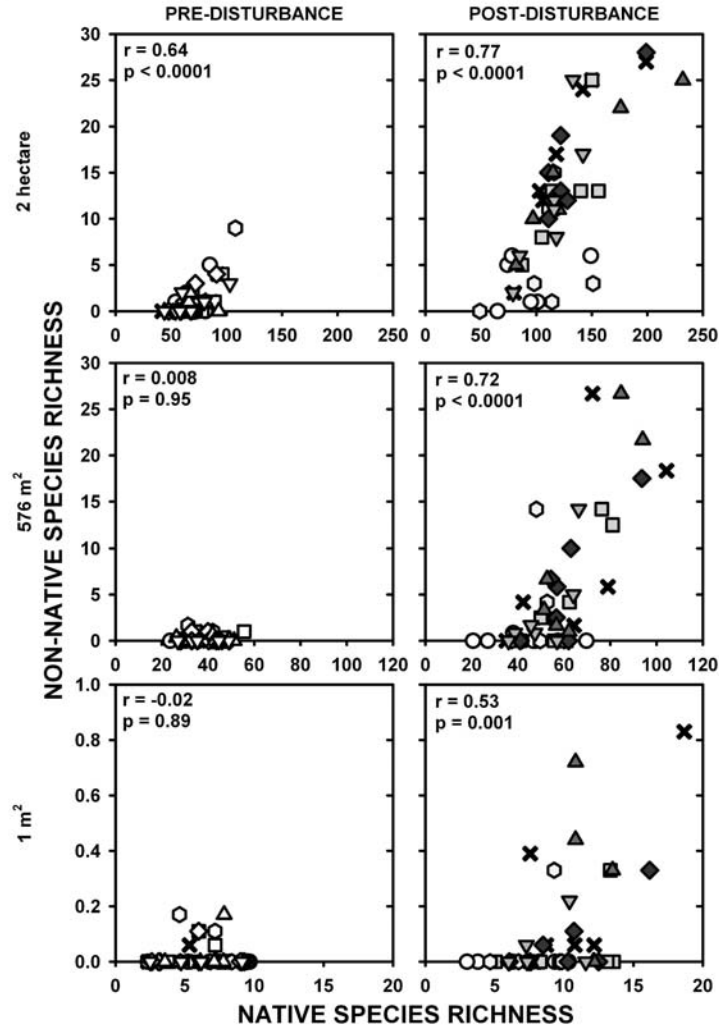
Figure 2.2. Relationship between native and non-native species richness at three spatial scales (2 ha, 576m^2, and 1m^2) before disturbance (pre-disturbance) and following disturbance (post-disturbance). Pearson's correlation coefficient and associated *p*-values are provided and indicate correlation between native and non-native species richness across disturbance treatments and sites. Symbols are open in left-hand pre-disturbance column and filled in right-hand post-disturbance column to indicate seven disturbance treatments (◯ = control, ◯ = understory herbicide, ☐ = group selection, ▽ = high-leave shelterwood, ◆ = leave-tree, ▲ = low-leave shelterwood, and ✖ = clearcut). Correlation coefficients for within treatment analyses are in Table 2.2.

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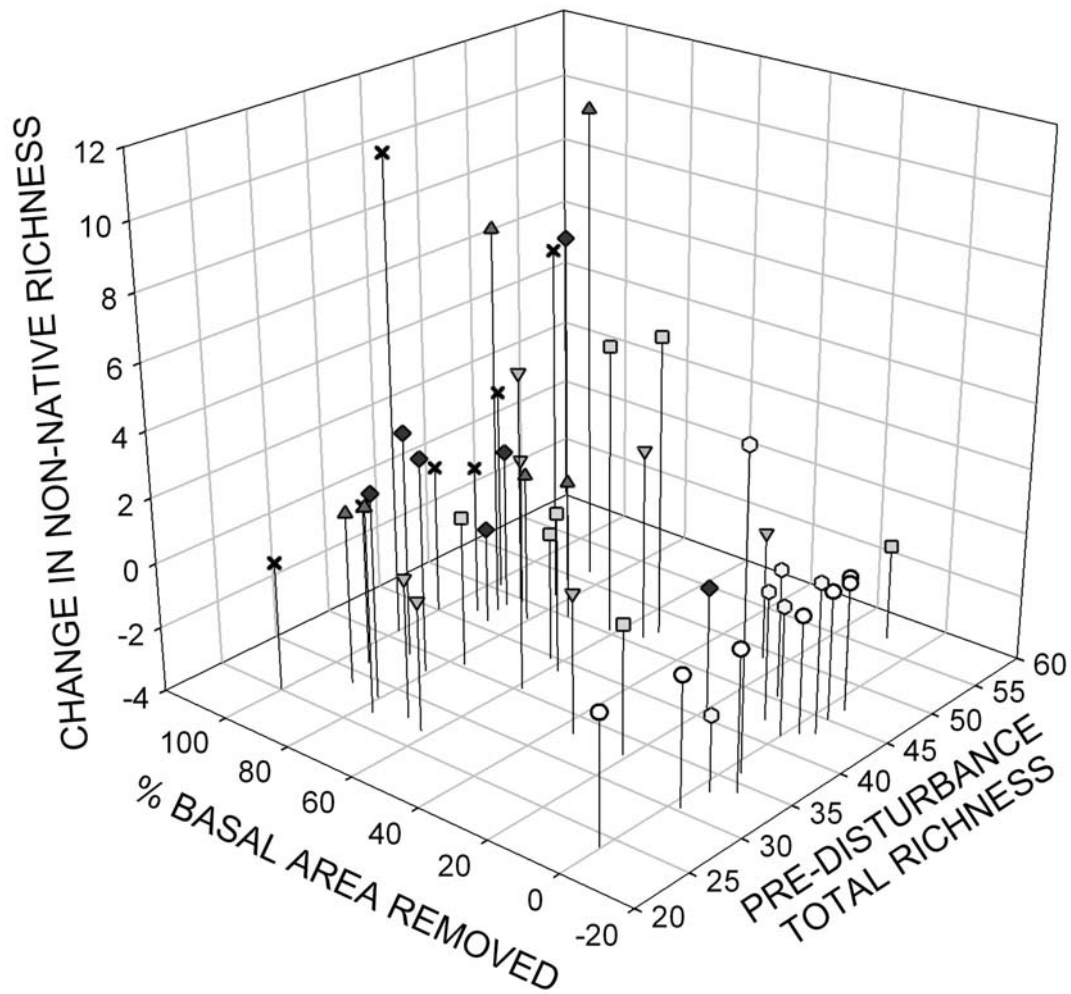
Figure 2.3. Relationship between pre-disturbance total diversity (sum of native and non-native species), % basal area removed, and increase in number of non-native species at 576 m^2 scale (pre-disturbance richness × % basal area removed interaction $p = 0.06$).
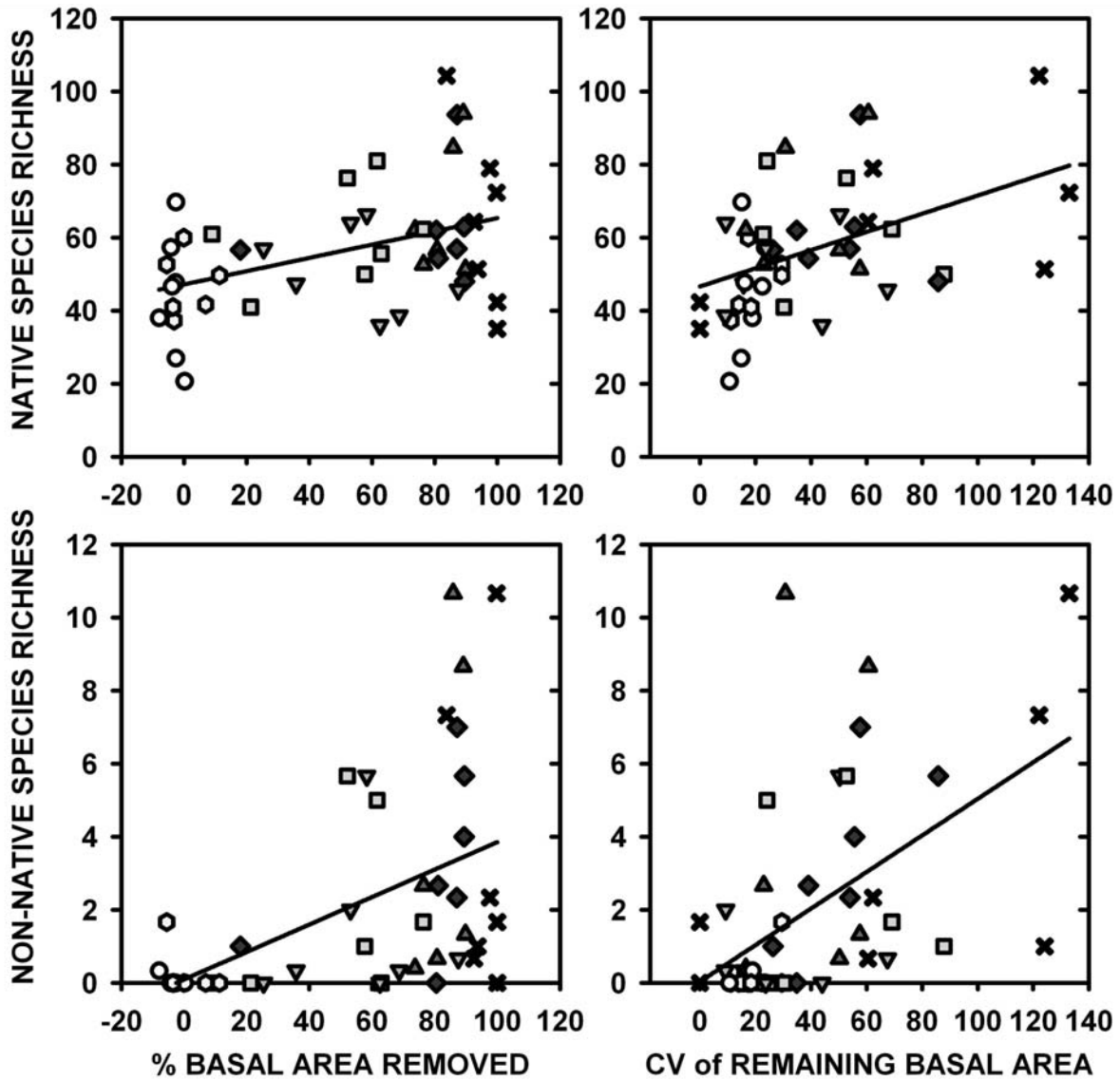
Figure 2.4. Relationships between % basal area removed and coefficient of variation (CV) of remaining basal area following disturbance with native and non-native species richness at the 576m^2 scale (○ = control, ◉ = understory herbicide, □ = group selection, ▽ = high-leave shelterwood, ◆ = leave-tree, ▲ = low-leave shelterwood, and ✖ = clearcut). Slope, R^2, and p-values for regressions are given in Table 2.4.

CHAPTER 3: TREE LEAF LITTER COMPOSITION AND NONNATIVE EARTHWORMS INFLUENCE PLANT INVASION IN EXPERIMENTAL FOREST FLOOR MESOCOSMS

R. Travis Belote and Robert H. Jones

ABSTRACT

Dominant tree species influence community and ecosystem components through the quantity and quality of their litter. Effects of litter may be modified by activity of ecosystem engineers such as earthworms. We examined the interacting effects of forest litter type and earthworm presence on invasibility of plants into forest floor environments using a greenhouse mesocosm experiment. We crossed five litter treatments mimicking historic and predicted changes in dominant tree composition with a treatment of either the absence or presence of nonnative earthworms. We measured mass loss of each litter type and growth of a model nonnative plant species (*Festuca arundinacea*, fescue) sown into each mesocosm. Mass loss was greater for litter of tree species characterized by lower C:N ratios. Earthworms enhanced litter mass loss, but only for species with lower C:N, leading to a significant litter × earthworm interaction. Fescue biomass was significantly greater in treatments with litter of low C:N and greater mass loss, suggesting that rapid decomposition of forest litter may be more favorable to understory plant invasions. Earthworms were expected to enhance invasion by increasing mass loss and removing the physical barrier of litter. However, earthworms typically reduced invasion success but not under invasive tree litter where the presence of earthworms facilitated invasion success compared to other litter treatments where earthworms were present. We conclude that past and predicted future shifts in dominant tree species may influence forest understory

invasibility. The presence of nonnative earthworms may either suppress of facilitate invasibility depending on the species of dominant overstory tree species and the litter layers they produce.

Keywords: *Ailanthus altissima*, *Castanea dentata*, decomposition, earthworms, invasional meltdown, leaf litter, *Lumbricus terrestris*; plant invasions

INTRODUCTION

Dominant species control many community and ecosystem processes (Wardle 2002). In forests, leaf litter inputs to the forest floor serve as an important mechanism by which trees regulate ecosystem functions including nutrient and energy cycling, tree regeneration, and the maintenance of biological diversity (Gilliam and Roberts 2003; Sayer 2006). The type and quality of dominant leaf litter controls these processes by mediating temperature, moisture, and nutrient inputs, and serving as a physical barrier to plant establishment (Facelli and Pickett 1991; Beatty 2003). Therefore, when humans directly or indirectly alter dominant tree species via disturbance, climate change, extinction, or facilitation of various biological invasions, additional biological invasions may be facilitated or resisted, depending on the properties of the dominant trees' litter. An understanding of how dominant tree species influence forest invasibility could prove very useful for land managers interested in minimizing nonnative plant invasions.

Several well-known changes in dominant tree species have taken place in the temperate forests of eastern North America. American chestnut (*Castanea dentata* (Marsh.) Borkh.) was once a dominant canopy tree (Russell 1987), but experienced widespread mortality when the nonnative chestnut blight fungus (*Cryphonectria parasitica*) was introduced to eastern North America. The functions that American chestnut provided within ecosystems are not fully understood, but it may have served as a "foundation species" by controlling the composition of

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understory species and mediating nutrient dynamics in soils and streams (Ellison et al. 2005). Other ongoing changes in these forests include the introduction of nonnative, invasive trees such as tree-of-heaven (*Ailanthus altissima* (P. Mill.) Swingle, hereafter Ailanthus), and disturbance-driven shifts in native species compositions favoring early successional species (Johnson et al. 2005). For example, timber harvesting can shift an oak (*Quercus* spp.) dominated to a yellow-poplar (*Liriodendron tulipifera* L.) dominated forest on mesic upland sites (Loftis and McGee 1992). Additional changes in dominant species composition are predicted in the future because of changes in climate, further invasions, growing demands for timber resource extraction, fire suppression, and potential interactions between these factors (Reich and Frelich 2002). These shifts in dominant tree composition will also change the litter layers of forests.

Changes in litter can also occur through the action of animals. Earthworms in particular have gained much attention because of their dramatic effects on litter layers and subsequent changes to structure and function of terrestrial ecosystems (Bohlen et al. 2004; Hobbie et al. 2006; Hendrix 2007). Earthworms are considered ecosystem engineers because of their ability to modify habitats, alter pools and fluxes of nutrients, and change understory community species composition (Jouquet et al. 2006). The introduction of nonnative earthworms into forested habitats that naturally lack them often dramatically changes the composition and diversity of the forest floor by removing the litter layer and exposing mineral soil (Hale et al. 2005; Frelich et al. 2006). Observational studies suggest that nonnative earthworms may be introduced following disturbance (Kalisz and Dotson 1989) and may facilitate nonnative plants through "invasional meltdown" – the process where invasion by one species facilitates additional invasions (Simberloff and Von Holle 1999; Heneghan et al. 2007). Mechanistic experiments that test this hypothesis are lacking.

The direct effects and potential interactions between changes in dominant tree species (through "extinction", invasions, and disturbance) and invasions of nonnative earthworms on the invasibility of temperate deciduous forests are poorly understood. While whole-stand manipulations to test the influence of changes in dominant species and earthworm invasions on ecosystem function or community composition are difficult, and impossible for certain species (e.g., American chestnut), it is possible to experimentally investigate these changes by manipulating leaf litter and monitoring subsequent changes in forest floor function and recruitment of plant species.

After considering historic, ongoing, and potential future changes to dominant species of forested ecosystems, we formulated and tested several hypotheses in a study using experimentally created forest floor mesocosms. First, we hypothesized that litter from different species (representing dominant tree compositional changes) would have different impacts on invasibility because of variation in litter quality (e.g., N content) leading to differences in decomposition rate and subsequent differences in physical barriers to plant establishment (Sayer 2006). Second, we hypothesized that plant invasion would also depend on the presence of nonnative earthworms because earthworms consume and bury litter (Frelich et al. 2006) or seeds (Milcu et al. 2006). Finally, we hypothesized that litter type and earthworm presence would have interacting effects on plant invasion reflecting variation in earthworm consumption or burial of different litter types.

METHODS

To test our hypotheses, we conducted a greenhouse study between 16 April and 16 June 2007. Simulated forest floor mesocosms were established by filling 18 L plastic tubs with silt

loam soils (classified as a Typic Dystrudepts) collected from the A and AB horizons of forested areas located in Montgomery County, Virginia, USA. Soil was sieved with a coarse metal screen (5 mm) to remove rocks, large root fragments, and macro-invertebrates (including earthworms) prior to filling the tubs. We filled the soil to a depth of 17 cm, leaving a 10 cm barrier to prevent earthworm escape from the top of the mesocosms. Each mesocosm included five drainage holes screened to allow drainage but prevent soil loss and earthworm escape. We added 0.5 L of water to each mesocosm every day for the first 4 weeks, and then reduced the watering frequency to every other day for the last half of the study. Average greenhouse temperature was maintained at 21° C throughout the experiment.

We collected senesced leaves from American chestnut, Ailanthus, yellow-poplar , and northern red oak (*Quercus rubra* L.) in October of 2006. Litter was collected from at least 12 individuals per species after senescence and before or immediately after abscission. American chestnuts still occur as stump sprouts in its native range and can overtop other tree species following canopy disturbance on certain sites before the blight induces mortality of the stem and tree crown (McCament and McCarthy 2005). We took advantage of one of these sites (a 10-year-old clearcut in Craig County, VA, USA where ~4 meter tall trees were relatively abundant) to collect litter of American chestnut trees. To mimic litter mass of typical hardwood forests of the area (Grigal and Gizzard 1975), we added 18.25 grams of air-dried litter to each mesocosm. These litter treatments represent past, current, and possibly future changes in dominant tree species and litter composition of the forest floor. A fifth treatment included the absence of litter as a control.

We added the nonnative anecic earthworm, *Lumbricus terrestris* to half of the mesocosms to cross litter treatments with presence or absence of earthworms. Earthworm

densities of three individuals per mesocosm were chosen to mimic densities observed in earthworm-invaded habitats (Kalisz and Dotson 1989). Mesocosms were randomly relocated on the greenhouse bench every 2 weeks during the experiment. At experiment termination, we investigated each mesocosm containing earthworms for the presence of castings on the soil surface and burrows below the soil surface to ensure that earthworms were active where they were added. Each treatment combination was randomly assigned to mesocosms and replicated 5 times resulting in a fully crossed multi-factorial completely randomized design (5 litter treatments × 2 earthworm treatments × 5 reps = 50 mesocosms).

To investigate how litter and earthworm treatment combinations influenced invasibility, one thousand seeds of a model invasive plant species (*Festuca arundinacea* Schreb., hereafter fescue) were sown into each of the mesocosms by evenly scattering onto soil surface prior to adding leaf litter and earthworms. We determined end of season production of fescue by harvesting above and belowground biomass as our measurement of invasion success. To test the prediction that decomposition would vary among treatment combinations, we collected litter from the soil surface at experiment termination and calculated per cent mass loss from initial litter mass. To investigate potential species-specific chemical characteristics of litter that might influence decomposition, five litter samples per species were drawn prior to establishing mesocosms and analyzed for initial percent C and N using a FlashEA 1112 Series Elemental Analyzer (CE Elantech, Lakewood, NJ); we used these data to calculate C:N ratios.

Statistical analysis

We used a two-way analysis of variance (PROC GLM; SAS 9.1) to test for main and interactive effects of litter treatment and earthworm treatment on two response variables, litter

mass loss and fescue biomass. Data were tested for normality and homogeneity of variance using Shapiro-Wilk's W statistic and Levene's test, respectively (Levene 1960; Shapiro and Wilk 1965). Data not meeting assumptions were log or arc-sin square root transformed. Post-hoc mean comparisons within treatments were performed using least square mean contrasts. One litter and earthworm control mesocosm (i.e., no litter or earthworms present) was eliminated from analyses because it was a statistical outlier where fescue grew very poorly, the result of clogged drainage holes causing standing water. To investigate how litter C:N, mass loss, and invasion success were related we performed three pairwise regressions. Specifically, we regressed mass loss on litter C:N ratios, fescue biomass on C:N, and fescue biomass on mass loss rates. Because we did not measure percent C and N of litter in each mesocosm, the two regressions involving C:N were conducted using mean values per treatment combination; for the remaining regression, individual data points for each mesocosm were included. We employed a critical alpha value of 0.05 for statistical significance.

RESULTS

Earthworm castings and burrows were observed in all of the mesocosms where we added earthworms. Litter mass loss depended on an interaction between species of litter and the presence of nonnative earthworms (Figure 3.1). Specifically, percent mass loss tended to be higher in litter of invasive Ailanthus and early-successional yellow-poplar than in American chestnut or northern red oak. Percent mass loss of Ailanthus and yellow-poplar were nearly twice as much and 1.4 times greater in the presence versus absence of earthworms, respectively, but mass loss rates of American chestnut and northern red oak did not differ between earthworm

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treatments (Figure 3.1). Litter mass loss tended to be lower for litter of species with lower percent leaf N and higher C:N ratios (Table 3.1; Figures 3.1 and 3.2).

Successful invasion by fescue was mediated by an interaction between the litter treatments and earthworm presence (Figure 3.3). Biomass of fescue tended to be highest in the absence of litter and under Ailanthus and yellow-poplar litter and lower under chestnut and red oak litter (Figures 3.3 and 3.4). Earthworms decreased the success of fescue in the absence of litter and presence of yellow-poplar litter, but had no significant effect in the other three treatments. In the presence of earthworms, the greatest fescue biomass occurred under litter of the invasive tree Ailanthus (Table 3.2; Figure 3.3). The effect of litter on invasion success (i.e., biomass of fescue) was related to litter C:N ratios and mass loss (Figure 3.2). Specifically, invasion success increased with increasing litter mass loss.

DISCUSSION

Results of this study supported all three of our hypotheses; i.e., that litter, earthworms, and their interactions can influence success of nonnative plant invasion into forest understories. The quality of the litter appeared to be driving these results. The effect of litter quality and recalcitrance from dominant species is known to influence multiple community and ecosystem components across diverse habitats (Facelli and Pickett 1991; Wardle 2002; Hättenschwiler et al. 2005; Sayer 2006). In our study, results suggest that litter layers of forests dominated by species with recalcitrant litter (i.e., slow decomposition rates) and high C:N ratios may be more resistant to understory plant invasions even if nonnative earthworms are introduced. Alternatively, forested stands with rapidly decomposing litter (and lower C:N ratios) may be particularly vulnerable to invasions by understory plant species. These results confirm predictions that

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changes in litter layers simulating historic, ongoing, or future shifts in tree composition may influence the resistance of forest floor ecosystems to invasions by nonnative plant species.

Recent studies suggest that "functionally extinct" American chestnut trees were a foundation species and that their litter played an important role in stream and soil nutrient dynamics (Ellison et al. 2005; Rhoades 2007). Our study suggests that chestnut litter may have served as a barrier to nonnative understory plant species compared to litter from species with faster decomposition rates. However, in many forests, oak species likely replaced chestnuts following blight mortality (Abrams et al. 1997) and we detected no significant difference between the main effects of chestnut litter and red oak litter on invasion success. This study also confirms personal observations that oak-dominated forests, which may be declining in abundance due to low rates of oak regeneration, altered disturbance regimes, and timber harvesting practices (Loftis and McGee 1992; McShea et al. 2007), appear particularly resistant to understory plant invasions, while forest stands dominated by yellow-poplar or invasive Ailanthus may be more vulnerable to understory plant invasions.

Nonnative earthworms had mixed effects on the success of plant invasions in this study. Earthworms typically reduced fescue biomass within litter treatments, but tended to have no negative influence under Ailanthus or northern red oak litter. Within litter treatments, earthworms likely buried or consumed seeds or new sprouts of fescue (Brown et al. 2004; Eisenhauer and Scheu 2008), which reduced its overall success. However, earthworms consumed or buried nearly 100% of the N-rich Ailanthus litter, which removed the physical barrier that litter creates. This led to fescue biomass tending to be greater under Ailanthus litter than other litter treatments where earthworms were present. Under highly recalcitrant northern red oak litter and where overall invasion success was lowest (main effect of litter), earthworms did not have a

negative effect on invasion success. The fact that earthworms preferentially consume or bury litter of certain species is well known (Darwin 1881; Perel and Sokolov 1964; Curry and Schmidt 2007). Litter from oak species has been observed to be relatively unpalatable to *Lumbricus terrestris* (Satchell 1983; Heneghan et al. 2007).

Ecologists have often observed that nonnative earthworms and nonnative plants frequently occupy the same habitats, suggesting potential facilitation between earthworm and plant invaders (Kourtev et al. 1999; Heneghan et al. 2007). However, understanding causality of these patterns has been limited by the observational nature of the studies. Some ecologists have suggested that nonnative plants may change soil characteristics, which allows for nonnative earthworms to invade (Ehrenfeld et al. 2001). Other hypotheses suggest that earthworms facilitate plant invasions, or that both nonnative earthworms and nonnative plants respond similarly to covarying factors such as disturbance or proximity to agricultural land use (Kalisz and Dotson 1989). While we did not test the hypothesis that plant invasions facilitate earthworm invasion, results from our study do suggest that invasion by a nonnative tree and the litter layer it produces, coupled with invasion by nonnative earthworms might directly facilitate further understory plant invasions.

The long-term effects of litter differences on earthworm populations or nonnative plants in not clear. Our experiment lasted only 2 months, which was insufficient to investigate treatment effects on humic and mineral soil layers and composition. Differences in humic layers and mineral soil chemical characteristics under litter layers may have longer term effects on invasibility and direct effects on earthworm populations. Moreover, while each tree species represented in our litter treatments can dominate forests on similar sites, the abundance and likelihood of dominance of the tree species in a particular area may depend on soil and site

characteristics, which can also influence invasive plant establishment and nonnative earthworm abundance (Frelich et al. 2006). For example, yellow-poplar typically replaces red oaks following disturbance only on mesic upland sites, but not on drier, less productive sites (Carmean and Hahn 1983). The same environmental factors that influence shifts in tree composition may also influence earthworm abundance and behavior.

The application of this study to natural systems is somewhat limited because it was conducted in a high light greenhouse environment using a model invasive species not typical of an understory plant invader. Our aim was to test specific mechanisms based on how changing litter layers may interact with earthworms to influence invasive plant establishment. However, differences in litter layers likely have important effects on native understory species as well (Gilliam and Roberts 2003). The effects of nonnative earthworms on native understory species depend on the traits or plant functional groups (Hale et al. 2005). Additionally, natural litter layers contain mixtures of litter from various species and support complex detrital foodwebs (Facelli 1994; Wardle 2002), which could also influence litter decomposition and understory invasibility. Clearly, more studies are needed to investigate the complex interaction between litter quality, earthworm invasions, native species, and nonnative plant invasions.

ACKNOWLEDGEMENTS

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Table 3.1. Mean percent C, N, and C:N ratios (± SE, N=5 samples) from initial litter prior to addition to mesocosms, and notes on ecology and abundance, for species used in a greenhouse test of invasibility of forest understories.   Means with different letters represent significant differences ($p < 0.05$).

Species	Common name	C %	N %	C:N	Current or historic trends
Ailanthus altissima	Tree-of-heaven	49.2 ± 0.2^a	2.24 ± 0.04^a	22.0 ± 0.4^a	Invasive in disturbed habitats
Liriodendron tulipifera	Yellow-poplar	47.9 ± 0.4^b	0.77 ± 0.02^b	62.4 ± 1.7^b	Early successional and dominant, can replace *Q. rubra* on mesic upland sites following disturbance
Castanea dentata	American chestnut	50.9 ± 0.2^c	0.62 ± 0.01^c	82.8 ± 0.7^c	Functionally extinct because of blight invasion, mostly replaced by oak and other hardwood species
Quercus rubra	Northern red oak	51.7 ± 0.6^c	0.69 ± 0.02^d	75.1 ± 1.6^d	Dominant canopy tree; local abundance can decline because of harvesting and gypsy moth defoliation; can be replaced by *L. tulipifera* following disturbance

Table 3.2. P-values for least square means contrasts of invasion success (fescue biomass) between the 5 litter treatments within earthworm treatments. Litter treatments are: NONE = no litter, control; AIAL = *Ailanthus altissima*, Ailanthus; LITU = *Liriodendron tulipifera*, Yellow poplar; CADE = *Castanea dentata*, American chestnut; QURU = *Quercus rubra*, Northern red oak.

	Earthworms absent				Earthworms present			
	NONE	AIAL	LITU	CADE	NONE	AIAL	LITU	CADE
NONE								
AIAL	0.01				0.07			
LITU	0.03	0.67			0.59	0.02		
CADE	<0.0001	0.007	0.002		0.03	0.0002	0.09	
QURU	<0.0001	0.01	0.003	0.90	0.19	0.003	0.44	0.33
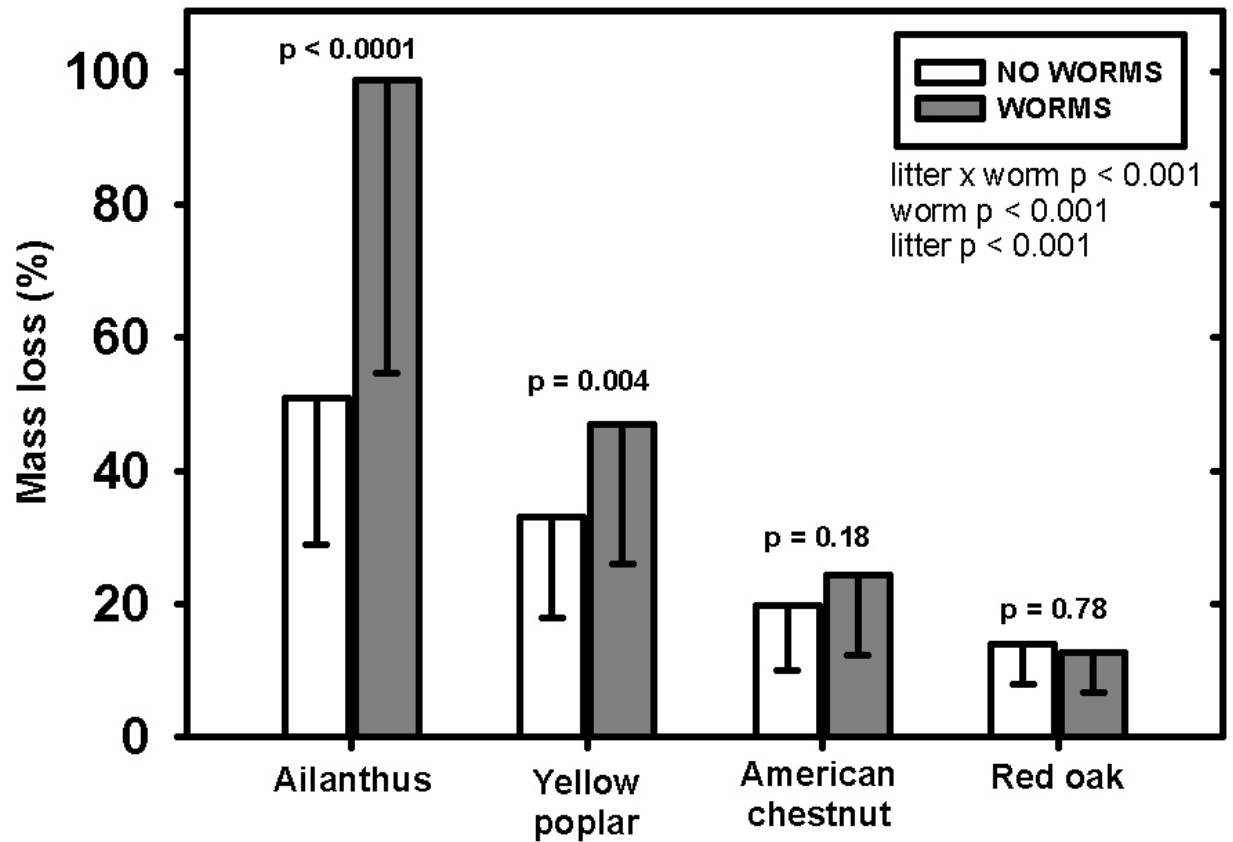
Figure 3.1. Mean percent mass loss of litter (-SE) from four species in mesocosms with or without nonnative earthworms, *Lumbricus terrestris*. P-values above graphs indicate contrasts between earthworm treatments within each litter treatment.
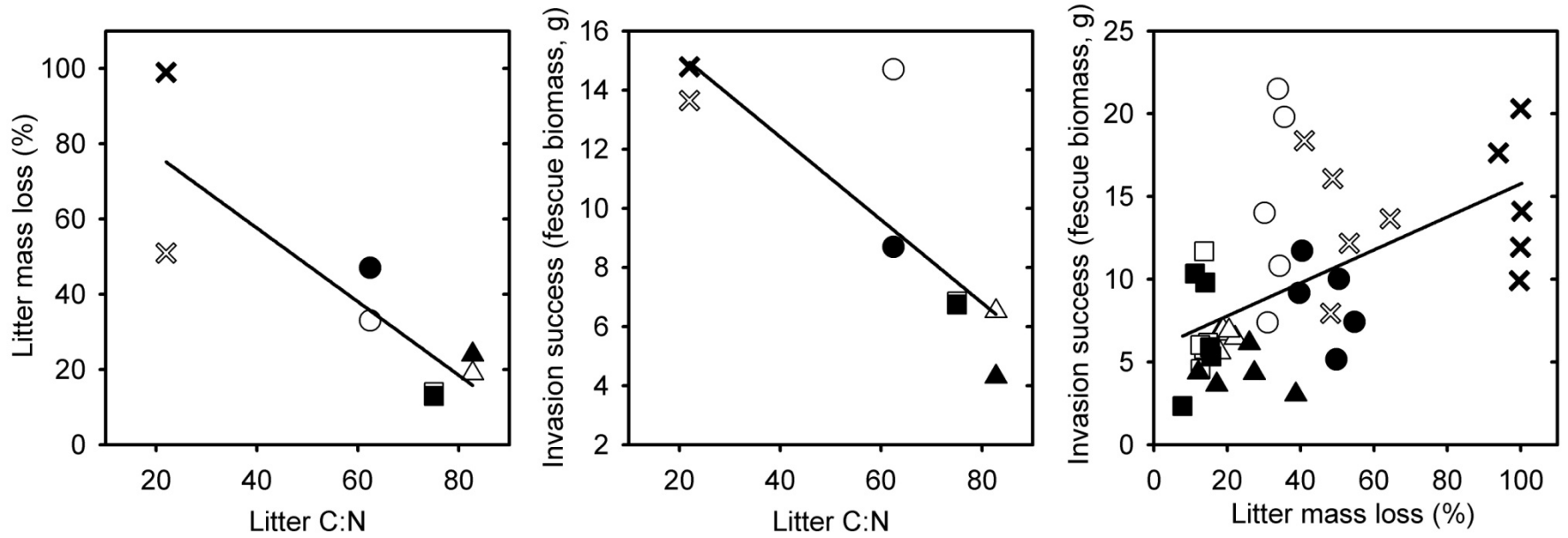
Figure 3.2. Pairwise regressions between litter C:N and mass loss ($R^2 = 0.73$, p = 0.007), litter C:N and invasion success ($R^2 = 0.70$, p = 0.01), and litter mass loss and invasion success ($R^2 = 0.30$, p < 0.001). Square symbols represent values of litter of northern red oak, triangles are values for litter of American chestnut, circles are values for litter of yellow-poplar, and × represents values from litter of Ailanthus. Filled symbols indicate values for mesocosms that included additions of nonnative earthworms; open symbols are values where earthworms were absent. C:N values were estimated based on litter sampled from the leftover pool of litter and not from litter used in each mesocosm.
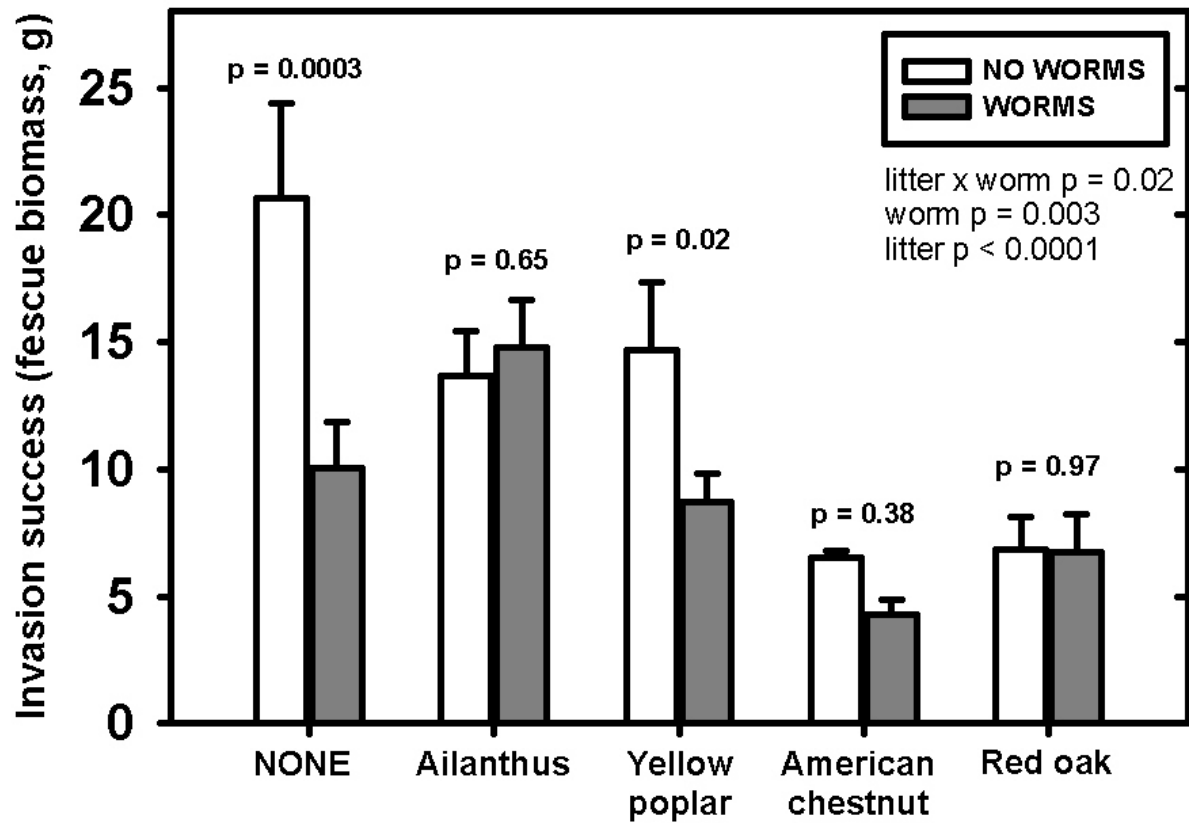
Figure 3.3. Invasion success of fescue (grams of biomass per mesocosm + SE) in mesocosms receiving crossed treatments of litter and earthworms. P-values above graphs indicate contrasts between earthworm treatments within each litter treatment. P-values for contrasts between litter treatments within earthworm treatments are in Table 3.2.
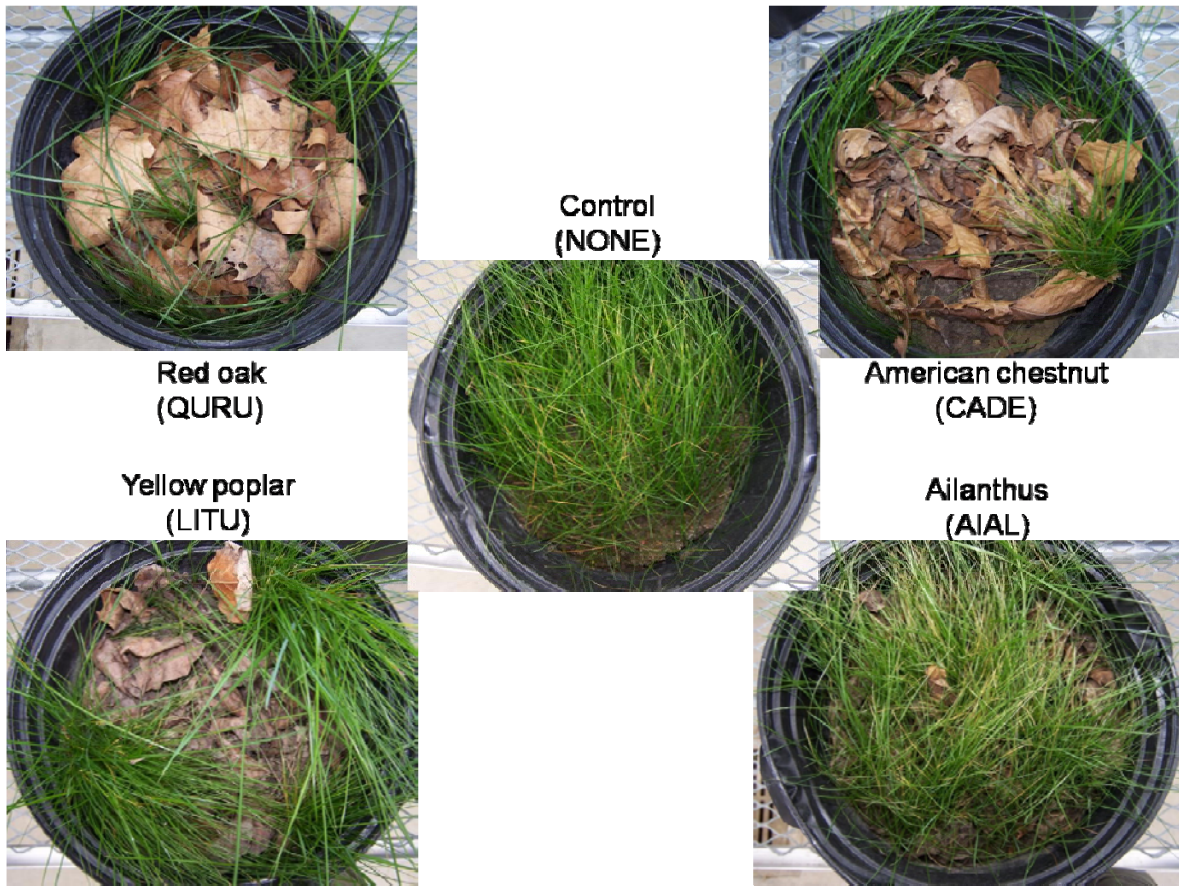
Figure 3.4. Sample photos of mesocosms showing main effects of each litter treatment on invasion success of fescue. Photos were taken by the author during the last week of the experiment.

CHAPTER 4: DISTURBANCE ALTERS LOCAL-REGIONAL RICHNESS RELATIONSHIPS IN APPALACHIAN FORESTS

R. Travis Belote, Nathan J. Sander, and Robert H. Jones

ABSTRACT

Relationships between local and regional species richness have been studied to identify the relative influence of regional versus local processes on community assembly and structure. In this paper, we investigate how an experimentally applied canopy disturbance gradient influenced local-regional richness relationships. Species richness was measured at three spatial scales (2 hectare = "regional"; 576 m^2 and 1 m^2 = local) and three times (one year pre-disturbance, one year post-disturbance, and ten years post-disturbance) across five disturbance treatments (uncut control through clearcut harvest) located in the Appalachian Mountains of western Virginia and West Virginia. We investigated whether species richness at 576 m^2 and 1m^2 depended on species richness at 2 hectares and whether this relationship changed through time before and after canopy disturbance through forest aggradation. We found that before disturbance, the relationship between local and regional richness was weak or nonexistent. One year after disturbance local richness was significantly related to regional richness, presumably because local sites received their propagules from the immediately adjacent region. Ten years after disturbance, the relationship was still significant, but the slopes defining the relationship had decreased by half. These results suggest that disturbance sets the stage for strong influences of regional species pools on local community assembly in temperate forests; however, as time passes after the disturbance, local controls of species composition begin to decouple relationships between regional and local diversity. Though we are unable to identify ecological

processes that led to our results, our data suggest that time since disturbance may be a critical

consideration when researching regional-local diversity relationships.

Keywords: Appalachian Mountains, disturbance, forest management, local-regional richness

relationships, succession

INTRODUCTION

Understanding the relative influence of regional and local processes on local community

diversity has become a focus of ecological study in recent years (Shurin and Srivastava 2005). In

particular, local-regional richness relationships (LRRs) have become a popular means for

exploring whether local diversity is more strongly limited by regional species pools or by local

interactions (Figure 4.1; Harrison and Cornell 2008). Saturating LRRs are often interpreted as an

indication that strong local interactions limit the number of species within local communities

(Cornell and Lawton 1992). Linear LRRs are interpreted as evidence that local diversity is not

limited by interactions but by the regional species pool (Caley and Schluter 1997; Stohlgren et al.

2008). Investigations of LRRs have been criticized for a number of reasons including statistical

problems (Srivastava 1999) or because the shape of LRRs can be determined by sampling

artifacts (Huston 1999; Loreau 2000) that do not reflect ecological processes (Hillebrand 2005).

Furthermore, because diversity measures are highly sensitive to the area being sampled

(Rosenzweig 1995), the definitions of "regional" and "local" areas become important, and

studies with different definitions may not be easily compared. Nevertheless, LRRs remain a

popular approach for elucidating the extent to which local and regional processes might shape

local communities.

Disturbance is widely recognized as an important process that influences diversity and composition of communities across both spatial (Collins et al. 2002) and temporal scales (Mouquet et al. 2003). Increased resource availability and decreased resource uptake immediately following disturbance reduces potential competitive exclusion by dominant species at local scales and allows habitats to be colonized by species adapted to disturbed environments (Huston 1999). At regional scales, disturbance can increase environmental heterogeneity and landscape-level diversity (Foster et al. 1998), but the influence of disturbance on LRRs has been little investigated (Huston 1999). In one of the only studies to date that assessed whether disturbance alters LRRs, Mouquet et al. (2003) developed a theoretical model to investigate local-regional richness relationships through time following disturbance. They predicted that LRRs would change during community assembly as the influence of colonization (during initial establishment) or competition (as the community reached equilibrium) determined local community richness (Figure 4.1). No studies, to our knowledge, have investigated LRRs by experimentally disturbing natural systems across a range in disturbance intensities and spatial scales, and then examining how LRRs respond through time (but see Starzomski et al. 2008).

In this paper, we use data from an ongoing experiment in forests of the southern Appalachian Mountains to investigate whether disturbance alters LRRs. The disturbance treatments represent a gradient of canopy removal and tree harvesting (Belote et al. 2008). In addition, we examined the LRRs over a 10-yr period following the initiation of the disturbance treatments. First, we predicted that there would be strong effects of disturbance on the LRRs but that the overall shape of the relationship would be asymptotic, suggesting species saturation in small scale plots (576 m^2 and 1 m^2). Second, we predicted that the shape of LRRs would change

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through time as local community processes intensify and prevent colonization of species from the surrounding region (Figure 4.1; Mouquet et al. 2003).

METHODS

Study Sites

Seven sites (experimental blocks) were chosen in the Ridge and Valley province and Appalachian Plateau region of southwest Virginia and northeastern West Virginia located on the Jefferson National Forest and the MeadWestvaco Corporation's Wildlife and Ecosystem Research Forest, respectively (Belote et al. 2008). Sites were selected to represent similar overstory composition and age and were dominated by *Quercus* spp. (red and white oaks) with *Acer rubrum* L. (red maple), *Carya* spp. (hickories), and other hardwood species common. The understory at the sites is diverse with native species exceeding 700 species, including a variety of understory trees (e.g., *Sassafras albidum* (Nutt.) Nees, *Nyssa sylvatica* (Marsh.)), shrubs (e.g., *Rhododendron* spp., *Vaccinium* spp.), lianas (e.g., *Smilax* spp.), graminoids (e.g., *Carex* spp., *Dichanthelium* spp.), and herbaceous monocots (e.g., members of Liliaceae and Orchidaceae) and dicots (e.g., species from Asteraceae and Rosaceae). Sites were located on similar topographic positions with generally south-facing, moderate slopes (10-40%) and intermediate elevations (600-1200 m). Soils at all sites are rocky, well-drained, acidic, and derived from sandstone and shale residuum and colluvium.

At each of the seven sites, seven two-hectare experimental units (EUs) were established with no buffer between units, but only five of the treatments were revisited and inventoried at all three sampling times (Figure 4.2). Nested within each EU, three permanent 576 m^2 (24 m × 24 m) plots were arranged so that they were 23 meters from the EU edge and were separated by an

azimuth of 120° from EU center. Six 1 m^2 subplots were nested within each 576 m^2 plot (subplots were located along plot perimeters). For additional information about the sites and plot designs see Hood (2001).

Disturbance Treatments

Disturbance treatments were applied to the 2-hectare experimental units between 1993 and 1998, during the non-growing season. Treatments were randomly assigned to EUs within each site, and included a range of overstory removal, from clearcut (95% basal area removed), leave-tree harvest (74% of basal area removed leaving a few dominants), shelterwood harvest (56% of basal area removed to "thin" the stand), understory herbicide (removal of suppressed trees via basal application of herbicide), to uncut control. Two additional treatments were originally included in the design but were not re-inventoried during the 10 year post-disturbance sampling. During tree harvest, limbs and branches were removed from main stems and typically left on site, except in the understory herbicide where trees were killed and left standing. Control treatments were intended to represent areas that experience no disturbance related to timber harvesting. However, during treatment application of nearby sites, some disturbance associated with skid trails and diffuse light from adjacent treatments occurred within some uncut control EUs; however, these disturbances were mostly restricted to the edges of the EUs. One West Virginia site did not include the understory herbicide treatments and we did not resample the leave-tree harvest treatment at this site ; thus the experimental set-up is an unbalanced randomized block design consisting of 47 EUs.

Data collection

All data were collected one year prior to disturbance treatment application with the exception of one site where pre-disturbance data were collected two years prior to harvesting disturbance (Hood 2001). Sites were resampled one or two years following disturbance and again nine to eleven years following disturbance. For all analyses we consider and refer to the initial post disturbance sampling as one year post disturbance and the second resample as ten year post disturbance. At each sampling period, presence of all herbaceous and woody plant species was recorded at each of the three scales (EU = 2 ha; plot = 576 m^2; and subplot = 1 m^2) and used to generate estimates of species richness at each scale (Figure 4.2). Richness was averaged across plots and subplots within experimental units to generate mean richness sampled at 576 m^2 or 1 m^2 respectively. Because the experimental units were large (2 hectares) we consider diversity at this scale to be "regional" richness compared to local diversity of plots and subplots (Huston 1999).

Statistical Analysis

We investigated relationships between species diversity of large experimental units ("regional", 2 hectares) and the smaller nested plots ("local", 576 m^2 or 1 m^2) at the three sampling times (pre-disturbance, one year post-disturbance, and ten year post-disturbance) using mixed analysis of covariance models (PROC MIXED, SAS 9.1). First, we modeled how plot and subplot richness were related to 2-ha richness, disturbance treatment, sampling time, and their interactions while accounting for random block effects of site using the entire dataset (N = 99). By controlling for random effects of site, we were able to address some statistical concerns of

previous LRR work by accounting for site variability (Srivastava 1999). Separate models were analyzed for 576 m^2 and 1 m^2 richness.

If the models detected significant interactions between variables, we then ran separate analyses within each sampling time across treatments controlling for random site effects (N = 33). To investigate potential species saturation, we ran separate linear and quadratic models and calculated Akaike's information criteria (AIC) for each model. To investigate whether disturbance affected the LRR, we analyzed data within each treatment within each sampling time (N = 7 or 6 depending on the treatment) using PROC GLM (SAS 9.1). We used PROC GLM for the within sampling time and treatment analyses to generate least square parameter estimates (slopes) and to compare R^2 values (PROC MIXED uses maximum likelihood parameter estimates).

We also investigated the effects of disturbance treatment and time on richness at each scale separately using a repeated measures analysis of covariance (PROC MIXED). Site was included in the model as a random blocking factor and pre-disturbance richness as a covariate to account for pre-disturbance variability in diversity.

RESULTS

When the entire dataset was analyzed together, local richness at the 1m^2 scale was a function of richness at the 2 hectare scale and sampling time (Figure 4.3; 2-ha richness × time: $P < 0.0001$) and treatment (2-ha richness × treatment: $P = 0.04$). Richness at the 576m^2 scale depended only on the interaction between 2-ha richness and time (Figure 4.3; $P = 0.007$). Within each sampling time (N = 33), quadratic models accounted for LRR relationships only one year after disturbance, and their fit was never better than linear models (Table 4.1). Therefore, all

subsequent analyses and discussion focus on linear models. Before disturbance, no relationship existed between 1m^2 richness and 2-ha richness (Table 4.1; Figure 4.3). However, one year after disturbance, 1m^2 richness was a function 2-ha richness (Figure 4.3), but by ten years after disturbance the relationship exhibited a shallower slope. The relationship between 576 m^2 richness and 2-ha richness was positive at all three sampling times, but the slope increased immediately after disturbance and became shallower after ten years, similar to the relationship between 1m^2 and 2 ha richness.

Relationships between local-regional richness within treatments depended on sampling time (Table 4.2). Before disturbance, no relationship existed between local and regional richness. One year following disturbance, the most disturbed sites tended to exhibit the steepest LRR compared to the less disturbed sites. Ten years following disturbance the only treatment to exhibit a positive LRR was the most disturbed (i.e., clearcut) treatment.

Richness at the regional scale (2 ha experiment unit) differed between treatments ($P < 0.001$) but did not differ with time (Figure 4.4; $P = 0.12$) or depend on a treatment × time interaction ($P = 0.67$). Richness at both local scales (576m^2 and 1m^2) depended on disturbance ($P < 0.001$) and time ($P < 0.001$) and only marginally on a treatment × time interaction ($P = 0.07$ for 576 m^2 and $P = 0.06$ for 1 m^2). Specifically, local richness tended to peak one year after disturbance in the most disturbed treatments and decreased after 10 years.

DISCUSSION

Our work suggests that disturbance mediates local-regional richness relationships (LRRs), and LRRs change through time following disturbance. Prior to disturbance local richness was not a function of regional richness at the smallest spatial scale. Immediately

following disturbance local richness was a function of regional richness, but the strength of the relationship depended on disturbance intensity. Specifically, local richness was most dependent on regional richness in the most disturbed plots. Consistent with our second prediction, the slopes of LRRs changed following disturbance and through time, and after 10 years LRRs appear to be returning to pre-disturbance conditions. Contrary to our prediction that the local-regional richness relationship would be asymptotic, we found no evidence for saturation of local species richness even at the smallest spatial scale (1 m^2) where saturation is expected, either because of sampling issues (Loreau 2000) or competitive exclusion (Huston 1999).

Disturbance intensity was positively related to diversity at all scales, which in turn led to positive LRRs after disturbance. The change in relationship between large-scale diversity and small-scale diversity suggests that disturbance leads to colonization of species after removing biological or environmental resistance to shade intolerant species (Chapter 5). Dominant overstory tree species likely control understory plant species diversity (e.g., Gilliam and Roberts 2003). Interestingly, Collins et al. (2002) showed that LRRs were stronger (more variance in the relationship explained) in less disturbed grasslands compared to those experiencing fire or bison grazing, which reduced competition from a dominant grass. These patterns differ from our results as well as Collins et al.'s own predictions. In our system, the control exerted by a closed canopy forest on the vascular plant community is reduced or temporarily eliminated by disturbance, and colonization subsequently becomes a relatively strong force influencing local species diversity (Chapter 5). But after 10 years of forest development, the effects of the canopy once again control local species diversity (Huston 1999). These results suggest that investigating temporal patterns of LRRs may be an important tool to understanding local controls of species diversity.

Our empirical results generally support previous attempts to model local-regional richness relationships following disturbance and through time (Mouquet et al. 2003). Mouquet et al. (2003) used simulations to investigate how community assembly following disturbance may determine LRRs. They predicted that the slope of the LRR should increase through time until the community reaches equilibrium at which time the LRR slope decreases to zero. Our results differ slightly from Mouquet et al. (2003) in that the LRR slopes were steepest immediately after disturbance, whereas their modeled LRR slopes initially became steeper with time before declining. These differences between studies may be due to the timing of colonists which increased for multiple years in Mouquet et al's model, but peaked one year after disturbance in our system and decreased after ten years (although the exact shape of the how local richness varied through time is unknown because we only resampled one and ten years post-disturbance). In an empirical study on microarthropods occupying moss beds, Starzomski et al. (2008) found that local richness did not depend on regional richness during any time of community assembly. Thus, it remains to be seen how, or whether, time since disturbance might affect LRRs across other communities.

LRRs are only patterns of an abstract measure of community structure (species richness), yet they are used to infer underlying community processes operating at either local or regional scales (Huston 1999; Harrison and Cornell 2008). In our case, we suspect that the underlying processes included disturbance, colonization, and post-disturbance shading of the understory by tree canopy closure. Disturbance was both a regional and local event. Immediately following disturbance, richness increased at all scales and after ten years remained relatively stable at the largest spatial scale, while decreasing at the smaller scales. Environmental heterogeneity at the largest spatial scale allowed for diversity following disturbance to be maintained even after

canopy closure particularly in patches of high light, which in this study system included skid trails used by logging machinery. At the largest spatial scales (2 ha) shade intolerant colonizers in many cases maintained populations or individuals in these patches. However, at the smaller spatial scales, plots and subplot typically occurred outside of these skid trails. As the canopy closed many colonizers were extirpated, presumably because light level decreased below their minimum maintenance level. Areas where diversity of shade intolerant species was maintained at the 2 hectare spatial scale even 10 years after disturbance are an example of local diversity influencing regional diversity. Canopy closure thus decreases diversity at small scales representative of a maturing forest, but heterogeneity caused by patches sampled across larger scales allows diversity of colonizers to be maintained after 10 years of canopy development (sensu Huston 1999).

We found little evidence of saturating LRRs in this study, but the slopes of LRRs revealed important processes in community reorganization after disturbance and through forest canopy closure. Typically a saturating LRR implies that competition leads to community saturation, where local communities can support a maximum number of species. Other hypothesized mechanisms for saturating LRRs suggest that at small spatial scales limiting numbers of individuals that can actually be sampled may lead to a saturating function, a pattern not necessarily related to competition or community saturation (Loreau 2000). Even at the smallest spatial scale where the number of individuals that can be sampled may result in a saturating LRR (1 m^2), no such saturating function was observed. Our results suggest that the slope of LRRs at different times may provide another important method of understanding the relative role of local and regional processes on the structure and dynamics of ecological communities.

ACKNOWLEDGEMENTS

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Table 4.1. Akaike's information criteria and p-values for linear and quadratic functions for local-regional richness relationships across disturbance treatments ($N = 33$) before canopy disturbance, one year, and ten years after disturbance. Data are shown in Figure 4.3.

		Pre-disturbance		1 year Post-disturbance		10 year Post-disturbance	
		AIC	P	AIC	P	AIC	P
$1\ m^2$	Linear	131.1	0.97	142.9	<0.001	133.8	0.007
	Quadratic	141.8	0.21	152.4	0.01	148.7	0.20
$576m^2$	Linear	200.3	<0.001	226.0	<0.001	226.2	<0.001
	Quadratic	210.1	0.61	234.5	0.03	239.8	0.83

Table 4.2. Slope, R^2, and p-value for within treatment regressions between species richness measured in 2 hectare experimental units and mean species richness measured within either eighteen 1 m^2 subplots or three 576 m^2 plots. $N=7$ for all treatments except herbicide and shelterwood where $N=6$.

		Pre-disturbance			1 year Post-disturbance			10 year Post-disturbance		
		slope	R^2	P	slope	R^2	P	slope	R^2	P
1 m^2	Control	-0.05	0.09	0.51	0.04	0.18	0.34	0.004	0.01	0.8
	Herbicide	-0.07	0.44	0.15	0.05	0.56	0.09	0.05	0.41	0.17
	Shelterwood	-0.03	0.13	0.43	0.06	0.72	0.02	0.01	0.16	0.36
	Leave tree	-0.07	0.06	0.64	0.06	0.52	0.10	0.04	0.49	0.12
	Clearcut	0.03	0.09	0.50	0.08	0.78	0.009	0.04	0.87	0.002
576 m^2	Control	0.11	0.03	0.71	0.42	0.61	0.04	0.21	0.51	0.07
	Herbicide	0.02	0.02	0.80	0.19	0.55	0.09	0.27	0.68	0.04
	Shelterwood	0.24	0.37	0.15	0.46	0.91	0.0008	0.29	0.89	0.002
	Leave tree	-0.06	0.01	0.89	0.39	0.97	0.0005	0.28	0.78	0.02
	Clearcut	0.24	0.36	0.15	0.53	0.96	0.0001	0.33	0.92	0.0007
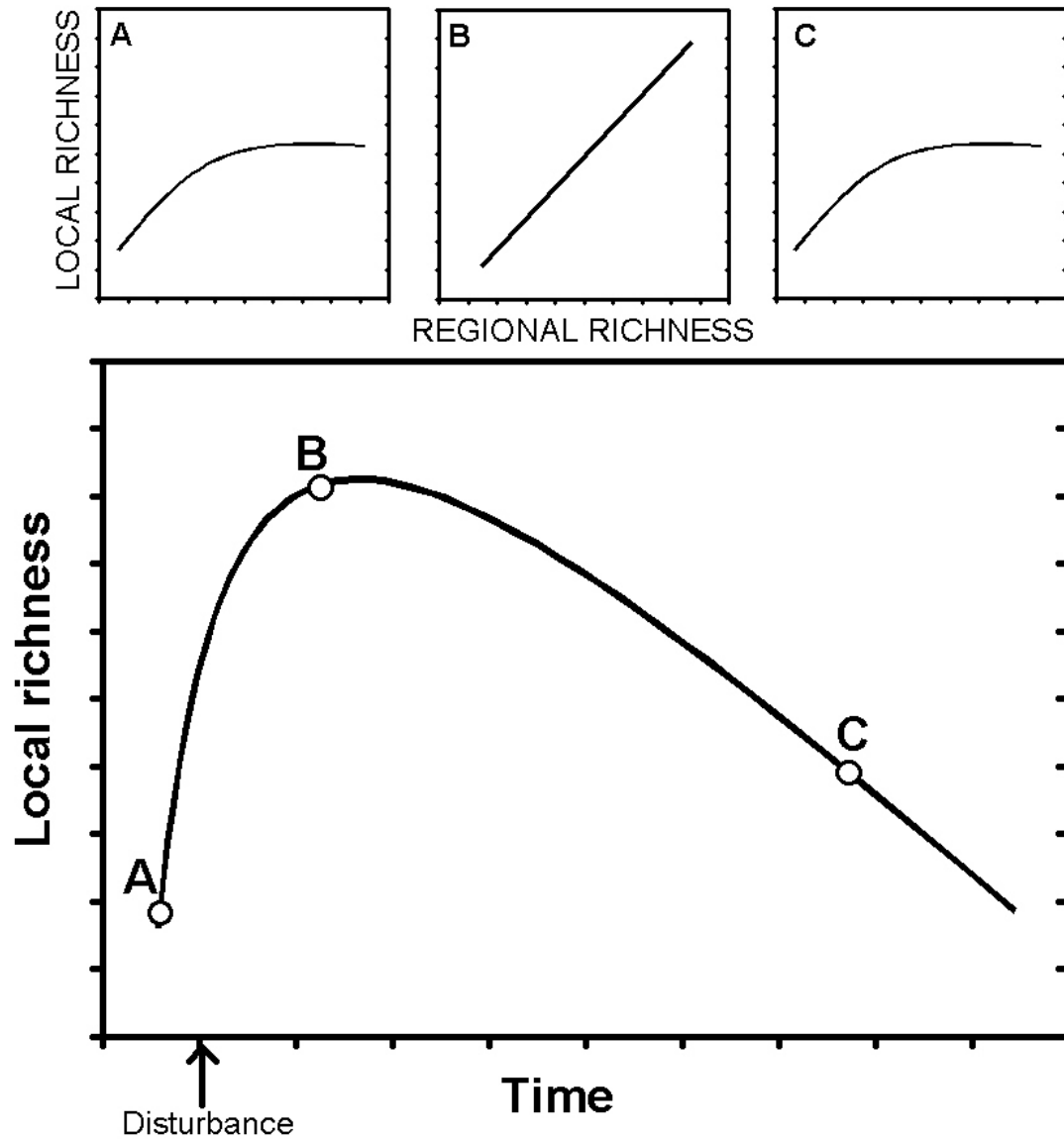
Figure 4.1. Predicted diversity response of forest plant communities following canopy

disturbance (after Mouquet et al. 2003 and Starzomski et al. 2008). Each point on the curve

represents a sampling period where local and regional richness relationships are assessed (shown

in top panels). Before disturbance, strong species interactions lead to saturating LRR (A).

Immediately following disturbance colonization of species leads to an unsaturated LRR (B).

After canopy closure dominant trees once again reduce local diversity leading to a saturating

LRR (C).
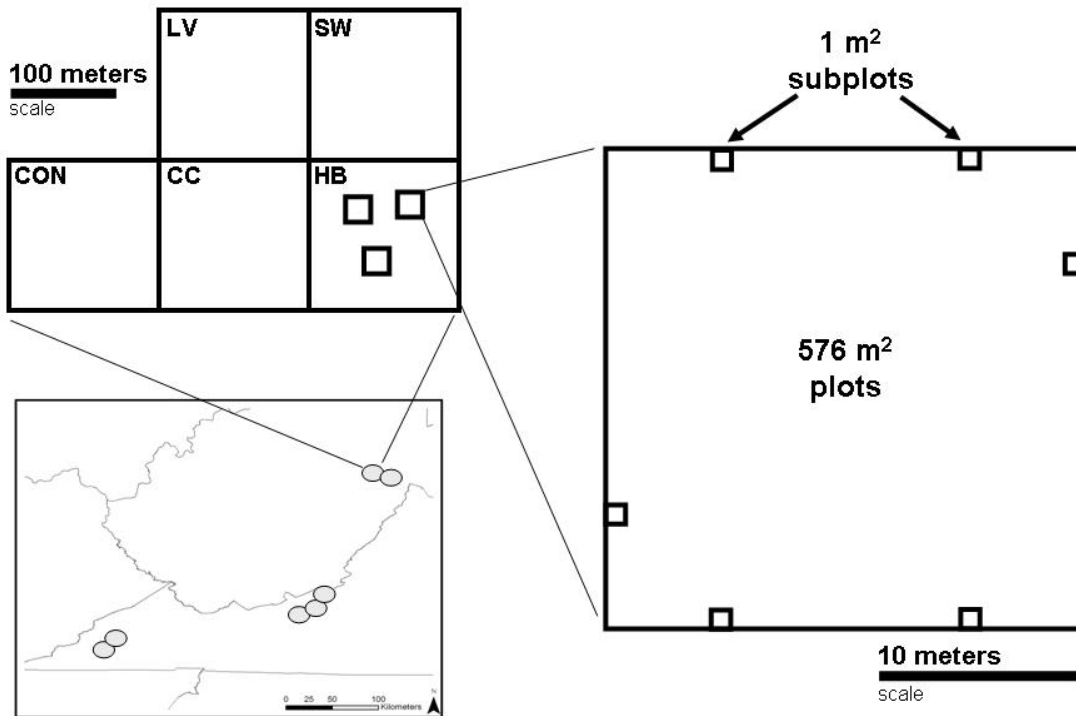
Figure 4.2. Study site locations within Appalachian region of Virginia and West Virginia with site and sampling design detailed. Regional richness was considered richness measured at the entire 2 hectare experimental unit and local richness was measured at either the 576 m^2 plots or 1 m^2 subplots.
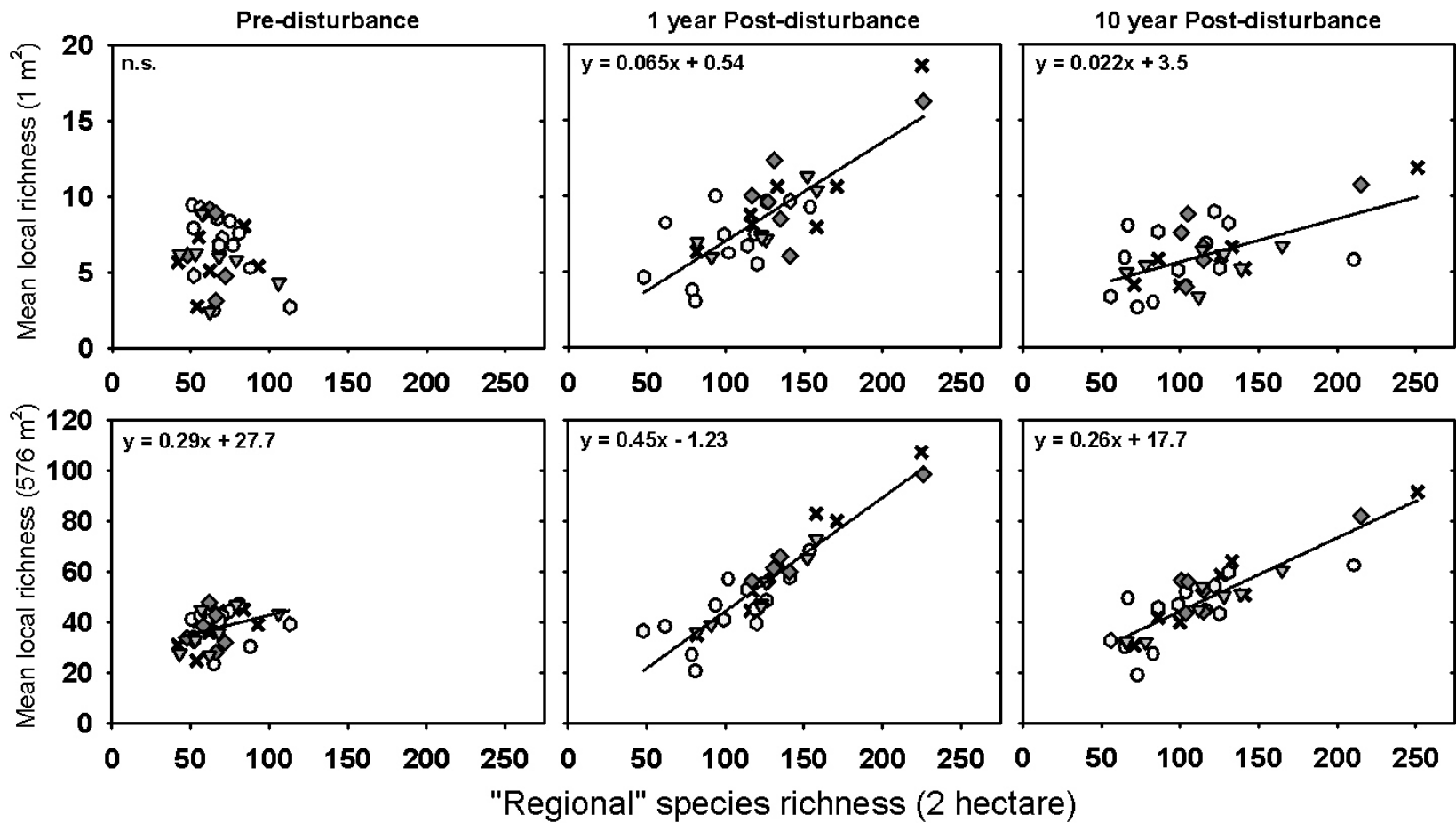
Figure 4.3. Local-regional richness relationships across five timber harvesting disturbance treatments and at three sampling times including pre-disturbance, one year post-disturbance, and ten years post-disturbance. Control treatments are circles, herbicide treatments are grey hexagons, shelterwood treatments are upside down grey triangles, leave tree treatments are dark grey diamonds, and clearcuts are black ×.
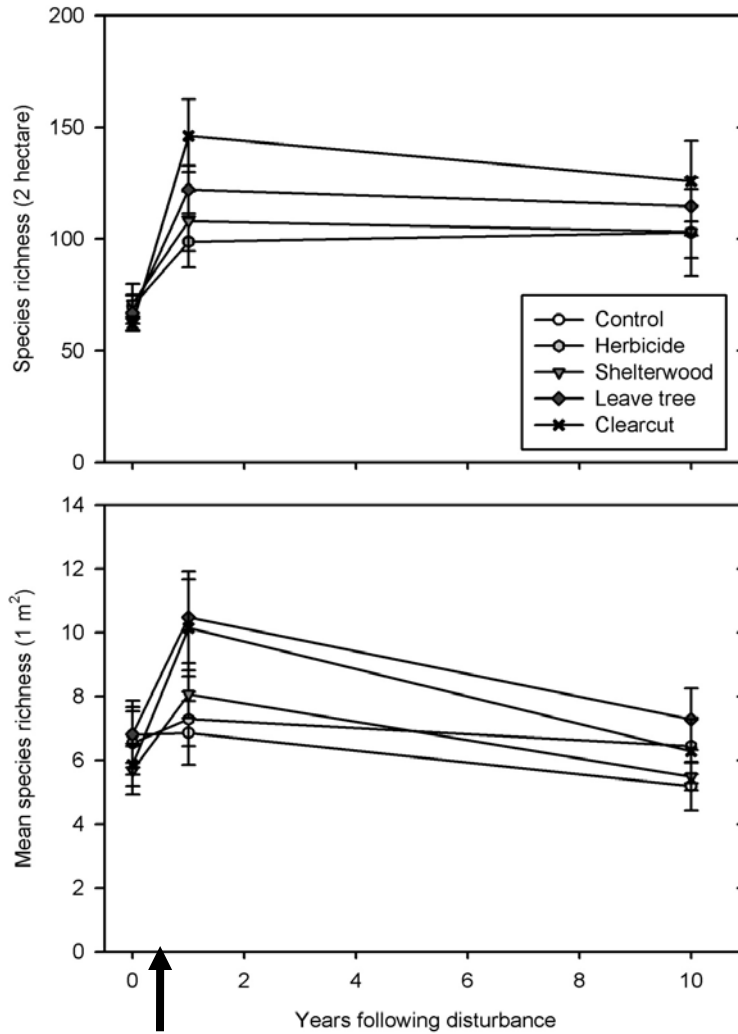
Figure 4.4. Richness at regional and 1m² local scales within each treatment and through time to emphasize the maintenance of diversity at regional scales but a decline in diversity at local scales during canopy development and recovery following disturbance. The arrow indicates time of disturbance treatment application. See Results section for treatment and time effects. Richness of treatments at the 576 m² scale is not shown because of similarities in patterns between 576 m² and 1 m² scales.

CHAPTER 5: STABILITY AND DIVERSITY OF VASCULAR PLANT COMMUNITIES FOLLOWING LOGGING DISTURBANCE IN APPALACHIAN FORESTS

ABSTRACT

Empirical data and theory suggest that the magnitude of species composition response to disturbance (i.e., resistance), and the rate of return to pre-disturbance conditions (i.e., resilience) can be influenced by either disturbance intensity, pre-disturbance diversity, or both. However, it remains difficult to predict which of these features (disturbance or pre-disturbance diversity) is more important, and whether community responses are driven by colonization or local loss of species. Responses of communities to disturbance likely depend on the scale of observation and may vary across species or functional group. In this study, we investigate the response of the vascular plant community to a gradient of timber harvesting disturbances, from control to clearcut, in Appalachian oak forests. We collected data at three spatial scales and three times including just before, one year post-, and ten year post-disturbance. We asked (1) how community compositional stability (resistance and resilience) and diversity were influenced by the interaction between disturbance intensity and pre-disturbance species diversity, (2) whether our conclusions would be influenced by the scale of observation, and (3) whether community responses were drive by colonization or extirpation of species. Resistance was estimated using community distance measures between pre- and one year post disturbance, and resilience using community distance between pre- and ten year post-disturbance conditions. The number of colonizing and extirpated species between sampling times were analyzed for all species combined and for six groups of species based on functional group. Resistance and resilience decreased with increasing timber harvesting disturbance; compositional stability was lower in the most disturbed plots, which was driven by colonization, but not extirpation, of species.

Resistance and resilience also depended on pre-disturbance richness. At intermediate spatial scales (576 m^2), the most diverse plots were least resistant and resilient to disturbance. At smaller spatial scales (1 m^2), results were the same when we used presence/absence data; however, when we analyzed species abundance data, we found a quadratic relationship between stability and pre-disturbance diversity, where intermediate levels of diversity were most stable. Most of the community-level responses were driven by post-disturbance colonization of native forbs and graminoids. In general, disturbance was a stronger force in shaping community composition and stability than was pre-disturbance diversity. Taken together, the results of this study are consistent with the theory that resources released by disturbance have strong bottom up impacts on species colonization and community composition. Additionally, few native species were extirpated following disturbance and many initially invading nonnative species did not persist through canopy closure. Therefore, the effects of management activities tested in this study, which span a gradient of timber harvesting disturbance, shift species composition largely via an increase in species colonization and diversity.

Key words: Appalachian Mountains; colonization; compositional stability; diversity-stability, disturbance, forest management

INTRODUCTION

In forests, human-caused disturbances (e.g., timber harvesting) generate considerable controversy amongst ecologists as well as the public (Meier et al. 1995). Land managers deliberately apply a variety of disturbances to forests to direct ecological structure or function to meet a variety of management objectives (Roberts and Gilliam 1995). For example, forest managers use fire and canopy removal (through tree harvesting) to maintain wildlife habitat

(McShea et al. 2007) and vegetation structure (Franklin et al. 2003), and to facilitate regeneration of favored tree species (Loftis 1990). If maintaining biodiversity is a goal of management, it is important to understand how alternative silvicultural practices and timber harvesting intensities affect species colonization and loss of understory species (Simberloff 1999). To build such understanding and apply it across multiple systems, it will be important to develop and test theories that predict how disturbance and species diversity interact to influence community stability (McCarthy 2003).

A long history of ecological research has shown that disturbance influences species composition and diversity through a variety of mechanisms that vary with the frequency, intensity, and spatial and temporal extent of the disturbance (Grubb 1977, Roberts 2004), which interact with the life history and physiological traits of individual species (McGill et al. 2006). Disturbance may directly affect community composition by causing mortality of individuals or groups of species, or indirectly through complex mechanisms including altering environmental conditions or resource availability and heterogeneity, which in turn permit colonization of new species (Pickett and White 1985) including nonnatives (Belote et al. 2008). The study of community assembly following disturbance has been instrumental to understanding the relative importance of biotic and environmental processes determining composition and diversity of communities (Clements 1916, Gleason 1926, Egler 1954, Simberloff and Wilson 1969).

The stability of communities in response to disturbance has intrigued ecologists for decades (Odum 1969, McCann 2000). Community stability can be defined as a function of both resistance and resilience (sensu Halpern 1988). Ecological resistance and resilience may be conceptualized using ecosystem-level functions (i.e., productivity or water retention) or community-level structure (i.e., species composition). In this paper, we consider resistance of

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communities as the ability of a community to maintain compositional integrity immediately

following a disturbance event (cf. Sankaran and McNaughton 1999, Foster et al. 2002), and

resilience as a measure of return to pre-disturbance conditions. The relative resistance and

resilience of communities is likely a function of the initial species composition of communities

(Halpern 1988) as well as regional species pools (Chapter 4).

Whether species-rich habitats are more or less stable than species-poor habitats remains

an important question in ecology (McCann 2000). Debates of diversity-stability relationships

arise because of site variability (Sankaran and McNaughton 1999), issues of spatial and temporal

scale (Valone and Hoffman 2003), and whether stability responses are measured at population,

community, or ecosystem levels (Tilman 1996). Predicting the stability of ecological

communities in response to natural resource management requires research examining the main

and interactive effects of management activities and species diversity.

In this study, we investigated how an experimentally applied forest canopy disturbance

gradient influenced species composition and diversity of Appalachian oak-dominated forests.

The disturbance gradient represents forest management options used in the Appalachian

Mountains to facilitate oak regeneration and harvest timber resources (Fox et al. 2006). Our goal

was to understand how disturbance intensity representing management alternatives influenced

stability and diversity of the vascular plant community. We hypothesized that stability

(resistance and resilience) of community composition would depend on disturbance intensity as

well as initial species diversity of sites. We also investigated whether these proposed

relationships depended on spatial scale of observation (Willis and Whitaker 2002), and whether

colonization or extirpation of species were the driving factors in shifts in species composition

following disturbance. Additionally, to better understand how species with shared life history

traits responded to disturbance (Rusch et al. 2003) and mediated compositional stability, we investigated how different functional groups of species responded to disturbance and through time across spatial scales ranging from 2 hectares to 1 m^2.

We predicted that greater disturbance intensity would lead to greater shifts in species composition that would be sustained through time via colonization and extirpation of species. Second, we predicted that initial diversity of sites would influence community shifts following disturbance. We asked whether the most diverse sites would be more or less resistant to compositional changes after disturbance following other hypotheses related to diversity-stability relationships (McCann 2000). Specifically, we predicted that areas with greater species richness would maintain greater compositional stability after disturbance through colonization of individuals (Seabloom 2007) or simply via a form of sampling artifacts (Huston et al. 2000). In other words, we predicted that sites with more species would be more resistant and resilient after disturbance because losses and gains of species would have less of a relative effect in species-rich compared to species-poor systems. Alternatively, we acknowledged that species-rich areas could be less compositionally stable (Sankaran and McNaughton 1999). Lastly, we predicted that disturbance intensity would increase diversity through colonization of native and nonnative species. We investigated these hypotheses and questions at various spatial scales to determine whether patterns depended on spatial scale.

METHODS

Study Sites

Seven sites (experimental blocks) were chosen in the Ridge and Valley province and Appalachian Plateau region of southwest Virginia and northeastern West Virginia located on the

Jefferson National Forest and the MeadWestvaco Corporation's Wildlife and Ecosystem Research Forest, respectively (Figure 5.1, Table 5.1). Sites were selected to represent similar overstory composition and age and were dominated by *Quercus* spp. (red and white oaks), *Acer rubrum* L. (red maple), yellow-poplar (*Liriodendron tulipifera* L.), and *Carya* spp. (hickories). The sites are floristically diverse with richness exceeding 700 species, including a variety of understory trees (e.g., *Sassafras albidum* (Nutt.) Nees, *Amelanchier arborea* (Michx. f.) Fernald, *Nyssa sylvatica* (Marsh.)), shrubs (e.g., *Rhododendron* spp., *Vaccinium* spp.), graminoids (e.g., *Carex* spp., *Dichanthelium* spp.), herbaceous monocots (e.g., members of Liliaceae and Orchidaceae) and dicots (e.g., species from Asteraceae and Roseaceae; hereafter forbs), vines (e.g., *Smilax* spp.), and ferns (e.g., *Osmunda* spp., *Dennstaedtia punctilobula* (Michx.) T. Moore). Sites were located on similar topographic positions with generally south-facing, moderate slopes (10-40%) and intermediate elevations (600-1200 m). Soils at all sites are rocky, well-drained, acidic, and derived from sandstone and shale residuum and colluvium. Precipitation is generally evenly distributed throughout the year.

At each of the seven sites, seven two-hectare experimental units (EUs) were established with no buffer between units. The experimental design includes seven treatments (Knapp et al. 2003), but we focus on five treatments in this study (Figure 5.2). Nested within each EU, three permanent 576 m^2 (24 m × 24 m) plots were randomly arranged so that they were 23 meters from the EU edge and were separated by an azimuth of 120° from EU center. Six 1 m^2 subplots were nested within each 576 m^2 plot; there were thus 18 subplots per experimental unit (Figure 5.1). For additional information about the sites, disturbance treatments and plot designs see Knapp et al. 2003, Belote et al. 2008, and Atwood et al. (in review).

Disturbance Treatments

Disturbance treatments were applied to the 2-hectare experimental units between 1993 and 1998, during the non-growing season. Treatments were randomly assigned to EUs within each site, and included a gradient of overstory removal including clearcut (95% basal area removed), leave-tree harvest (74% of basal area removed leaving a few dominants), shelterwood harvest (56% of basal area removed to "thin" the stand), understory herbicide (removal of suppressed trees via basal application of herbicide), and uncut control. During tree harvest, limbs and branches were removed from main stems and typically left on site. Control treatments were intended to represent areas that experience no disturbance related to timber harvesting. However, during treatment application of nearby EUs, some minor disturbance associated with skid trails and diffuse light from adjacent treatments occurred within some uncut control EUs. These disturbances were mostly restricted to the edges of the EUs. The five treatments were applied to examine the influences of alternative management strategies on multiple system components including plant (Wender 2000, Hood 2001) and animal diversity (Knapp et al. 2003; Homyack in review), invasions by nonnative species (Belote et al. 2008), oak regeneration (Atwood et al. in review), and soil ecosystem processes (Sucre and Fox 2008). One West Virginia site did not include the understory herbicide treatment and we were not able to resample the leave-tree treatment at 10 years post-disturbance because of time constraints; thus the experimental set-up is an unbalanced randomized block design consisting of 33 EUs.

Data collection

Pre-disturbance and initial post disturbance data were collected one year prior to and one or two years following disturbance treatment application with the exception of one site where pre-disturbance data were collected two years prior to harvesting disturbance (Hammond et al.

1998, Wender 2000, Hood 2001). Sites and permanently marked plots were revisited and sampled 9 or 11 years following disturbance depending on site (Atwood et al. in review). Here, we refer to the 9 or 11 year post-disturbance sampling effort as 10 year post-disturbance. Presence of all herbaceous and woody plant species was recorded at each of the three scales (EU, plot, and subplot). At the subplot scale, species-specific canopy cover was estimated using modified Daubenmire cover classes (Daubenmire 1959). All scales were sampled twice during the growing season to account for seasonal differences in species composition; i.e., data were collected in May or June and again in late August or September. Data from both samples were combined and analyzed together. Using number of species present, we generated estimates of richness of native and nonnative species at each scale and at each sampling time. We classified all species using six functional groups based on typical growth form and life history characteristics including tree, shrub, forb, graminoid, vine, or fern.

Statistical analysis

Using the nested sampling design within each experimental unit, we calculated frequency and importance values of all species observed in plots and subplots, respectively. Plot frequency was calculated as the number of plots a species occurred in within each EU. Subplot importance values (IV) were calculated as the sum of relative cover (cover of species / total cover) and relative frequency (frequency / total frequency) as described in Mueller-Dombois and Ellenberg (1974). A list of species observed in subplots and mean IV by treatment for each sampling time is in Appendix D.

We determined the number of colonizing and extirpated species within each functional group one year following disturbance at each spatial scale. Extirpated species were those

observed in EUs, plots, or subplots before disturbance but not one year after disturbance. Colonizing species were those observed after but not before disturbance. We also determined the number of species within each functional group that colonized after 1 year but were extirpated after 10 years, and species that colonized between the 1 year and 10 year post-disturbance sampling.

Community stability, Resistance and Resilience

We used a blocked multi-response permutation procedure (MRPP) to investigate overall compositional differences between the disturbance treatments while accounting for experimental blocking by site. MRPP uses distance measures and randomization tests to investigate whether assigned groups (e.g., disturbance treatments) are compositionally different (McCune and Grace 2002). We ran separate MRPPs using Euclidean distances for pre-disturbance, 1 year post-disturbance, and 10 year post-disturbance data to investigate if compositional differences between treatments were detected at each of the sampling periods. Separate analyses were also performed on the community data collected at the plot and subplot scales using relative frequency data and importance values, respectively, so that six total MRPPs were conducted (3 sampling times × 2 spatial scales). Because blocked MRPPs require balanced designs, we omitted data from the WV1 site for this analysis; WV1 is the only incomplete site without all treatments.

To quantify community resistance and resilience following disturbance, we calculated distance measures on the sample × species matrix using relative frequency data at the plot scale and importance values at the subplot scale as abundance measures. Resistance is defined as the inverse of the initial displacement following disturbance (small changes in community

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composition represent greater resistance than larger changes). Resilience is defined as the inverse of the distance between pre-disturbance and ten year post disturbance (compositional return to near pre-conditions indicates greater resilience). Plot and subplot analyses were performed separately to investigate the effects of spatial scale on community stability. We also calculated distance measures at both scales using presence-absence data to better understand how shifts in abundance compared to shifts in species composition to determine resistance and resilience of communities. For instance, if patterns of resistance and resilience differed between analysis conducted using abundance data compared to presence-absence data, then compositional shifts may be more related to abundance shifts than changes in species composition.

To investigate the robustness of patterns, we also chose to employ two different measures of community distance and dissimilarity as measures of community resistance and resilience. Specifically, we used both Euclidean distances and the Sorensen dissimilarity index to quantify compositional shifts (McCune and Grace 2002). We performed both detrended correspondence analysis (DCA) using Euclidean distances (hereafter, ED) and non-metric multideminsional scaling (NMS) using Sorensen dissimilarity (hereafter, SD) values to display compositional relationships. Both ordinations yielded similar patterns (the DCA ordinations are shown in Figures 5.3 and 5.4). Successional vectors that connect repeatedly measured samples through time were overlaid onto the ordination to visualize compositional shifts of samples from pre-disturbance, to one year post-disturbance, and ten year post-disturbance (Figure 5.4). All multivariate distance measures were calculated using PC-ORD v. 5 (MjM Software).

We analyzed the effects of disturbance treatment and pre-disturbance diversity on resistance and resilience estimates (using both ED and SD) with a mixed analysis of covariance (ANCOVA) using PROC MIXED (SAS 9.1; Littell et al. 2006) with the model:

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$$Distance = \mu + treatment + diversity + treatment \times diversity + site + \varepsilon$$

Distance represents the response variable and was either ED or SD. *Disturbance* is the fixed effect of disturbance treatment; *diversity* is pre-disturbance diversity, and *site* is the random block effect. After plotting the data we observed that several relationships between pre-disturbance diversity and distances followed a quadratic form, so we tested both linear and quadratic *diversity* terms in the models. Because we analyzed ED and SD, as well as abundance and presence-absence data, sixteen total models were run (2 distance measures × abundance v. presence-absence × resistance or resilience × 2 spatial scales).

To investigate whether initial compositional changes were related to compositional return to pre-disturbance conditions we calculated Pearson correlation coefficients between values of resistance and resilience. We also used t-tests within treatments to determine whether initial compositional resistance differed from compositional resilience. Specifically, we tested whether initial compositional differences between pre-disturbance and 1 year post disturbance increased, decreased, or remained the same after 10 years. At the subplot scale, we calculated change in species evenness (Pielou's *J*; McCune and Grace 2002) between pre-disturbance and one year post-disturbance and plotted pre-disturbance richness against initial change in evenness, and change in evenness against initial compositional change using both ED and SD.

Colonization and extirpation

To investigate how additions or losses of species mediated compositional changes through time, we calculated richness of colonizing and extirpated species between our sampling times. Specifically, we calculated the number of species that colonized EUs, plots and subplots between pre-disturbance and 1 year post-disturbance samples. We also calculated the number of

initial colonizing species that became extirpated after 10 years, as well as the number of new colonizing species after 10 years. For the two nested scales, we composited the species lists across the plots and subplots within each experimental unit to generate richness values from the three 576 m^2 plot and eighteen 1m^2 subplots per EU. We investigated whether colonization and extirpation of species within functional groups differed between disturbance treatments with mixed model ANOVAs with site entered as a random blocking factor. We calculated Spearman rank correlation coefficients between pre-disturbance richness and total richness of colonizing and extirpated species to investigate how colonization and extirpation were related to initial diversity. We also calculated Spearman rank correlation coefficients between richness of colonizing and extirpated functional groups with measures of resistance and resilience to investigate whether colonization or extirpation may have been responsible for compositional stability.

Richness of native and nonnative species

Total species richness was calculated as the number of species encountered at each spatial scale. Effects of disturbance on total species richness were analyzed separately at each spatial scale through time using a repeated measures randomized complete block ANCOVA with the mixed model:

Richness = μ + *Treatment* + *Site* + *Time* + *Treatment × Time* + *Pre-treatment richness* + *ε*

Where μ is the overall mean; *richness* is the number of species observed at each scale; *treatment* is the effect of each disturbance treatment; *site* is the random block effect of site; *time* is the effect of time; *pre-treatment richness* is a covariate to account for variation in initial richness; and *ε* is the residual error. Residuals of all models were tested for normality using Shapiro-

Wilk's W statistic (Shapiro and Wilk 1965); data not meeting this assumption were log transformed.

RESULTS

Compositional stability, Resistance and Resilience

Differences in species composition at the plot and subplot scales were apparent between sites and revealed differences in physiographic provinces of the Appalachian region (Figure 5.3); these compositional differences between sites were accounted for in the blocked MRPP analysis. As expected, compositional differences between treatments were not detected before disturbances were applied for either plot (MRPP; $P = 0.85$) or subplot ($P = 0.98$) scales. Following disturbance, treatments differed in species composition at the plot ($P = 0.0003$) but not the subplot scale ($P = 0.14$). After 10 years, compositional differences between treatments were still apparent at the plot ($P = 0.02$) and still not detected at the subplot scale ($P = 0.23$).

Resistance and resilience varied by disturbance treatment and pre-disturbance richness. Disturbance effects were relatively consistent across analyses; specifically, the most disturbed plots tended to be less resistant and resilient (i.e., community displacement and dissimilarity were greater in more intensively disturbed treatments and were less similar to pre-disturbance conditions; Table 5.2-5.3, Figures 5.4-5.8, especially Figure 5.8). Compared to the clear impact of disturbance, the apparent influence of pre-disturbance richness on both resistance and resilience was somewhat more dependent on the type of analysis and scale of observation, though broadly speaking, communities with more species tended to be less resistant and resilient than those with fewer species (but with several exceptions outlined below).

Of the sixteen analyses performed investigating relationships between richness and stability, we observed the following four general patterns: (1) quadratic relationships in six cases showing maximum stability at intermediate levels of richness; (2) a positive linear relationship in five cases showing maximum stability at the lowest levels of richness; (3) no significant relationship in three cases; and (4) an interaction between disturbance treatment and pre-disturbance richness in two cases (Figures 5.5-5.7).

Specifically, resilience of plots depended on which distance measure was employed. The relationship between pre-disturbance richness and ED resistance was linearly increasing, so that the most diverse plots were less resilient. However, SD exhibited a quadratic form of the relationship where plots with intermediate levels of pre-disturbance diversity were most resilient. Patterns in resistance and resilience did not differ whether we used abundance or presence-absence data at the plot scale (Table 5.2-5.3); specifically, significance of factors in models did not change depending on whether abundance or presence-absence was used.

Similar to the plot scale, subplots that experienced the most intense disturbance were less resistant and resilient (Table 5.2-5.3; Figure 5.6-5.7). The relationship between pre-disturbance diversity and resistance and resilience at the subplot scale depended on whether data were analyzed using abundance (importance values) or the presence-absence community matrix. The community matrix which included abundance values exhibited quadratic relationships between both resistance and resilience and pre-disturbance richness, where subplots with intermediate levels of pre-disturbance richness were the most resistant and resilient (Table 5.2; Figure 5.6). In contrast, when ED was used, the presence-absence data exhibited positive relationships between pre-disturbance diversity and shifts in composition (resistance) and dissimilarity after 10 years (resilience). When SD was used, relationships between abundance and presence-absence data

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exhibited overall similar patterns except that resistance based on SD from the presence-absence data was not statistically related to pre-disturbance diversity (Table 5.3, Figure 5.7). In only one instance, did we find a significant interaction between the quadratic form of diversity and disturbance treatments (i.e., subplot resilience from abundance data; Table 5.2, Figure 5.6).

Resistance and resilience values were positively correlated ($r \geq 0.70$, $p < 0.0001$; Appendix E); the least resistant plots and subplots were also the least resilient. Resistance and resilience values did not differ in most treatments (Figure 5.8) at either scale with some exceptions. At the plot scale, the leave-tree and clearcut sites tended to be more similar to pre-disturbance conditions after 10 years than after 1 year. At the subplot scale, we found little difference between resistance and resilience values, although the control and herbicide treatment tended to be more dissimilar after 10 years than after 1 year following disturbance (Figure 5.8). Relationships between change in evenness and initial shifts in composition were nonlinear. Subplots that experienced a decrease in evenness tended to shift composition more, whereas increases in evenness had little effect on compositional shifts (Appendix F).

Colonization and extirpation

Colonization of total species tended to be greater in more disturbed treatments and at all spatial scales (Table 5.4; Figure 5.9). Colonization of all functional groups, except vines and ferns, increased at the EU and plot scale with greater disturbance intensities. At the subplot scale, only the colonization of trees and forbs increased as disturbance increased. One year after disturbance the number of species extirpated across all or any functional group did not differ by treatment at any scale (Table 5.4; Figure 5.9).

After ten years and across all treatments 42%, 51%, and 57% of the initial colonizers were extirpated from EUs, plots, and subplots, respectively. Extirpation of initial colonizers was

higher in more disturbed plots (Table 5.5; Figure 5.10). Tree and forb colonizers were extirpated in the most disturbed sites at all scales and colonizing graminoids at EU and plot scales after ten years of canopy development (Table 5.5; Figure 5.10). Total colonization of all species between one and ten years post-disturbance did not vary between treatments. During this time, colonization of tree species tended to be greater in the herbicide treatments than in other treatments at the plot scale, and graminoid species colonized leave-tree and clearcut more than other treatments at the subplot scale.

Total initial colonization and colonization by all functional groups, except vines, was strongly positively correlated with community resistance and resilience at the plot scale (Appendix G). Total colonization was positively correlated with resilience of subplots, but not resistance. Total initial extirpation was uncorrelated with resistance and resilience at either scale, but extirpation of trees was positively correlated with resilience. Extirpation was not correlated with resistance or resilience of subplots. Pre-disturbance richness and richness of colonizing species were not correlated at the plot ($r = 0.01$, $P = 0.96$) or subplot ($r = 0.24$, $P = 0.19$) scale. Pre-disturbance richness was not correlated with richness of extirpated species at the plot scale ($r = -0.15$, $P = 0.42$), but was positively correlated with richness of extirpated species at the subplot scale ($r = 0.68$, $P < 0.01$).

Richness of native and nonnative species

Richness of all native and nonnative species sampled at the EU scale increased following disturbance (Table 5.6; Figure 5.11). Native species richness was maintained through time, but nonnative species richness decreased 10 years after disturbance (Table 5.6; Figure 5.11). Neither native nor nonnative richness at the experimental unit scale depended on a treatment × time

interaction. Native richness at the plot scale depended on a disturbance treatment × time interaction (Table 5.6; Figure 5.11). Nonnative richness was greater in more disturbed plots but did not depend on time. At the subplot scale, native richness depended on disturbance treatment and time, but not on their interaction (Table 5.6; Figure 5.11). Nonnative richness in the subplots only marginally depended on disturbance treatment.

DISCUSSION

As observed elsewhere throughout the Appalachian Mountains (Elliott and Knoepp 2005) and other forested regions (Thomas et al. 1999, Halpern et al. 2005, McDonald et al. 2008), timber harvesting tended to shift species composition and increase overall diversity. Resistance and resilience of community composition following disturbance were mediated by several factors including intensity of timber harvesting disturbance, initial diversity of the community, and colonization of species.

Our first prediction that stability of composition would depend on disturbance intensity was supported. As in other forested systems (Halpern 1988, Rydgren et al. 2004), species composition tended to shift more dramatically and remained more dissimilar in the most disturbed treatments even after ten years when stump sprouting and seed regeneration formed a dense stand of small diameter trees with a closed canopy (Atwood et al. in review). Compositional differences caused by the initial colonization of species immediately following disturbance prevented many sites from returning to pre-disturbance compositions, even though nearly half of the colonizers were extirpated after 10 years following canopy closure.

Effects of diversity on compositional stability

We found mixed support of our second prediction, that pre-disturbance diversity of communities would influence their compositional stability. Similar to other studies investigating different measures of temporal stability, our results depended on the methods we employed (Cottingham et al. 2001). Our objective was to quantify resistance (i.e., 1 year compositional shifts) and resilience (i.e., 10 year return to pre-disturbance conditions) using several methods to investigate the robustness of patterns in compositional shifts. The relationship between measures of compositional shifts (i.e., resistance and resilience) and pre-disturbance diversity depended on several factors including spatial scale, whether distance or dissimilarity indices were used, and whether abundance or presence-absence matrices were used.

Questions regarding the relationship between biodiversity and stability have a long history in ecology (MacArthur 1955, Elton 1958, Hutchinson 1959, Odum 1969, May 1972, Goodman 1975, McNaughton 1977, Tilman 1999, McCann 2000). Some of the lack of agreement on diversity-stability relationships may be related to whether stability is defined at the population, community, or ecosystem-level. Population-level stability may decrease across diversity gradients, whereas ecosystem-level stability (e.g., maintenance of productivity) may increase with diversity (Tilman 1996). However, how diversity influences or is correlated with compositional stability has only recently been explored (Sankaran and McNaughton 1999, Foster et al. 2002, Krushelnycky and Gillispie 2008). Previous studies have found that compositional stability decreased with increasing diversity (Halpern 1988, Foster et al. 2002). Sankaran and McNaughton (2000) found that diversity-stability relationships were sensitive to how compositional stability was measured. Similarly, our results suggest that compositional stability is sensitive to how, and at what scale, stability is measured.

We commonly found the most diverse communities were also the least resistant compared to less diverse communities regardless of spatial scale. This may be due to the fact that plots and subplots with more species tended to occur in areas with greater regional species pools (sensu Chapter 4) or richer metacommunities (Liebold et al. 2004). Therefore after disturbance the community sampled at the smallest subplot spatial scale could be colonized by a greater diversity of species, thus leading to greater community shifts. However, this hypothesis is unsupported by the lack of correlation between pre-disturbance richness and colonization of species.

One of the more interesting patterns we found between diversity and stability was a U-shaped relationship, wherein intermediate levels of diversity are most resilient to disturbance, at least at some scales of analysis. To our knowledge this is the first study to detect maximum compositional stability at intermediate levels of diversity. This pattern may be the combined result of shifts in dominance and evenness, increases in colonization, and complex site factors that covary with diversity (sensu Huston 1997). Additional research is needed to understand the ecological or statistical properties of why intermediate levels of diversity might be more compositionally stable.

Interestingly, we found no interaction between disturbance treatment and pre-disturbance diversity on resistance suggesting that shapes of diversity-resistance curves did not change with disturbance intensity. Overall resistance was lower in the most disturbed plots but the influence of diversity on compositional stability did not depend on disturbance. However, resilience of subplots based on abundance did depend on a diversity × disturbance interaction where less disturbed treatments (controls and herbicide) tended to exhibit no relationship between diversity and disturbance, but more disturbed treatments (clearcut) exhibited a U-shaped curve.

In sum, the exact processes and mechanisms leading to complex nonlinear relationships between compositional stability and pre-disturbance diversity are difficult to elucidate. However, our results suggest that diversity does not typically yield compositional stability.

Extirpation, diversity, and compositional stability

In subplots, pre-disturbance richness and richness of extirpated species were correlated, suggesting that species rich sites may be more prone to local extirpation events than species poor sites. Sankaran and McNaughton (1999) found similar patterns in savanna-grassland communities of India, which they attribute to the presence of greater numbers of infrequent species in the most diverse sites before disturbance. Infrequent species had a greater tendency to be locally extirpated after disturbance, which is likely true in our system. While extirpation was greater in more diverse site, richness of extirpated species was not related to resistance or resilience and did not vary by treatment.

In contrast, colonization was not correlated with pre-disturbance richness but did influence compositional stability. The relative effects of species colonization and changes in evenness on compositional shifts may have led to diversity-stability relationships, which have been observed in other plant communities (Sankaran and McNaughton 1999). In the least diverse sites, colonization by only a few species may lead to significant compositional shifts compared to pre-disturbance conditions. Alternatively, dominance of single species after disturbance may lead to greater compositional changes, which did occur in some of our most disturbed and least diverse sites and has also been observed in grasslands following disturbance (Foster et al. 2002). There tended to be less of a change in evenness at intermediate levels of pre-disturbance diversity, which may partially explain U-shaped relationships between diversity and stability.

Moreover, shifts in composition tended to be greater in subplots where evenness decreased more, but a proportional increase in evenness influenced compositional shifts little. These patterns were observed whether using ED or SD. In our system, dominance by *Smilax rotundifolia* L. and *Rubus* spp. in some subplots decreased evenness and led to significant compositional changes following disturbance.

Other studies have documented potential long-term effects of extirpation of species in the Appalachian region following timber harvesting (Duffy and Meier 1992), but these initial results were met with considerable criticism (Johnson et al. 1993, Elliot and Loftis 1993). Duffy and Meier (1992) compared old-growth forests with second-growth forests and found old-growth forests to be more diverse than second growth forests. Additionally, they found that the oldest second-growth forests had as few species as the younger second-growth forests, suggesting lasting suppression of species diversity after timber harvesting. Our sites differed in composition of dominant tree species to those studied by Duffy and Meier (1992), but our results in conjunction with other studies conducted in the central Appalachians (Gilliam 2002) suggest that timber harvesting may not have the suppressive effect on plant species diversity reported by Duffy and Meier (1992). However, at the time of our ten year post-disturbance sample, our uncut control sites were only slightly older (60-100 years old) than the second-growth forests Duffy and Meier (1992) sampled (45-87 years old). Therefore, it is possible that species may have been extirpated during the historic timber harvests that occurred across our sites during the early to mid 1900s. In other words, the pre-disturbance richness of our un-disturbed forests may have been influenced by historic timber harvests, although we have no way of testing this hypothesis.

Many understory species in Appalachian oak forests are perennial and maintain belowground roots and stems which contribute to their individual resilience to disturbance (i.e.,

the ability to persist following intense harvesting disturbance). Appalachian oak forests have historically experienced various disturbances or perturbations other than timber harvesting including windthrow (Everham and Brokaw 1996), fire (Delcourt and Delcourt 1997, Reilly et al. 2006), and ice damage (Hooper et al. 2001) among others (Roberts and Gilliam 2003). While many species can persist following disturbance events (cf. Dietze and Clark 2008), more research is needed to understand species-specific and site-specific responses to timber harvesting (Gilliam and Roberts 2003).

Colonization and diversity

Colonization of species after disturbance not only contributed to compositional shifts, but also influenced species richness at the sites. Despite differences across our sites, we found that disturbance treatments tended to increase colonization and diversity. Colonization was greatest in the most disturbed treatments and most colonizing species were forbs and graminoids. Graminoids and forbs are also the most diverse functional groups across all of the sites and typically possess traits that make them good dispersers into new habitats (Gilliam and Roberts 2003). Many of these colonizing species did not persist through canopy closure, probably because of their intolerance to shade cast by tree regeneration. After 10 years, extirpation of colonizers led to a decrease in diversity at smaller spatial scales. However, at the largest spatial scale, diversity of native species did not tend to decrease after 10 years, but nonnative species richness decreased. The fact that native diversity was maintained at the largest spatial scales even during stem exclusion stage of forest succession was likely the result of spatial heterogeneity, wherein native shade intolerant forbs persisted or new species colonized patches where canopy closure did not occur due to skid trail networks.

Skid trails that were established during timber harvesting were in some cases maintained after ten years. Grass species were sown into trails immediately after timber harvesting to prevent soil erosion, which may competitively exclude tree seedling establishment. Alternatively, increased soil compaction of the trails may have prevented tree regeneration. Soil compaction may have been maintained even after the initial establishment via deer and researchers who frequently used the trails. These hypotheses were not tested in the current study, but other studies suggest that soil compaction (Zenner et al. 2007) or other complex interactions (Rudgers et al. 2007) can limit tree establishment in grass dominated sites and contribute to differences in species composition (Zenner and Berger in press). Whatever the mechanisms, skid trail patches remained sites for shade intolerant forbs and graminoids to persist. Other recent studies have documented dramatic shifts in species composition in skid trails (Zenner and Berger in press), which may provide refugia for ruderal species including nonnative species to persist during canopy closure. Additional research is needed to understand how skid trails contribute to larger scale diversity following timber harvesting (Chapter 4), and serve as potential sources of soil erosion (Hood et al. 2002) and nonnative species propagules (Call and Nilsen 2003, Zenner and Berger *in press*).

Variability in site responses to disturbance limits our ability to predict how timber harvesting affects species diversity and compositional responses (Roberts and Gilliam 1995). While all sites in this study were dominated by oak species (Atwood et al. in review), there is considerable site and regional compositional differences of species, which made investigating individual species responses to treatments difficult. There were several generalist forb species that colonized disturbed treatments at multiple sites including *Erechtites hieraciifolia* (L.) Raf. ex DC., *Potentilla* spp., *Hieracium* spp., *Lobelia inflata* L., *Conyza canadensis* L. Cronquist,

Solidago spp., *Pseudognaphalium obtusifolium* (L.) Hilliard & B.L. Burtt, *Symphyotrichum* spp. Nees, and *Phytolacca americana* L. Graminoids that colonized multiple sites after disturbance included *Agrostis* spp., *Dactylis glomerata* L., *Danthonia* spp., *Andropogon virginicus* L., and *Dichanthelium* spp. (Hitchc. & Chase) Gould. Woody species that colonized multiple sites included the tree *Robinia pseudoacacia* L. and species of shrubs from the genera *Rubus* spp.

Compositional dynamics in uncut controls

Compositional shifts within the uncut control treatments were significant, which may be an indication of several factors. First, observer bias in species identification could explain some colonization and extirpation events. Dubious shifts in composition might be detected if a species was identified differently between years. To investigate this potential, we examined compositional and diversity patterns at the genera level, where misidentification would be less likely and found very similar patterns in all analysis of stability and diversity. Second, disturbance associated with edges of experimental units and skid trail roads may have impacted the uncut control treatments. Control treatments were typically located next to treatments receiving significant canopy disturbance and in some cases skid trails used by logging machinery bisected small portions of the control experimental units. This undoubtedly led to increases in diversity at the experimental unit scale and may have led to changes in composition and diversity at the nested scales. However, within the nested plots and subplots, no direct disturbance was observed in control treatment units. The third hypothesis explaining changes in composition and diversity of control plots is typical temporal dynamics of species between years, which may be due to various biotic and abiotic mechanisms such as precipitation, herbivory, competition, seed production, and gap formation. Control treatments, while not experiencing timber harvesting, did

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occasionally experience natural disturbances throughout the duration of the study including windthrow and ice damage. Lastly, all sites were harvested within the past 60 to 100 years prior to experiment initiation. Bunn et al. (in press) recently found that diversity of understory plant communities decreased between 1978 and 2007 in plots that were logged in the 1920s, whereas plant diversity did not change in historically unlogged plots. While different from patterns observed in our system over ten years, dynamics in our control plots may be the result of long-term changes during forest aggradation (Bormann and Likens 1979). Clearly, compositional shifts occur in forest understories through time, which complicates our ability to quantify compositional resilience as a return to some "stable" pre-disturbance condition.

Conclusions

Results from our study suggest that stability of plant communities following logging depends on complex factors including disturbance intensity, initial diversity of habitats, spatial scale, and how resistance and resilience is measured. In general, compositional stability decreased with disturbance intensity; i.e., species composition shifted more dramatically in the most disturbed areas and tended to be dissimilar even after 10 years of forest aggradation. The relationship between diversity and stability was more complex following disturbance. Intermediate levels of diversity were more stable in some instances, whereas areas with fewer species were more stable in other instances. Moreover, colonization of species following disturbance tended to mediate compositional stability. While compositional shifts were significant, our initial results suggest that few species are extirpated due to disturbance. The forest management disturbance alternatives tested in this experiment may actually maintain species and structural diversity across forest landscape mosaics. More research is needed to

understand (1) species-specific responses to disturbance and (2) the complex mechanisms determining compositional stability.

ACKNOWLEDGEMENTS

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Table 5.1. Richness of six plant functional groups observed at seven Appalachian forest sites. Values represent total richness of all species observed across sampling periods and disturbance treatments.

Site	Tree	Shrub	Forb	Graminoid	Vine	Fern
Blacksburg 1 (BB1)	60	19	240	78	10	12
Blacksburg 2 (BB2)	46	18	151	40	9	15
New Castle (NC)	37	14	112	42	8	6
Clinch 1 (CL1)	44	13	145	45	5	10
Clinch 2 (CL2)	34	12	163	47	6	12
West Virginia 1 (WV1)	37	11	91	46	6	11
West Virginia 2 (WV2)	31	9	123	58	7	11

Table 5.2. P-values for ANCOVA terms investigating measures of resistance and resilience of vascular plant community composition to five disturbance treatments (treatment) and pre-disturbance richness (diversity) based on abundance data. Quadratic terms of diversity were tested after plotting data (Figures 5.5 and 5.6).

		Plots (576 m^2)		Subplots (1m^2)	
		Euclidean distance	Sorensen dissimilarity	Euclidean distance	Sorensen dissimilarity
Resistance	Treatment	<0.01	<0.01	0.01	<0.01
	Diversity	0.05	0.94	0.04	0.26
	Diversity × Treatment	0.92	0.87	0.01	0.22
	Diversity^2 (quadratic term)	0.86	0.21	<0.01	0.03
	Diversity^2 × Treatment	0.70	0.58	0.25	0.78
Resilience	Treatment	<0.01	<0.01	0.05	<0.01
	Diversity	<0.01	0.53	0.32	0.01
	Diversity × Treatment	0.78	0.59	0.02	0.02
	Diversity^2 (quadratic term)	0.16	0.02	0.22	0.72
	Diversity^2 × Treatment	0.33	0.44	0.01	0.01

Table 5.3. P-values for ANCOVA terms investigating measures of resistance and resilience of vascular plant community composition to five disturbance treatments (treatment) and pre-disturbance richness (diversity) based on presence-absence data. Data for subplots are shown in Figure 5.7. Plot data not shown because patterns were similar to Figure 5.5.

		Plots (576 m^2)		Subplots (1m^2)	
		Euclidean distance	Sorensen dissimilarity	Euclidean distance	Sorensen dissimilarity
Resistance	Treatment	<0.01	<0.01	0.02	0.01
	Diversity	0.01	0.89	<0.01	0.71
	Diversity × Treatment	0.88	0.70	0.73	0.37
	$Diversity^2$ (quadratic term)	0.71	0.36	0.38	0.09
	$Diversity^2$ × Treatment	0.59	0.58	0.98	0.97
Resilience	Treatment	<0.01	<0.01	0.02	0.07
	Diversity	<0.01	0.53	<0.01	0.04
	Diversity × Treatment	0.32	0.19	0.96	0.53
	$Diversity^2$ (quadratic term)	0.30	0.08	0.05	0.08
	$Diversity^2$ × Treatment	0.73	0.61	0.58	0.46

Table 5.4. P-values for mixed model investigating disturbance treatment effects on the number of species colonized (1 year colonizers) and extirpated (1 year extirpated) at three spatial scales one year after experimental forest harvests treatment applications. Means for each treatment and scale are in Figure 5.9.

		Experimental unit	Plot	Subplot
1 year colonizers	All	<0.01	<0.01	<0.01
	Tree	0.08	<0.01	<0.01
	Shrub	0.02	0.02	0.54
	Forb	<0.01	<0.01	0.02
	Graminoid	<0.01	<0.01	0.16
	Vine	0.49	0.39	0.61
	Fern	0.75	0.50	0.26
1 year extirpated	All	0.19	0.64	0.50
	Tree	0.83	0.14	0.32
	Shrub	0.07	0.06	0.29
	Forb	0.30	0.73	0.60
	Graminoid	0.56	0.24	0.32
	Vine	0.68	0.38	0.33
	Fern	0.29	0.88	0.06

Table 5.5. P-values for mixed model investigating disturbance treatment effects on the number of species that colonized between one and ten years post-disturbance (10 year colonizers) and species that colonized after 1 year but were extirpated ten years following experimental forest harvests treatment (10 year extirpated). Means for each treatment and scale are in Figure 5.10.

		Experimental unit	Plot	Subplot
10 year colonizers	All	0.84	0.05	0.49
	Tree	0.18	0.01	0.87
	Shrub	0.27	0.85	0.05
	Forb	0.73	0.17	0.27
	Graminoid	0.99	0.37	<0.01
	Vine	0.01	0.88	0.54
	Fern	0.86	0.12	0.55
10 year extirpated	All	<0.01	<0.01	<0.01
	Tree	0.01	0.03	<0.01
	Shrub	0.62	0.35	0.31
	Forb	<0.01	<0.01	<0.01
	Graminoid	<0.01	<0.01	0.32
	Vine	0.39	0.57	0.05
	Fern	0.86	0.41	0.37

Table 5.6. *P*-values for disturbance treatment and time effects and their interaction on richness of native and nonnative species at 3 spatial scales. Means and standard errors are shown in Figure 5.11.

		Native	Nonnative
Experimental unit	Treatment	<0.01	0.05
	Time	0.56	<0.01
	Treatment × Time	0.38	0.29
Plot	Treatment	<0.01	<0.01
	Time	0.01	0.13
	Treatment × Time	<0.01	0.28
Subplot	Treatment	<0.01	0.08
	Time	<0.01	<0.01
	Treatment × Time	0.16	0.78
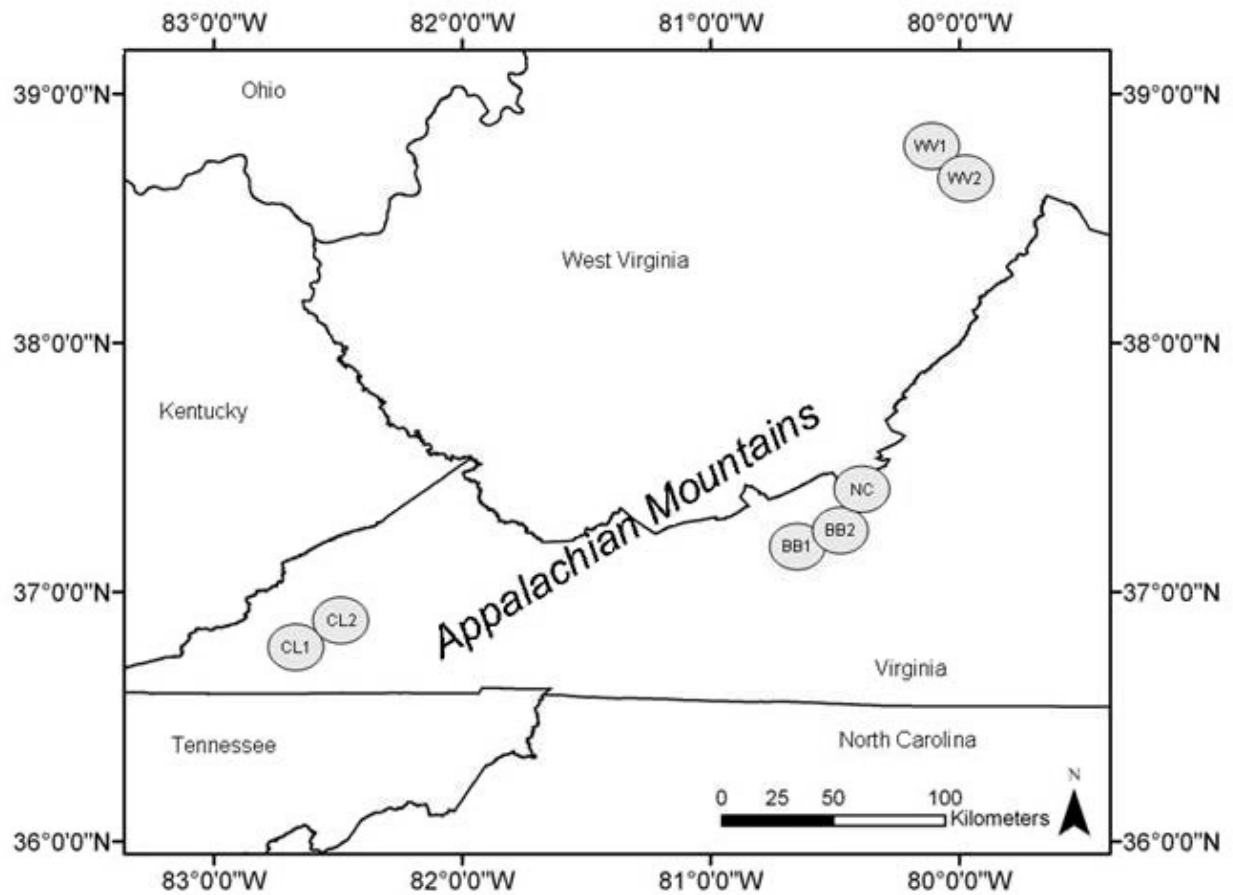
Figure 5.1. Location of seven sites (experimental blocks) in the Appalachian Mountains of western Virginia and West Virginia that received disturbance treatments investigating timber harvesting effects on plant composition and diversity.
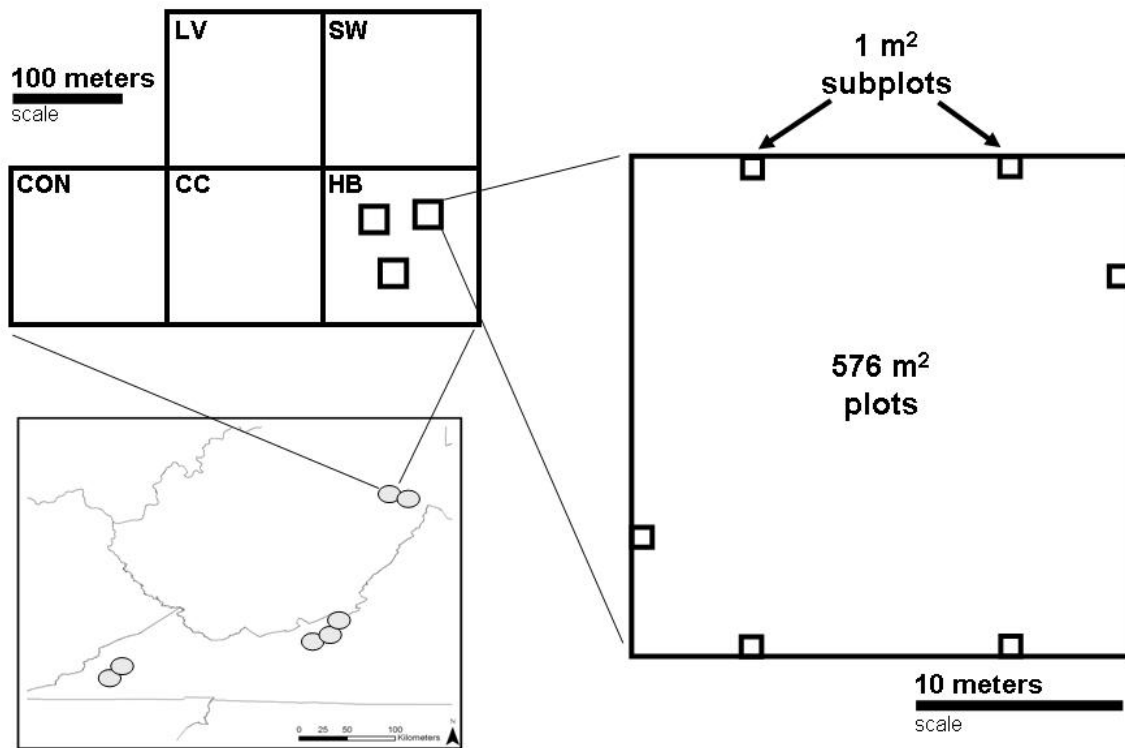
Figure 5.2. Typical site and sampling layout of permanently marked experimental units, plots, and subplots in experiment investigating effects of disturbance on diversity and stability of plant community. Treatments were randomly applied to each experimental unit within each site.
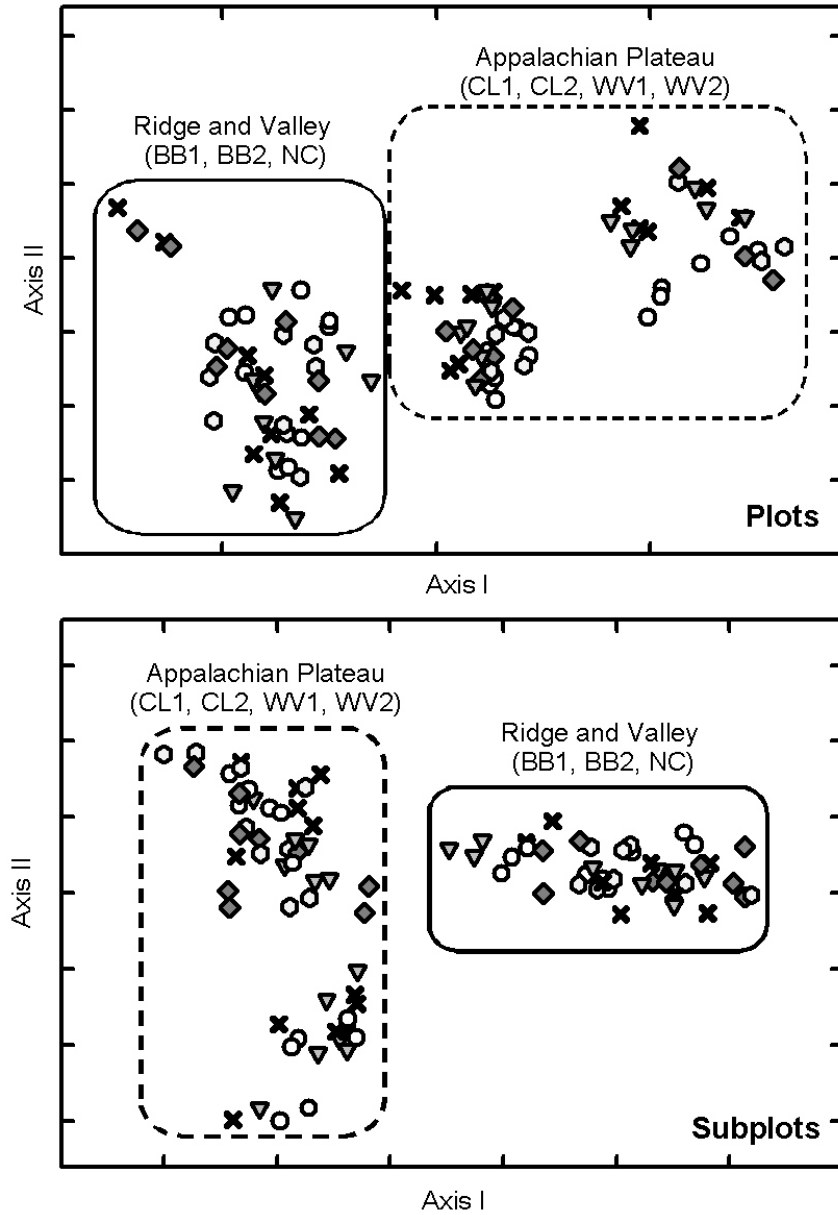
Figure 5.3. Detrended correspondence analysis (DCA) ordination of plots (top panel) and
subplots (bottom panel) across all sites and times highlighting compositional differences between
sites occurring in different ecoregions (EPA level III) based on species abundance (Appalachian
Plateau or Ridge and Valley). Open circles = control; grey hexagon = herbicide; grey upside
down triangle = shelterwood; grey diamonds = leave-tree; black × = clearcut.

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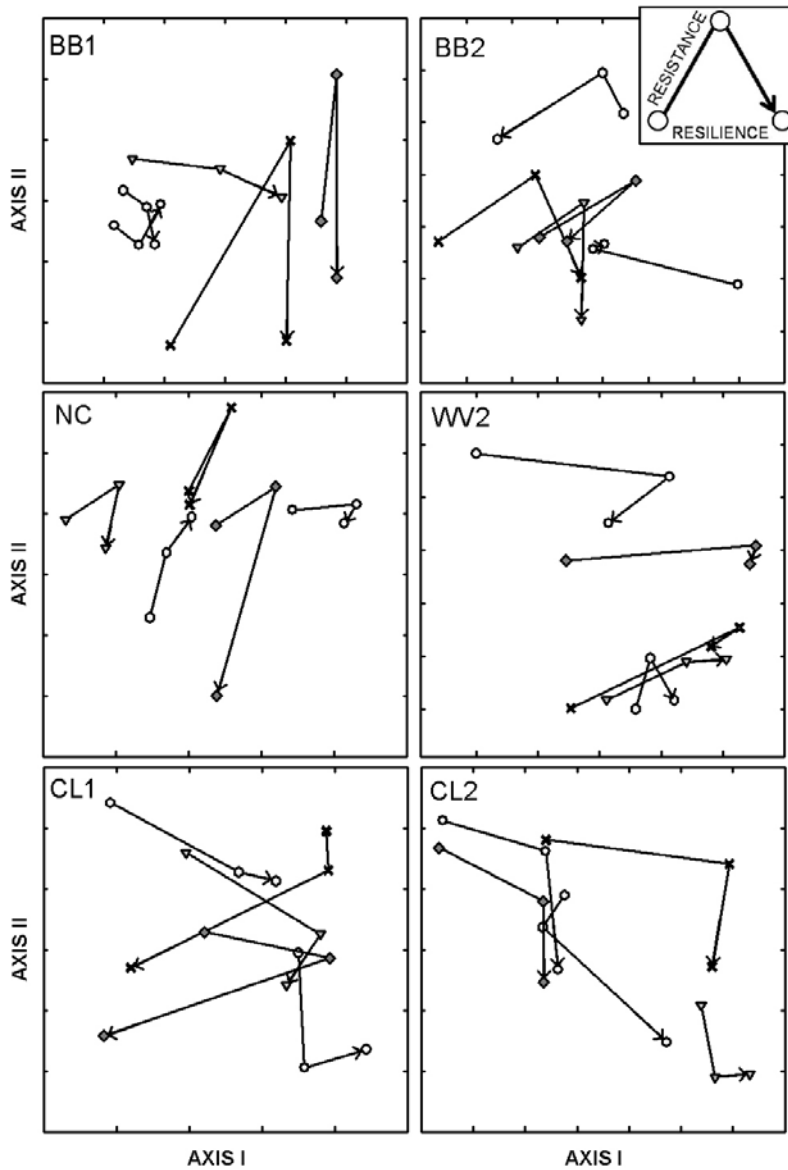
Figure 5.4. DCA ordination of subplots with "successional vectors" (sensu Halpern 1988) connecting repeatedly sampled subplots receiving five disturbance treatments within six of the seven sites (symbols for each disturbance are same as Figure 5.3). Figures provide a visual of compositional changes through time (arrow head ending with the 10 year post-disturbance sample). Each panel is scaled only for one site and visual distances should not be compared across sites.
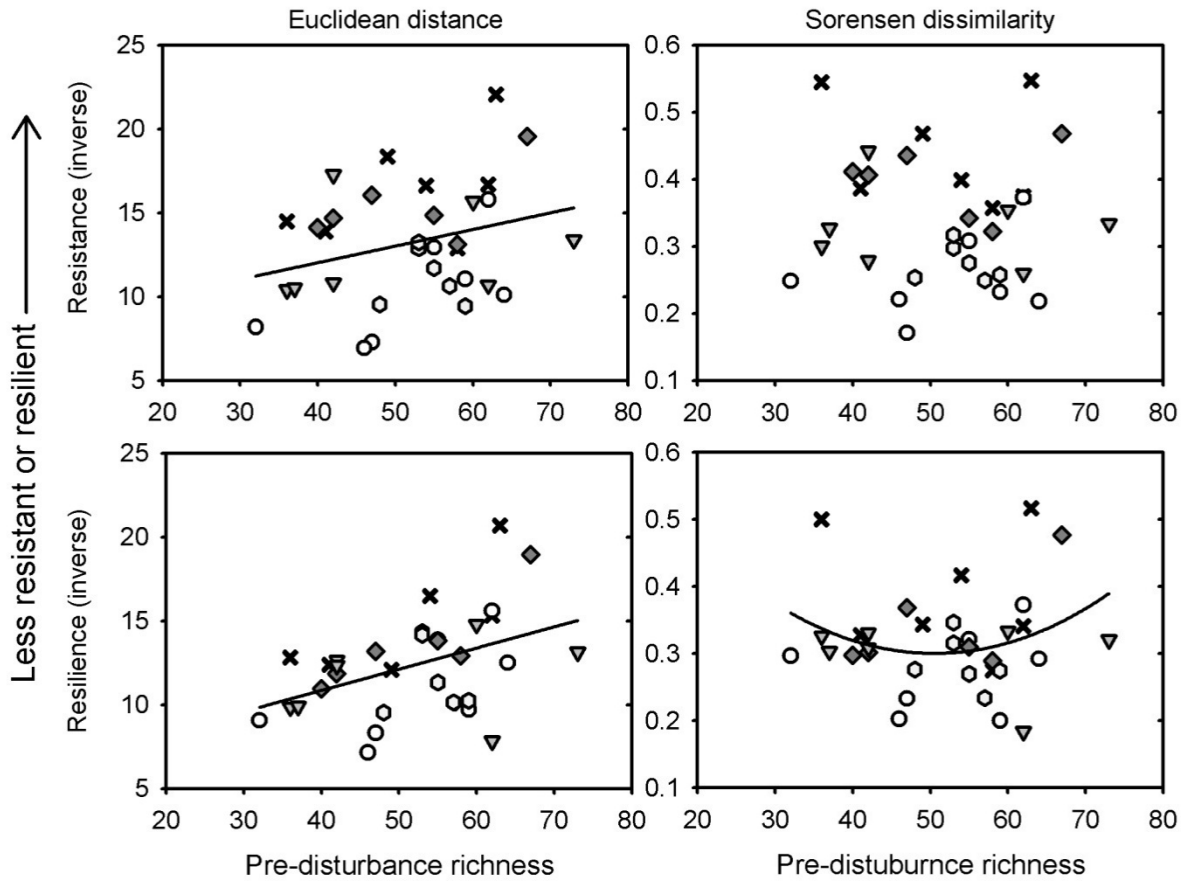
Figure 5.5. Plot-scale relationships between pre-disturbance richness and measures of resistance and resilience based on species frequency. Plotted lines represent relationship between pre-disturbance richness and resistance or resilience across disturbance treatments to highlight overall relationship and because no richness × treatment interaction was found. Symbols representing disturbance treatments are same as Figure 5.3. Statistics for effects of disturbance treatment and richness are in Table 5.2.
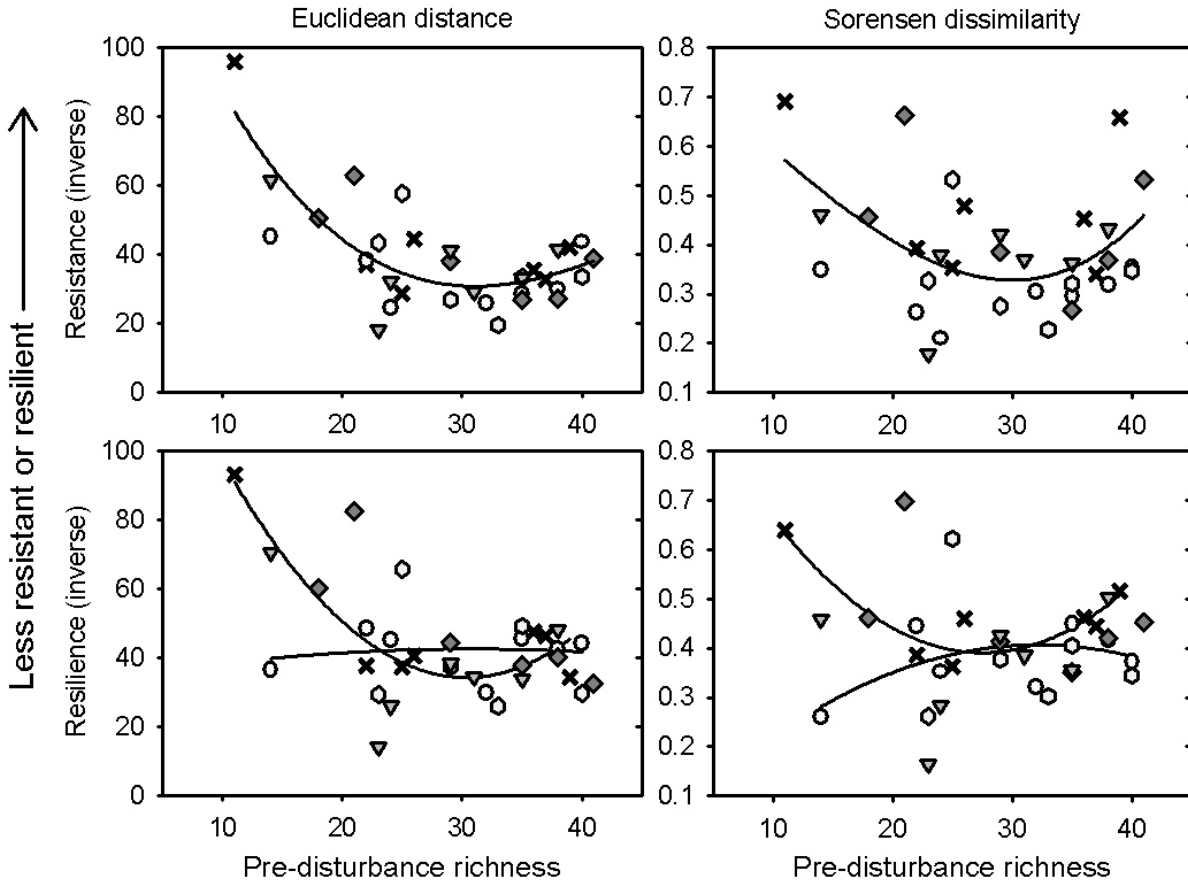
Figure 5.6. Subplot-scale relationships between pre-disturbance richness and measures of resistance and resilience based on species importance values. Symbols are same as Figure 5.3. Because the resilience depended on an interaction between pre-disturbance richness and disturbance treatment, models across treatments are not shown. Quadratic models for the clearcut (U-shaped curves) and control treatments are shown to emphasize statistical interaction between richness and resilience (other treatment models were excluded for clarity). Statistics for effects of disturbance treatment and richness are in Table 5.2.
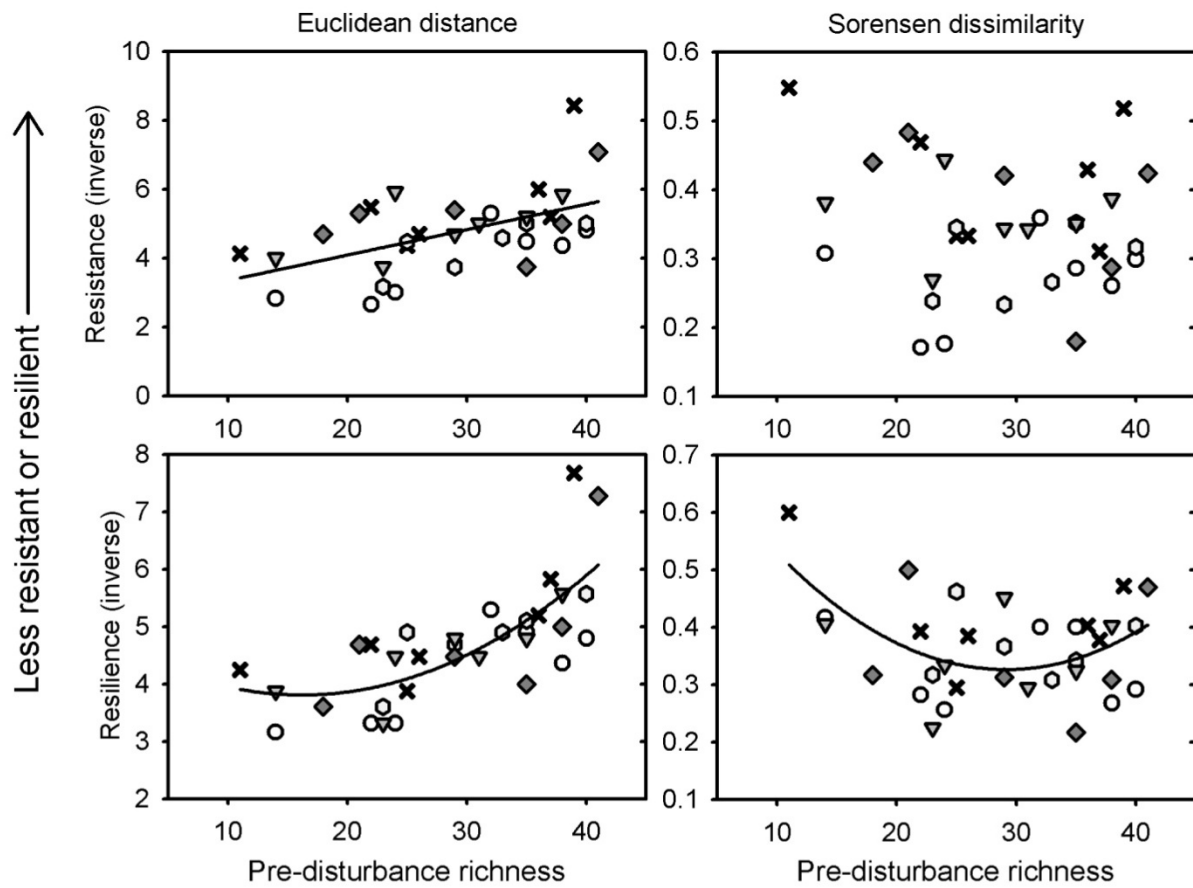
Figure 5.7. Subplot-scale relationships between pre-disturbance richness and measures of resistance and resilience based on species presence-absence. Symbols are same as Figure 5.3. Statistics for effects of disturbance treatment and richness are in Table 5.3.
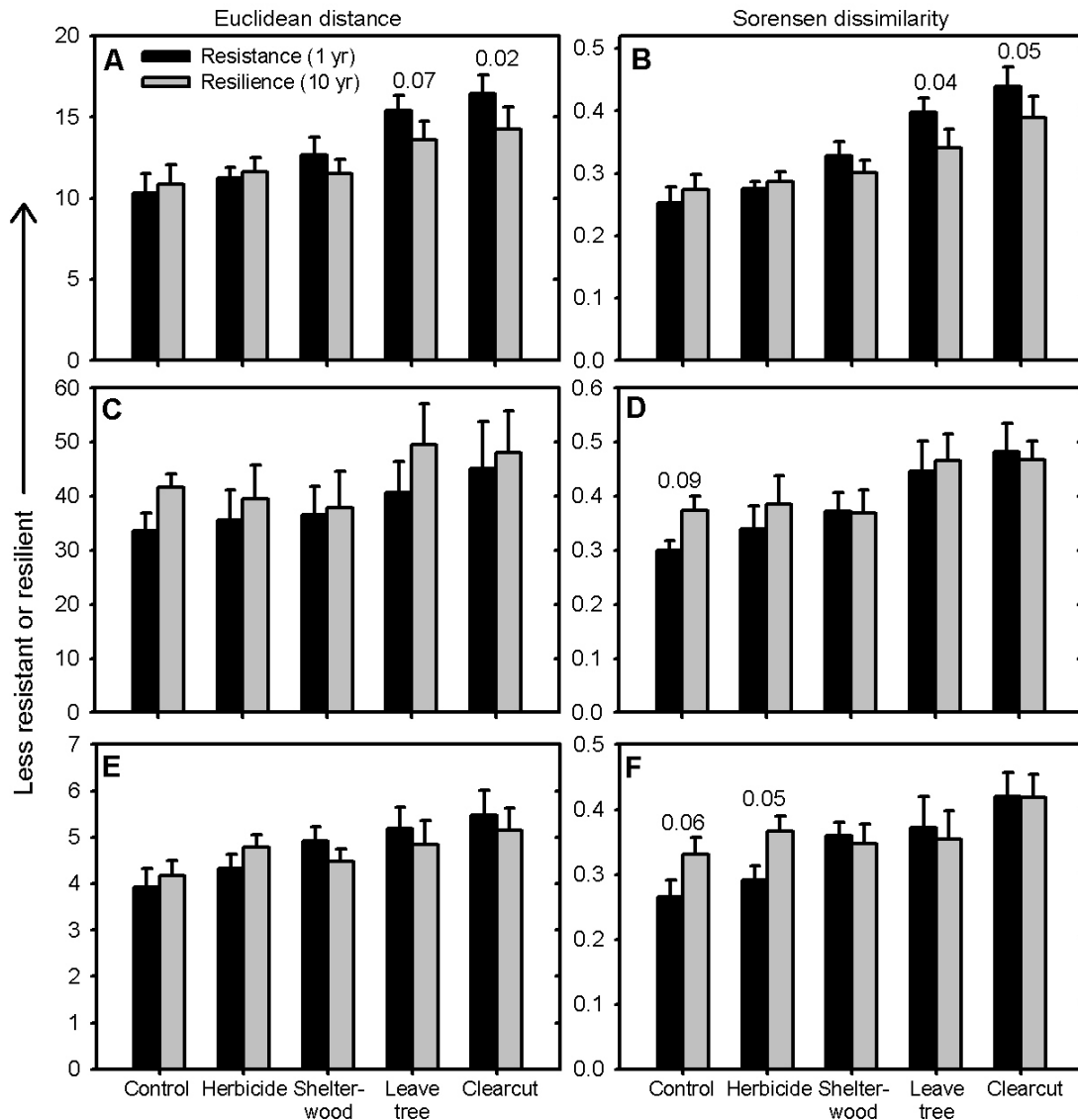
Figure 5.8. Mean (+SE) resistance and resilience of community composition within each disturbance treatment as measured by Euclidean distances or Sorensen dissimilarity index. A and B are resistance and resilience values for plots based on frequency. C and D are values based on importance values of subplots. E and F are values based on presence-absence of subplots. Statistics for disturbance treatment effect are in Tables 5.2 and 5.3; *P*-values are shown above resistance and resilience values within treatment when they were < 0.10 to highlight changes in compositional difference between 1 and 10 year post-disturbance.

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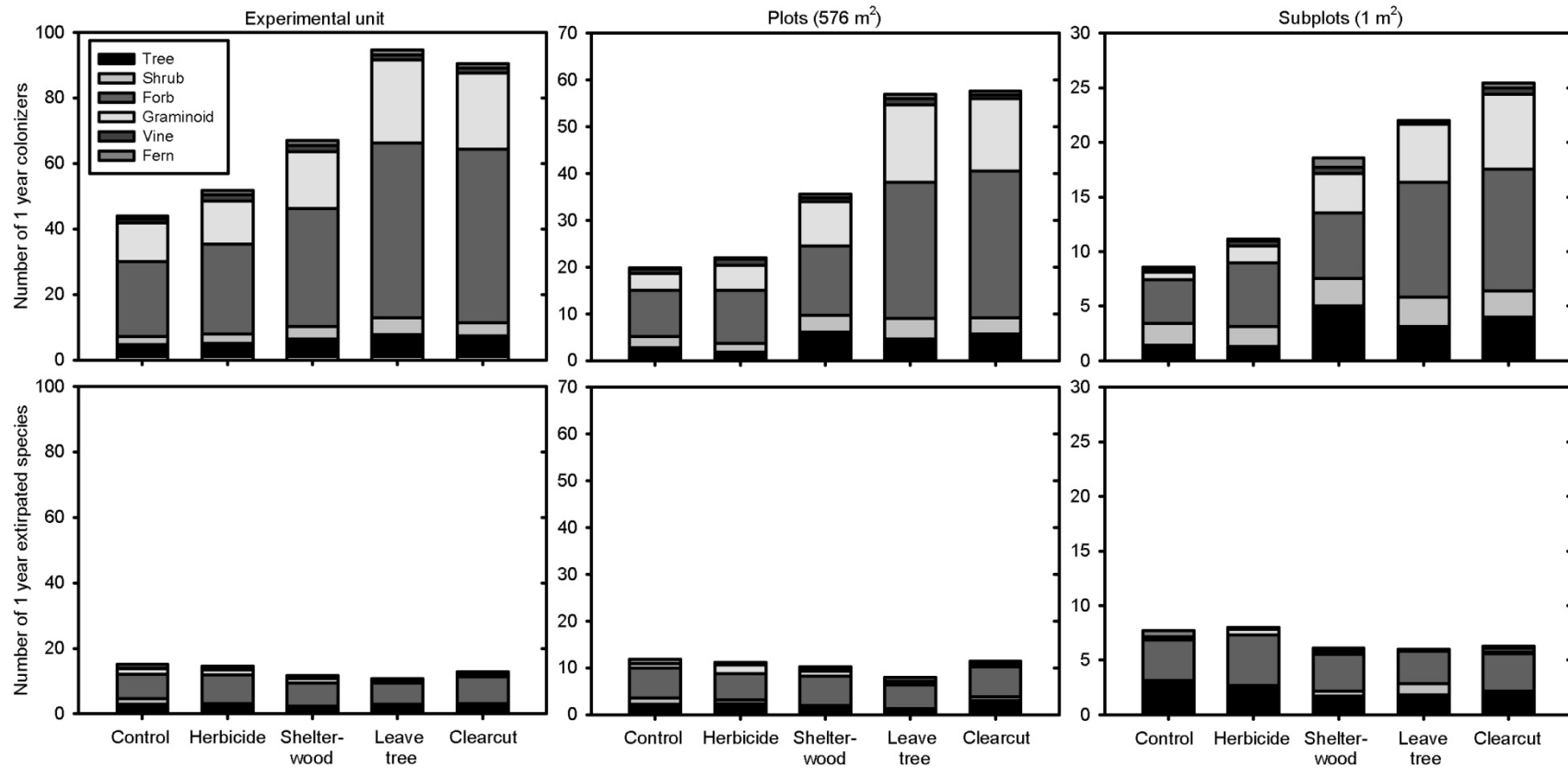
Figure 5.9. Contribution of six plant functional groups to total richness of colonizers one year after disturbance (1 year colonizers; top) and contribution of functional groups to total richness of extirpated species one year after disturbance (1 year extirpated species; bottom) in five disturbance treatments and three spatial scales (2 hectare = experimental units; plots = 576m^2; subplots = 1 m^2). Statistics for total and within functional group tests are in Table 5.4.
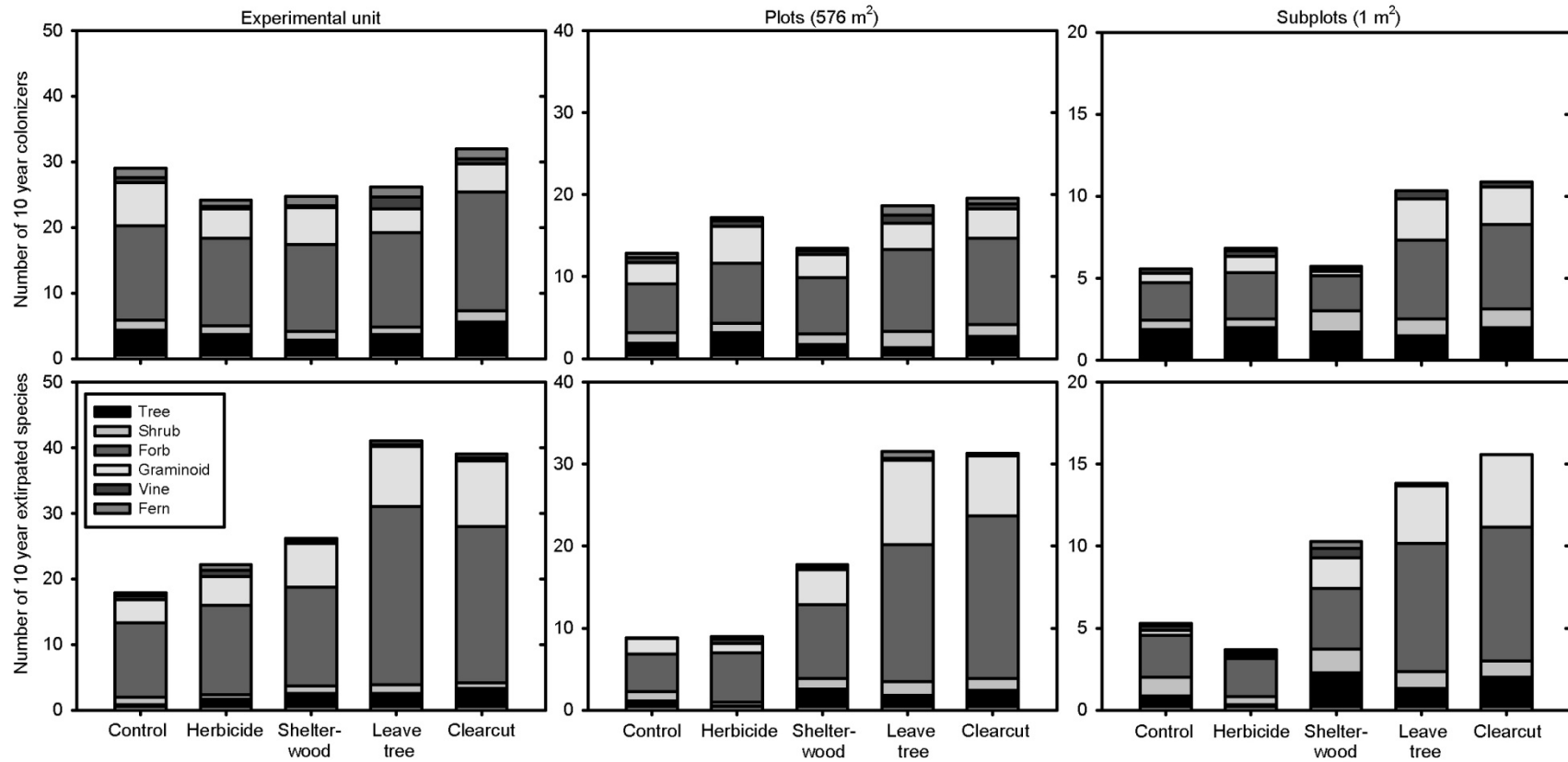
Figure 5.10. Contribution of six plant functional groups to total richness of species that colonized after ten years (10 year colonizers; top) and richness of functional groups that colonized sites after one year but did not persist after 10 years (10 year extirpated species; bottom) in five disturbance treatments and at three spatial scales (2 hectare = experimental units; plots = 576m^2; subplots = 1 m^2). Statistics for total and within functional group tests are in Table 5.5.
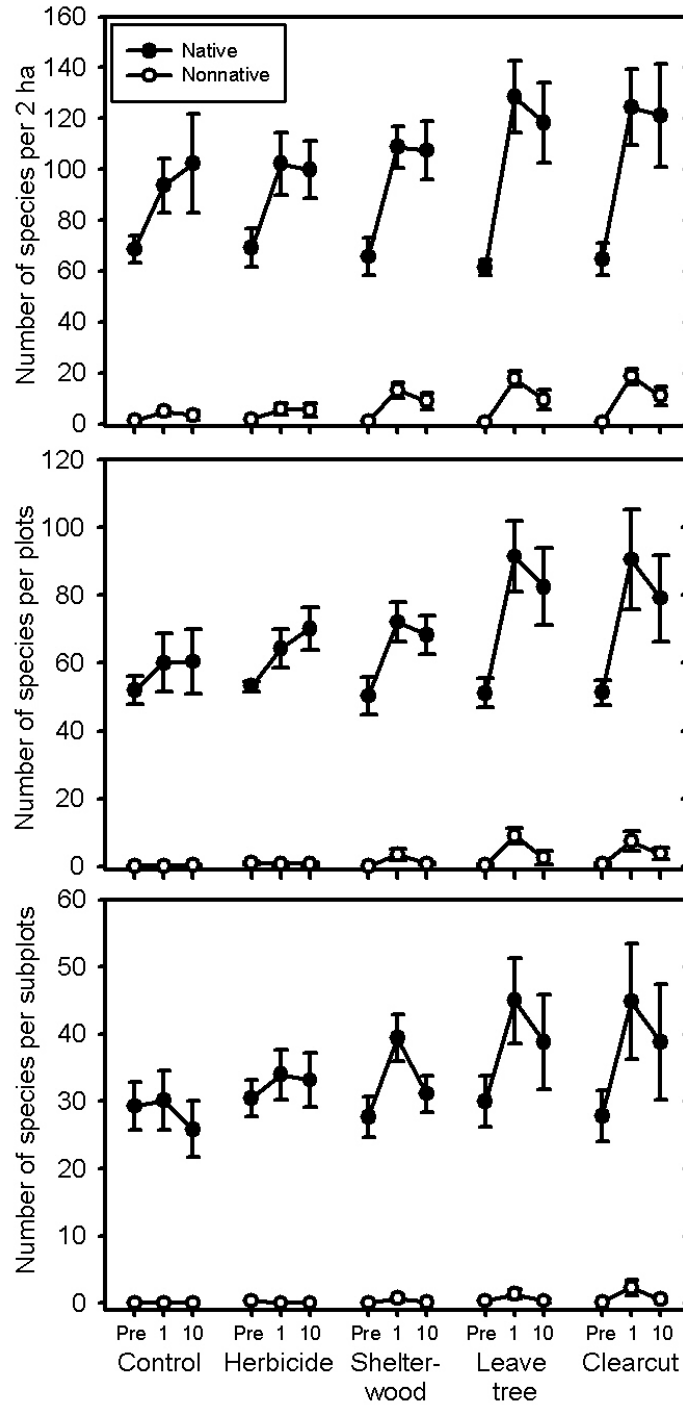
Figure 5.11. Changes in mean (± SE) richness of all native and nonnative species through time within five disturbance treatments and at three spatial scales. Statistics for treatment and time effects are in Table 5.6.

CHAPTER 6: SYNTHESIS, CAVEATS, AND FUTURE DIRECTIONS

Human populations and their use of natural resources continue to increase. At the same time, we become increasingly concerned about managing our natural resources sustainably while maintaining biodiversity, compositional integrity, and functioning of ecological communities. Therefore, management objectives are complex and at times include conflicting goals. Daunting challenges exist to understand and predict consequences of management actions on ecosystems. Difficulty in predicting how management actions will influence ecosystems results because of variability of sites including differences in soil, topographic, and climatic factors, as well differences in species distributions, life histories, and species interactions within their communities.

Numerous ecological theories have been developed that at times may provide predictions about how management actions influence ecological communities. However, many of these theories have been untested in forested systems, under realistic conditions, and in the context of natural resource management. In this dissertation, I have attempted to link natural resource management with current theories from community ecology with the hopes of providing information to both forest managers and theoretical ecologists.

In Chapter 2, I tested theories of species invasions relating to native diversity and disturbance intensity. While predictions derived from classic theory suggest species-rich areas would be less prone to invasion by nonnative species, I found that the most species-rich sites were invaded by more nonnative species than species-poor sites. The pattern is likely due to site differences related to regional species pools or soil resource availability, which are correlated with both native and nonnative species diversity. Nonnative species invasion tended to be higher in more disturbed sites, but many nonnative species did not persist through canopy closure. In

some cases, nonnative trees (e.g., *Paulownia tomentosa*) did persist in disturbed sites and should be monitored or removed before the possibility of spreading propagules. In fact, during the reentry and removal of the overstory in the shelterwood treatments at one of the sites in 2008, individuals of *Paulownia tomentosa* were left on site. Given the copious seed production of *P. tomentosa*, I recommend that this species be removed during a stand reentry in shelterwood treatments.

In Chapter 3, I tested the "invasional meltdown" hypothesis that nonnative species facilitate further invasions. I investigated how litter layers from different tree species (including an invasive tree) interact with nonnative earthworms to influence invasion by a model nonnative plant species. Results suggest that nonnative earthworms can decrease invasibility and that invasibility may be greater in forested stands dominated by trees with high quality litter (higher nitrogen content). Also, results suggest that one mechanism of oak forests resistance to some nonnative plants is the recalcitrance of its litter (i.e., it decomposes more slowly). Thus, while treatments that facilitate oak regeneration may benefit nonnative species invasion initially because of disturbance (sensu Chapter 2), management for oak stand dominance may provide longer term biotic resistance in the form of recalcitrant leaf litter layers. However, monitoring of sites following initial establishment of nonnative species may be important because many invasive species persist during a lag phase where abundance is low for years before increasing in abundance and becoming a pest.

In Chapter 4, I investigated whether local species diversity is a function of regional species pools. Conceptual models predict saturation of local-regional species richness relationships when interactions between species limit local diversity, but unsaturated relationships in non-interacting communities. I found that local diversity did not depend on

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regional diversity before disturbance, but after disturbance local species richness depended

heavily on regional richness. After 10 years when tree regeneration created a dense and closed

canopy, local diversity depended less on regional diversity. These results generally support

theoretical predictions that strong interactions, in this case interactions between canopy trees and

understory species, can limit diversity of local communities even as regional diversity increases.

In Chapter 5, I investigated several factors that can potentially influence compositional

stability after timber harvesting disturbance. Theory suggests that more diverse sites would

maintain greater temporal stability after disturbance. Disturbance intensity decreased resistance

and resilience of species composition. Species diversity of communities before timber harvests

affected resistance and resilience in complex ways, which depended on spatial scales and

methods used. At intermediate spatial scales (576 m^2), the most diverse sites tended to be less

resistant and resilient after disturbance. At smaller spatial scales (1 m^2) areas with intermediate

levels of diversity were most resistant and resilient when considering abundance of species.

However, if only presence or absence of species was considered, the most diverse areas tended to

be less resistant and resilient. Thus, based only on species without regard to changes in

abundance, the most diverse sites appear to be less stable after disturbance. This result

contradicts classic theory, but supports similar recent studies in other community types.

Caveats

An important caveat to these results is my inability to clearly tease apart whether

diversity per se influences invasibility and compositional stability. In fact, diversity of sites

likely correlates with other site factors that influenced many of our response variables (e.g.,

invasibility, resistance, resilience). Other important factors influencing community response to

disturbance include site history, soil characteristics, regional land use and species pools, and abundance of herbivores, among others. However, if one attempts to predict the number of nonnative species that will invade, or how much the composition of communities will shift after disturbance, species diversity may be important to consider whether or not diversity serves as a mechanism of invasibility or stability. For example, the number of species present before harvest is an easily measurable attribute of the community that can be used to predict various responses after timber harvesting including invasion and compositional shifts.

More studies should be conducted to investigate species-specific responses to timber harvesting. For instance, while we found no difference in extirpation of species across disturbance treatments, some species might have been detrimentally affected by timber harvesting. For example, black cohosh (*Actea racemosa*), which was present before timber harvests at Blacksburg 1, was extirpated from subplots after clearcutting. Unfortunately, we were unable to statistically investigate such species-specific responses because of variability in species composition among sites.

The responses of plant communities to forest management disturbances are complex and are mediated by disturbance intensity and possibly diversity of sites. Additional research should address potential treatment by site interactions, as well as mechanisms mediating species-specific and community responses to disturbance. Even the considerable variability across the sites sampled within the studies of this dissertation includes just a portion of potential site variability within hardwood forests of the eastern US. For example, the SASAB sites were located on sandstone and shale residuum and colluvium with acidic soils (mean pH of 4.4, ranging from 3.6 to 5). Other forested sites with richer soils support a different suite of understory plant species and may respond differently to disturbance and invasion. Based on my observations, sites with

richer soils (higher base saturation) are much more likely to be dominated by nonnative understory plant species (e.g., *Alliaria petiolata* (M. Bieb.) Cavara & Grande), especially near disturbed areas. Therefore, results from this dissertation should not be extrapolated across the entire Appalachian region, and may only apply to Appalachian oak forests occurring on sites similar to those described herein.

Conclusions

Theories of diversity, invasibility, and stability are often developed and tested in model ecosystems, particularly grasslands. Recent experimental work in grasslands tends to suggest that species-rich sites resist invasions (references cited in Chapter 2) and are more stable following perturbations (references cited in Chapter 4). These results generally contrast those that we observed in forests, which may be due to several factors. First, observations in experimental work are typically small (≤ 3 m^2) and do not incorporate natural heterogeneity. Second, grassland and forested systems differ in the traits of the common species, importance of key resources (e.g., water vs. light), and the interactions between traits and resource availability. Results emerging from tests of theories in model systems (e.g., grasslands) may not apply across the diverse communities and ecosystems that occur on Earth.

Taken together, these studies suggest that timber harvesting in Appalachian oak forests may interact with plant species diversity to influence community invasibility and composition. While questions about species responses and specific mechanisms remain, results generally suggest that the management options investigated in this dissertation and the disturbances they produce may not negatively impact plant species diversity. In sum, diversity, invasibility, species saturation, and compositional stability all depend on disturbance in Appalachian oak forests.

APPENDIX A. SITES, BASAL AREA REMOVED AND YEAR OF SAMPLE.

Seven sites used in the Southern Appalachian Siliviculture and Biodiversity (SASAB) study; mean percent basal area removed from five disturbance treatments representing silvicultural alternatives and a disturbance gradient at each site; year treatments were completed and the vegetation was sampled before disturbance (pre-disturbance sample), 1 year post-disturbance and 10 year post-disturbance. Vegetation sampling consisted of an inventory of all vascular plant species at 3 spatial scales: 2 hectare experimental units, 576 m^2 plots and 1 m^2 subplots. See text for details (adapted from Wender 2000 and Hood 2001). *Disturbance treatments followed best management practices to protect streamside zones.

| Site | Basal area removed (%) | | | | | Year | | | |
	Control	Herbicide	Shelter-wood	Leave-tree	Clearcut	Treatment application completed	Pre-disturbance sample	1 year-post disturbance sample	10 year-post disturbance sample
Blacksburg 1	0	trace	36	87	83	1995	1993	1996	2006
Blacksburg 2	0	trace	63	88	100	1996	1995	1998	2006
New Castle	0	trace	69	89	94	1996	1995	1998	2006
Clinch 1	0	10	54	81	93	1998	1993	2000	2007
Clinch 2	0	8	26*	18*	98	1998	1995	1999	2007
West Virginia 1	0	NA	87	NA	100	1997	1996	1999	2007
West Virginia 2	0	trace	61	81	100	1998	1997	2000	2007
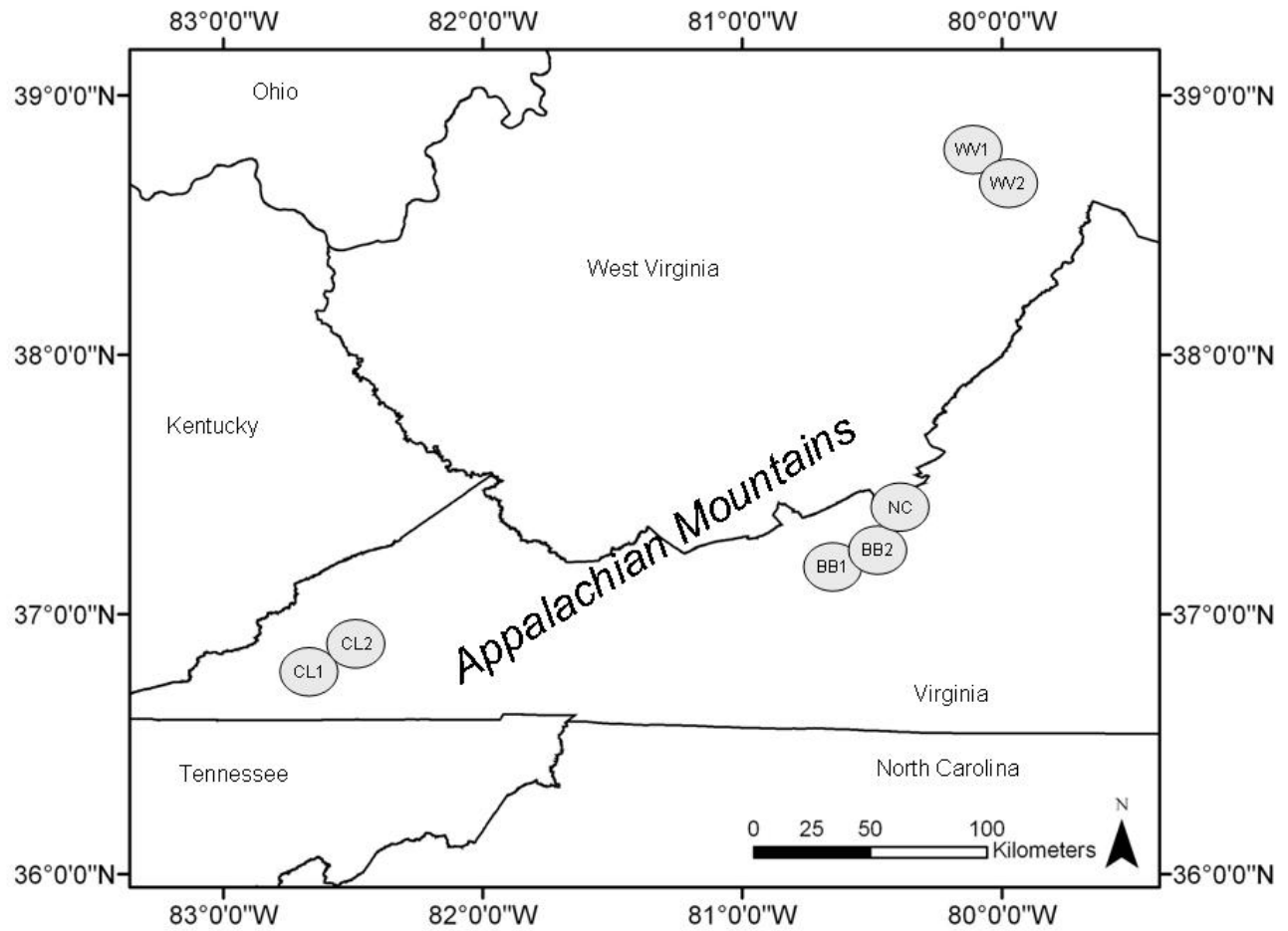
Appendix B1. Approximate locations of the seven study sites (blocks) within the Appalachian Mountains of western Virginia and West Virginia. BB1 = Blacksburg District site 1; BB2 = Blacksburg District site 2; CL1 = Clinch District site 1; CL2 = Clinch District site 2; NC = New Castle District site; WV1 = Westvaco Corporation site 1; WV2 = Westvaco Corporation site 2.
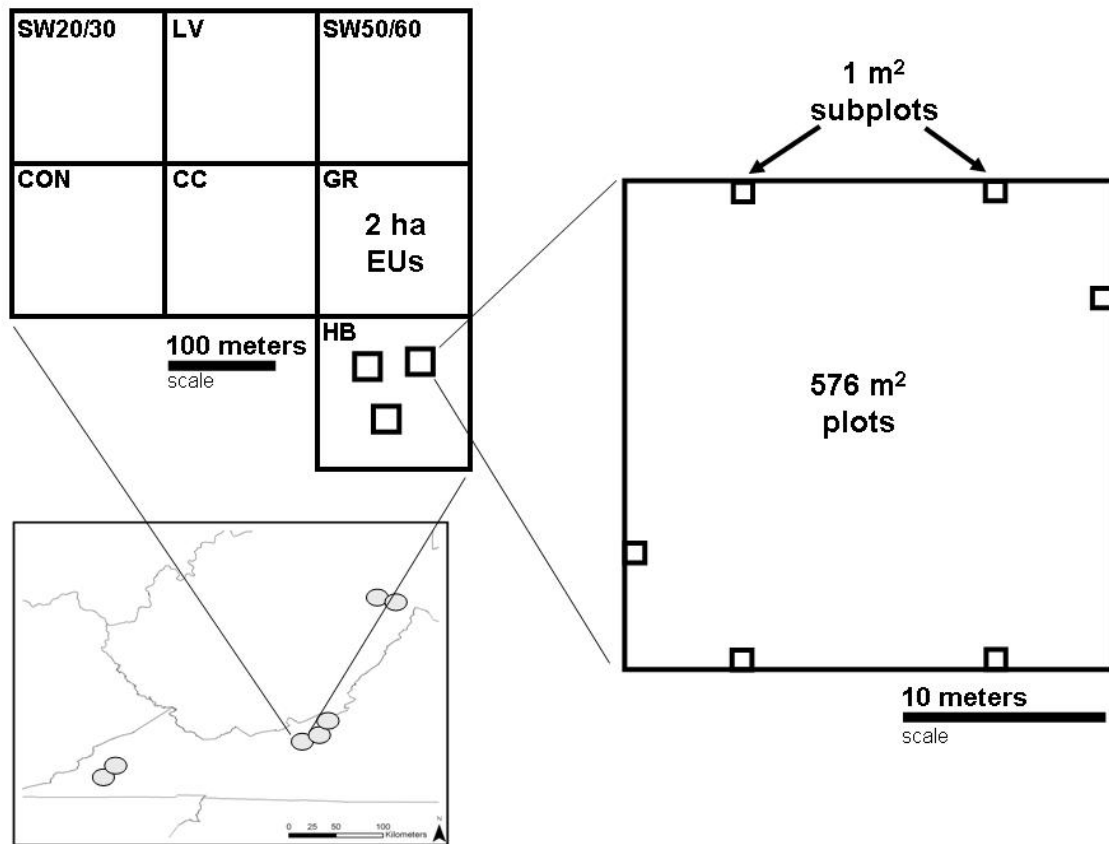
Appendix B2. Typical layout of the experimental units within each site and arrangement of nested plots and subplots to illustrate sampling scheme. Richness of native and non-native vascular plant species was recorded at the 2 hectare experimental units (EUs), 576m^2 plots, and 1m^2 subplots. Disturbance treatment codes are included in the EUs as an example to illustrate that each treatment was randomly assigned to EUs within each site. CON = uncut control; HB = understory herbicide; GR = group selection; SW50/60 = high leave shelterwood; LV = leave tree harvest; SW20/30 = low leave shelterwood; CC = clearcut.

APPENDIX C. NONNATIVE SPECIES AT EACH SITE

Non-native species occurring in the seven sites; presence within a site is represented by '×'. BB1 = Blacksburg District site 1; BB2 = Blacksburg District site 2; CL1 = Clinch District site 1; CL2 = Clinch District site 2; NC = New Castle District site; WV1 = Westvaco Corporation site 1; WV2 = Westvaco Corporation site 2. Taxonomic authorities can be found at USDA PLANTS Database (http://plants.usda.gov/).

Non-native species	BB1	BB2	CL1	CL2	NC	WV1	WV2
Achillea millefolium	×	×	×	×	×		×
Agrostis capillaris			×			×	×
Agrostis gigantean	×	×				×	×
Ailanthus altissima	×	×	×		×		
Allium vineale	×						
Anthoxanthum odoratum	×	×	×	×		×	×
Arabidopsis thaliana		×					
Arctium minus	×	×		×			
Arrhenatherum elatius				×			
Barbarea verna		×					
Barbarea vulgaris	×		×				
Berberis thunbergii					×		
Bromus japonicus			×				
Cardamine hirsuta	×			×			
Carduus acanthoides	×	×			×		
Carduus nutans	×						
Cerastium glomeratum	×	×		×			
Cirsium arvense	×						
Cirsium vulgare	×	×	×	×	×		
Convolvulus arvensis					×		
Crepis capillaris	×	×			×		
Dactylis glomerata	×	×	×	×	×	×	×
Daucus carota	×	×	×				
Digitaria ischaemum			×			×	×
Elaeagnus umbellata	×			×			

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Species							
Festuca arundinacea	×	×	×	×	×	×	×
Festuca ovina							×
Glechoma hederacea	×						
Hieracium pilosella	×			×			
Hieracium pratense	×	×	×	×	×	×	×
Holcus lanatus	×	×	×	×	×	×	×
Humulus lupulus	×						
Hypochaeris radicata	×	×	×	×	×	×	×
Ipomoea purpurea		×			×		
Kummerowia stipulacea			×				
Lactuca scariola	×						
Lepidium campestre	×		×				
Lespedeza bicolor					×		
Lespedeza cuneata	×	×	×	×	×		
Leucanthemum vulgare			×	×		×	×
Lolium perenne						×	×
Lonicera japonica	×						
Lotus corniculatus						×	×
Medicago lupulina	×		×				
Melilotus officinalis				×		×	
Microstegium vimineum			×				
Miscanthus sinensis	×						
Paulownia tomentosa	×	×	×		×		
Perilla frutescens	×						
Phleum pratense			×	×		×	
Plantago lanceolata	×	×	×	×			×
Poa compressa	×		×	×			×
Polygonum persicaria	×			×			
Prunus avium	×						
Rosa multiflora	×	×			×		×
Rubus phoenicolasius	×	×			×		
Rumex acetosella	×	×	×	×	×	×	×
Rumex obtusifolius	×						×
Salix caprea							×
Salix purpurea							×
Secale cereale			×				

Species							
Securigera varia		×	×	×	×		
Setaria faberi	×						
Setaria viridis	×						
Solanum dulcamara	×						
Sonchus asper	×		×	×			
Spiraea japonica						×	×
Taraxacum officinale	×	×	×	×	×	×	
Trifolium campestre	×						
Trifolium hybridum			×			×	×
Trifolium pratense	×	×	×	×		×	×
Trifolium repens	×		×		×		×
Tussilago farfara	×	×	×	×		×	×
Verbascum blattaria	×						
Veronica officinalis	×	×	×	×	×	×	×

APPENDIX D. IMPORTANCE VALUES OF SPECIES SAMPLED IN SUBPLOTS

All species encountered in subplots and their importance values in five disturbance treatments before disturbance (PRE), one year post-disturbance (POST 1), and ten years post-disturbance (POST 10); habits represent functional life form groups (T = tree; S = shrub; F = forb; G = graminoid; V = vine; Fe = fern). Nativity represents whether a species is considered native to the eastern United States (N) or introduced and nonnative to the eastern US (Int).

Scientific Name	Family	Habit	Nativity	Control			Herbicide			Shelterwood			Leave Tree			Clearcut		
				Pre	Post 1	Post 10	Pre	Post 1	Post 10	Pre	Post 1	Post 10	Pre	Post 1	Post 10	Pre	Post 1	Post 10
Acer pensylvanicum	Aceraceae	T	N	6.0	9.2	4.2	12.1	10.0	10.6	3.8	2.7	6.5	11.3	5.4	3.0	5.2	3.1	2.6
Acer rubrum	Aceraceae	T	N	17.2	18.2	29.7	11.1	13.2	13.7	18.7	12.6	23.3	12.2	8.6	18.8	16.9	8.3	19.0
Acer saccharum	Aceraceae	T	N	1.6	1.0	1.5	2.2	1.6	36.0	--	--	1.9	0.9	2.1	2.2	--	--	4.0
Actaea racemosa	Ranunculaceae	F	N	--	--	--	--	--	--	--	--	--	1.0	1.0	--	1.2	--	--
Ageratina altissima	Asteraceae	F	N	--	--	--	--	--	0.8	--	--	--	--	--	1.4	--	--	--
Agrimonia sp.	Rosaceae	F	N	--	--	--	--	--	--	--	--	--	--	--	0.6	--	--	--
Agrimonia parviflora	Rosaceae	F	N	--	--	--	--	--	--	--	--	--	--	--	--	--	1.5	--
Agrostis capillaris	Poaceae	G	Int	--	--	--	--	--	--	--	--	--	--	1.1	--	--	--	--
Agrostis gigantea	Poaceae	G	Int	--	--	--	--	--	--	--	--	--	--	--	--	1.9	3.9	--
Agrostis perennans	Poaceae	G	N	--	--	--	--	--	0.7	--	--	--	--	0.5	--	--	1.1	1.5
Ailanthus altissima	Simaroubaceae	T	Int	--	--	--	--	--	--	--	1.6	2.1	--	1.9	--	--	0.4	--
Allium tricoccum	Liliaceae	F	N	--	--	--	2.2	--	--	--	--	--	--	--	--	--	--	--
Ambrosia artemisiifolia	Asteraceae	F	N	--	--	--	--	--	--	--	--	--	--	0.5	--	--	--	--
Amelanchier arborea	Rosaceae	T	N	3.9	3.4	4.7	6.6	5.7	11.0	5.6	3.0	3.6	2.7	1.7	3.1	4.9	1.7	2.7
Amphicarpaea bracteata	Fabaceae	V	N	--	--	--	--	--	1.3	--	--	--	--	--	0.6	--	--	0.5
Andropogon virginicus	Poaceae	G	N	--	--	--	--	--	--	--	1.1	1.0	--	--	1.9	--	3.2	7.2
Anemone quinquefolia	Ranunculaceae	F	N	12.5	13.3	12.4	19.6	6.0	3.9	4.4	5.7	1.8	14.7	5.4	5.9	8.9	5.2	5.4
Angelica venenosa	Apiaceae	F	N	--	--	--	1.6	--	--	--	--	--	--	--	--	--	0.8	--
Arisaema triphyllum	Araceae	F	N	--	--	--	1.5	1.6	0.8	--	1.7	--	--	0.6	--	4.0	--	--
Aristolochia macrophylla	Aristolochiaceae	V	N	--	--	--	--	--	--	1.6	--	--	5.1	--	--	--	--	--
Aristolochia serpentaria	Aristolochiaceae	F	N	--	--	1.5	--	--	1.3	--	--	--	--	--	--	--	--	--
Arnoglossum atriplicifolium	Asteraceae	F	N	--	--	--	--	--	--	--	--	--	--	--	0.6	--	--	--

Asclepias quadrifolia	Asclepiadaceae	F	N	1.2	--	--	--	--	--	--	--	--	--	--	--	--	0.4	--
Aster sp.	Asteraceae	F	Unk	--	--	--	--	--	--	--	--	--	--	--	1.7	--	--	0.5
Athyrium filix-femina	Dryopteridaceae	Fe	N	1.0	0.8	--	--	--	2.2	0.9	3.3	2.5	0.8	0.7	1.4	--	--	--
Aureolaria flava	Scrophulariaceae	F	N	1.1	--	--	1.1	--	--	--	--	--	--	--	--	--	--	--
Aureolaria laevigata	Scrophulariaceae	F	N	--	--	--	--	0.9	0.8	--	--	--	1.0	--	--	--	0.8	--
Baptisia tinctoria	Fabaceae	F	N	--	--	--	--	--	--	--	--	--	--	0.8	--	--	0.8	--
Betula lenta	Betulaceae	T	N	3.8	3.2	2.1	2.7	2.3	6.8	6.4	5.1	17.2	--	18.9	26.7	5.7	8.1	17.4
Botrychium virginianum	Ophioglossaceae	Fe	N	--	1.2	--	--	--	--	--	--	--	--	--	--	--	--	--
Brachyelytrum erectum	Poaceae	G	N	--	--	--	--	1.6	1.5	--	0.6	--	--	--	--	--	--	--
Campanula divaricata	Campanulaceae	F	N	--	--	--	--	--	--	--	--	--	--	1.1	--	--	0.5	--
Carex sp.	Cyperaceae	G	N	--	--	3.0	--	--	1.0	--	--	1.1	--	--	1.4	--	--	1.9
Carex aestivalis	Cyperaceae	G	N	--	--	--	--	--	--	--	0.9	--	--	--	--	--	2.0	--
Carex blanda	Cyperaceae	G	N	--	--	--	--	--	--	--	--	--	--	1.0	--	--	--	--
Carex debilis	Cyperaceae	G	N	--	--	2.4	--	--	--	2.8	6.0	2.7	--	7.3	1.1	--	8.4	2.1
Carex digitalis	Cyperaceae	G	N	--	1.0	1.2	--	--	--	--	0.9	1.1	--	2.6	0.8	--	1.8	0.5
Carex hirsutella	Cyperaceae	G	N	--	--	--	--	--	--	--	--	--	--	--	--	--	0.6	--
Carex laxiflora	Cyperaceae	G	N	1.2	--	--	--	4.7	4.9	--	--	--	4.3	9.6	--	--	0.7	--
Carex leptonervia	Cyperaceae	G	N	--	--	--	--	1.6	4.4	--	--	--	4.3	2.0	1.1	--	--	--
Carex nigromarginata	Cyperaceae	G	N	--	--	--	--	--	--	--	0.6	1.1	--	2.6	0.9	--	0.8	0.5
Carex pensylvanica	Cyperaceae	G	N	--	--	--	--	--	1.3	--	--	--	--	--	--	--	--	0.5
Carex rosea	Cyperaceae	G	N	--	--	--	--	--	--	--	--	--	--	0.5	--	--	--	--
Carex stipata	Cyperaceae	G	N	--	--	--	--	--	--	--	--	--	--	0.6	--	--	--	--
Carex swanii	Cyperaceae	G	N	--	--	--	0.9	--	--	--	--	--	--	1.0	--	--	2.0	0.5
Carex umbellata	Cyperaceae	G	N	--	--	--	--	--	--	--	--	--	--	2.6	--	--	0.4	--
Carex virescens	Cyperaceae	G	N	--	--	--	--	0.8	0.7	--	1.8	--	--	3.1	0.8	--	1.5	--
Carex willdenowii	Cyperaceae	G	N	--	--	--	--	--	--	--	--	--	--	0.5	--	--	6.5	--
Carpinus caroliniana	Betulaceae	T	N	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1.8
Carya alba	Juglandaceae	T	N	2.3	1.1	3.1	8.9	1.5	4.4	2.3	0.6	7.1	4.1	1.0	2.5	6.2	1.3	3.4
Carya glabra	Juglandaceae	T	N	1.6	1.2	1.5	2.9	3.0	7.5	2.3	3.1	3.7	2.0	0.9	1.9	1.2	1.7	0.8
Castanea dentata	Fagaceae	T	N	3.5	2.3	2.3	5.3	1.6	--	5.1	2.2	2.1	10.8	2.8	3.4	4.4	3.5	4.8
Castanea pumila	Fagaceae	T	N	--	1.0	1.2	--	--	--	--	9.0	4.0	--	--	--	--	--	--
Ceanothus americanus	Rhamnaceae	F	N	--	1.2	--	--	--	--	--	0.8	--	--	--	--	--	--	--
Cerastium glomeratum	Caryophyllaceae	F	Int	--	--	--	--	--	--	--	--	--	--	--	--	--	0.8	--
Chamaelirium luteum	Liliaceae	F	N	--	--	0.9	--	--	--	--	--	--	--	1.3	--	--	--	--
Chimaphila maculata	Pyrolaceae	F	N	4.4	4.5	2.6	4.0	5.0	5.4	3.4	1.0	3.0	9.2	1.3	9.4	6.0	0.5	4.2
Claytonia caroliniana	Portulacaceae	F	N	--	--	--	8.3	--	--	--	--	--	--	--	--	--	--	--
Clintonia umbellulata	Liliaceae	F	N	0.8	3.2	1.7	--	--	0.7	0.9	0.6	1.2	--	1.3	0.7	4.0	--	--

Species	Family																	
Collinsonia canadensis	Lamiaceae	F	N	--	--	--	--	--	--	--	--	--	--	0.5	--	0.9	--	0.8
Conopholis americana	Orobanchaceae	F	N	1.7	2.6	3.1	2.0	1.2	1.7	2.8	3.7	--	2.1	1.3	1.6	2.4	--	--
Convallaria majuscula	Liliaceae	F	N	--	--	--	--	--	--	--	--	--	2.4	1.0	1.5	--	0.8	--
Conyza canadensis	Asteraceae	F	N	--	--	--	--	--	--	--	0.6	--	--	--	--	--	1.2	--
Coreopsis major	Asteraceae	F	N	1.0	0.9	--	1.8	1.4	0.8	1.6	1.0	--	1.0	0.5	0.6	1.7	--	--
Cornus florida	Cornaceae	T	N	2.2	--	--	1.8	2.1	2.1	1.6	0.9	3.8	3.5	3.7	1.7	1.8	1.6	1.0
Corylus americana	Betulaceae	S	N	--	--	--	--	--	--	--	--	--	--	--	--	--	0.4	--
Crataegus sp.	Rosaceae	T	N	1.1	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Cypripedium acaule	Orchidaceae	F	N	--	--	--	--	--	--	--	--	--	--	--	--	1.5	--	--
Dactylis glomerata	Poaceae	G	Int	--	--	--	--	--	--	--	0.6	--	--	0.6	--	--	0.8	--
Danthonia compressa	Poaceae	G	N	--	--	1.2	--	5.0	5.5	--	1.3	4.4	--	1.1	1.1	--	0.7	1.7
Danthonia sericea	Poaceae	G	N	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1.8
Danthonia spicata	Poaceae	G	N	--	3.8	1.2	--	--	0.8	--	--	--	--	--	1.1	--	9.3	2.1
Daucus carota	Apiaceae	F	Int	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1.2
Dennstaedtia punctilobula	Dennstaedtiaceae	Fe	N	4.1	4.9	3.1	10.0	5.6	6.0	11.3	4.9	5.1	17.0	13.9	6.5	12.8	12.7	7.4
Desmodium glabellum	Fabaceae	F	N	--	--	--	--	--	2.5	--	--	--	--	--	--	--	--	--
Desmodium nudiflorum	Fabaceae	F	N	5.2	5.4	4.0	6.9	17.7	10.1	12.2	5.0	2.2	3.9	3.2	2.7	2.0	1.5	0.8
Desmodium paniculatum	Fabaceae	F	N	--	7.4	--	--	--	--	--	0.6	--	--	0.8	--	--	--	--
Desmodium rotundifolium	Fabaceae	F	N	--	--	--	--	--	--	--	--	--	--	--	--	--	0.4	0.5
Dicentra cucullaria	Fumariaceae	F	N	--	--	--	2.2	--	--	--	--	--	--	--	--	--	--	--
Dichanthelium sp.	Poaceae	G	N	--	--	--	--	--	--	--	--	--	--	--	--	1.1	--	1.4
Dichanthelium acuminatum	Poaceae	G	N	--	--	--	--	--	--	--	--	--	--	--	1.0	--	2.4	--
Dichanthelium boscii	Poaceae	G	N	--	--	--	--	--	--	--	0.6	--	--	1.6	1.0	--	5.3	2.0
Dichanthelium clandestinum	Poaceae	G	N	--	--	--	--	--	--	--	--	--	--	0.8	3.6	--	--	--
Dichanthelium commutatum	Poaceae	G	N	--	--	--	0.9	1.4	1.7	2.8	3.1	1.5	--	6.6	1.4	1.2	4.5	3.3
Dichanthelium depauperatum	Poaceae	G	N	--	--	--	--	--	--	--	--	--	--	1.0	--	--	--	--
Dichanthelium dichotomum	Poaceae	G	N	--	1.9	--	--	--	--	--	3.4	1.8	--	3.0	1.7	--	2.3	3.0
Dichanthelium latifolium	Poaceae	G	N	--	0.8	1.8	2.2	2.0	1.5	--	6.4	4.3	4.3	6.3	1.2	--	6.3	4.0
Dichanthelium linearifolium	Poaceae	G	N	--	--	--	--	--	--	--	--	--	--	--	--	--	5.3	--
Dioscorea quaternata	Dioscoreaceae	F	N	6.9	--	--	1.1	--	--	1.5	--	--	--	--	--	--	--	--
Dioscorea villosa	Dioscoreaceae	F	N	6.7	5.7	7.1	4.9	4.2	4.7	3.8	2.3	2.6	6.9	5.3	4.2	3.3	2.0	2.5
Doellingeria infirma	Asteraceae	F	N	1.1	1.0	--	--	--	--	--	--	--	--	--	--	--	--	--
Dryopteris intermedia	Dryopteridaceae	Fe	N	4.3	--	--	4.3	4.7	5.8	6.9	2.6	3.9	12.8	0.6	--	3.8	1.0	1.4
Epigaea repens	Ericaceae	F	N	--	0.9	--	1.3	0.9	--	2.7	3.2	4.0	1.3	--	0.9	5.1	1.4	4.5
Erechtites hieraciifolia	Asteraceae	F	N	--	--	--	--	7.8	--	--	3.1	--	--	8.8	--	--	6.9	--
Erigeron annuus	Asteraceae	F	N	--	--	--	--	--	--	--	--	--	--	--	--	0.6	--	--
Eupatorium sp.	Asteraceae	F	N	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0.8

Species	Family																	
Eupatorium purpureum	Asteraceae	F	N	1.6	--	--	--	--	--	4.7	0.9	2.4	--	--	--	--	--	--
Eupatorium sessilifolium	Asteraceae	F	N	--	--	--	--	--	--	--	--	--	--	--	0.6	--	--	0.5
Eupatorium steelei	Asteraceae	F	N	--	3.2	2.4	--	--	--	--	2.5	4.3	--	0.6	1.4	--	--	2.7
Eurybia divaricata	Asteraceae	F	N	--	1.0	--	--	0.9	1.0	4.7	2.4	2.6	--	--	--	9.5	4.1	1.2
Eurybia macrophylla	Asteraceae	F	N	1.6	--	1.6	--	--	--	--	--	--	--	--	--	--	--	--
Euthamia graminifolia	Asteraceae	F	N	--	--	--	--	--	--	--	0.9	--	--	--	--	--	--	--
Fagus grandifolia	Fagaceae	T	N	13.4	--	18.0	--	--	--	2.8	4.8	11.8	--	--	--	13.0	8.4	12.7
Festuca sp.	Poaceae	G	Unk	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0.5
Festuca filiformis	Poaceae	G	Int	--	--	--	--	--	--	--	--	--	--	0.6	--	--	--	--
Fraxinus americana	Oleaceae	T	N	2.2	1.9	3.3	1.1	2.4	1.4	2.4	--	--	2.0	1.0	2.0	7.5	2.8	4.2
Fraxinus pennsylvanica	Oleaceae	T	N	--	--	--	--	0.9	--	--	--	--	--	--	--	--	0.4	--
Galax urceolata	Diapensiaceae	F	N	3.5	6.3	5.1	2.9	2.7	2.6	3.1	3.9	3.2	5.3	3.8	2.8	3.9	1.9	2.1
Galearis spectabilis	Orchidaceae	F	N	--	--	1.6	--	--	--	--	--	--	--	--	--	--	--	--
Galium circaezans	Rubiaceae	F	N	1.7	--	--	2.1	--	--	--	0.6	--	1.0	0.5	1.1	2.5	0.4	1.5
Galium lanceolatum	Rubiaceae	F	N	--	--	0.9	--	1.6	--	--	0.6	--	--	--	--	--	0.5	--
Galium latifolium	Rubiaceae	F	N	--	--	--	--	--	--	--	--	--	--	1.0	--	--	--	0.5
Galium pilosum	Rubiaceae	F	N	--	--	--	--	--	--	--	--	--	--	--	--	--	0.4	--
Gamochaeta purpurea	Asteraceae	F	N	--	--	--	--	--	--	--	--	--	--	0.6	--	--	--	--
Gaultheria procumbens	Ericaceae	F	N	12.0	8.4	8.5	11.4	9.5	9.1	2.7	1.6	1.1	--	--	--	6.0	2.6	1.9
Gaylussacia baccata	Ericaceae	S	N	17.8	14.0	20.8	1.3	0.9	2.9	32.4	27.7	21.7	2.7	5.4	8.0	13.0	7.6	10.8
Gentiana decora	Gentianaceae	F	N	--	1.3	1.8	--	2.5	1.1	--	2.5	0.9	--	1.1	--	--	0.6	1.4
Geranium maculatum	Geraniaceae	F	N	1.2	1.2	--	--	--	--	--	--	--	4.1	1.0	1.1	7.5	2.0	2.4
Geum sp.	Rosaceae	F	N	--	--	--	--	--	--	--	--	--	--	--	1.1	--	--	1.9
Geum virginianum	Rosaceae	F	N	--	--	--	--	--	--	--	--	--	--	0.5	--	--	--	--
Gillenia trifoliata	Rosaceae	F	N	--	0.9	1.2	--	0.9	0.8	--	--	--	--	0.5	1.0	--	--	--
Glyceria sp.	Poaceae	G	N	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0.5
Goodyera pubescens	Orchidaceae	F	N	1.0	0.9	1.1	--	0.9	0.8	--	--	--	1.3	0.5	--	--	--	--
Goodyera repens	Orchidaceae	F	N	0.8	--	--	--	--	--	--	--	--	1.0	--	--	--	--	--
Hamamelis virginiana	Hamamelidaceae	T	N	2.5	4.3	1.7	1.8	1.5	1.8	4.8	2.9	5.3	5.6	5.6	25.9	3.7	1.2	1.1
Heuchera sp.	Saxifragaceae	F	N	--	--	1.2	--	--	--	--	--	--	--	--	0.6	--	--	0.5
Heuchera americana	Saxifragaceae	F	N	--	1.0	--	--	--	--	--	1.0	--	--	0.5	--	--	--	--
Hieracium gronovii	Asteraceae	F	N	--	--	--	--	--	--	--	--	--	--	--	--	--	0.6	--
Hieracium paniculatum	Asteraceae	F	N	--	1.9	--	2.0	--	0.8	0.9	--	--	--	0.8	0.8	--	0.6	0.8
Hieracium venosum	Asteraceae	F	N	--	--	--	5.1	4.7	1.7	--	--	--	--	--	0.6	--	--	--
Holcus lanatus	Poaceae	G	Int	--	--	--	--	--	--	--	--	--	--	--	0.6	--	--	--
Houstonia longifolia	Rubiaceae	F	N	--	--	--	--	--	--	--	--	--	--	--	--	1.2	2.0	--
Houstonia purpurea	Rubiaceae	F	N	--	--	--	--	0.8	0.7	--	3.7	0.9	--	--	--	--	--	--

Species	Family																	
Hypericum hypericoides	Clusiaceae	F	N	--	--	--	--	--	--	--	--	--	--	--	--	--	1.6	0.9
Hypericum mutilum	Clusiaceae	F	N	--	--	--	--	--	--	--	--	--	--	--	--	--	0.4	--
Hypericum punctatum	Clusiaceae	F	N	--	--	--	--	--	--	--	--	--	--	0.5	--	--	--	0.6
Hypoxis hirsuta	Liliaceae	F	N	--	--	--	--	--	--	--	--	--	--	0.8	1.1	--	--	0.5
Ilex ambigua	Aquifoliaceae	T	N	--	--	--	0.9	--	--	--	--	--	--	--	--	2.4	--	--
Ilex montana	Aquifoliaceae	T	N	0.9	2.4	2.1	--	1.5	6.9	2.8	3.4	5.2	--	0.9	1.4	0.9	1.8	2.3
Ilex opaca	Aquifoliaceae	T	N	0.8	--	--	0.9	--	--	0.9	--	--	--	--	--	1.2	--	--
Ipomoea pandurata	Convolvulaceae	V	N	--	1.2	--	--	1.9	2.0	--	--	--	--	0.5	1.8	--	--	--
Ipomoea purpurea	Convolvulaceae	V	Int	--	--	--	3.5	--	--	--	--	--	1.3	--	--	--	--	--
Iris verna	Iridaceae	F	N	--	--	--	--	--	--	1.1	--	--	--	--	--	--	2.4	1.0
Isotria verticillata	Orchidaceae	F	N	1.8	--	--	--	--	--	2.2	2.1	1.1	1.5	0.7	--	3.4	--	--
Juncus sp.	Juncaceae	G	N	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0.5
Juncus effusus	Juncaceae	G	N	--	--	--	--	--	--	--	--	--	--	--	--	--	0.4	--
Juncus marginatus	Juncaceae	G	N	--	--	--	--	--	--	--	--	--	--	0.5	--	--	0.4	--
Juncus subcaudatus	Juncaceae	G	N	--	--	--	--	--	--	--	--	--	--	--	--	--	0.4	--
Juncus tenuis	Juncaceae	G	N	--	--	--	--	--	--	--	--	--	--	1.0	--	--	1.2	--
Kalmia latifolia	Ericaceae	S	N	3.3	1.8	12.0	--	--	--	1.3	1.0	2.1	6.7	1.9	--	1.5	4.6	4.5
Lactuca canadensis	Asteraceae	F	N	--	--	--	--	0.9	--	--	--	--	--	--	--	--	--	--
Laportea canadensis	Urticaceae	F	N	--	--	--	--	1.6	2.2	--	--	--	--	--	--	--	--	--
Lechea racemulosa	Cistaceae	F	N	--	--	--	--	--	--	--	--	--	--	1.0	--	--	0.6	--
Leersia virginica	Poaceae	G	N	--	--	--	--	--	--	--	--	--	--	--	--	--	0.8	--
Lespedeza sp.	Fabaceae	F	Unk	--	--	--	--	--	--	--	--	--	--	0.8	--	--	--	--
Lespedeza bicolor	Fabaceae	F	Int	--	--	--	--	--	--	--	--	--	--	0.8	--	--	--	--
Lespedeza cuneata	Fabaceae	F	Int	--	--	--	--	--	--	--	0.6	--	--	--	--	--	--	--
Lespedeza frutescens	Fabaceae	F	N	--	--	--	--	--	--	--	--	--	--	1.6	--	--	--	--
Lespedeza hirta	Fabaceae	F	N	--	--	--	--	2.1	--	--	--	--	--	0.8	--	--	1.2	--
Lespedeza procumbens	Fabaceae	F	N	--	--	--	--	--	--	--	--	--	--	--	--	--	0.4	1.2
Lespedeza repens	Fabaceae	F	N	--	--	--	--	--	--	--	--	--	--	0.8	--	--	--	--
Lilium michauxii	Liliaceae	F	N	--	--	--	--	--	--	--	--	--	--	0.8	--	--	0.4	--
Lindera benzoin	Lauraceae	S	N	--	1.9	--	0.9	--	--	--	--	--	--	0.5	2.6	--	--	--
Liriodendron tulipifera	Magnoliaceae	T	N	2.5	1.5	8.5	3.1	2.7	2.6	2.2	6.9	6.4	9.4	9.0	10.7	2.9	6.1	9.4
Lobelia inflata	Campanulaceae	F	N	--	--	--	--	--	--	--	0.6	--	--	5.3	--	--	7.8	--
Lobelia spicata	Campanulaceae	F	N	--	--	--	--	--	--	--	--	--	--	0.5	--	--	0.4	--
Lotus corniculatus	Fabaceae	F	Int	--	--	--	--	--	--	--	--	--	--	0.6	--	--	--	--
Ludwigia alternifolia	Onagraceae	F	N	--	--	--	--	--	--	--	--	--	--	0.5	--	--	0.4	--
Luzula echinata	Juncaceae	G	N	--	--	--	--	--	--	--	--	--	--	--	--	--	0.5	0.8
Lycopodium obscurum	Lycopodiaceae	F	N	--	--	--	--	--	--	--	--	--	12.6	1.4	1.6	--	--	--

Species	Family																	
Lysimachia quadrifolia	Primulaceae	F	N	2.3	1.0	--	1.4	0.9	0.8	1.9	1.6	0.9	2.2	1.7	0.7	2.7	1.1	1.1
Magnolia acuminata	Magnoliaceae	T	N	4.2	6.1	7.0	6.6	5.5	7.1	6.6	3.2	3.8	6.8	6.3	6.9	11.6	5.1	7.1
Magnolia fraseri	Magnoliaceae	T	N	4.9	5.4	10.7	3.5	8.1	8.4	9.8	6.7	9.1	8.0	9.9	20.6	16.7	4.8	17.6
Maianthemum racemosum	Liliaceae	F	N	3.2	2.1	2.5	2.5	2.3	1.9	3.0	1.9	1.1	3.5	1.5	1.3	3.4	1.4	1.2
Malus coronaria	Rosaceae	T	N	--	--	--	--	--	0.8	--	--	--	--	--	--	--	--	--
Medeola virginiana	Liliaceae	F	N	7.4	6.7	7.3	5.3	4.6	5.8	5.0	2.5	1.8	5.2	2.7	3.6	3.1	2.0	3.4
Melampyrum lineare	Scrophulariaceae	F	N	--	--	--	--	--	--	--	--	--	--	--	--	--	0.4	--
Mitchella repens	Rubiaceae	F	N	17.7	3.7	4.1	--	--	--	16.5	5.2	3.7	4.3	--	--	11.8	2.3	1.4
Monotropa uniflora	Monotropaceae	F	N	--	--	1.8	--	--	--	3.5	--	--	0.8	0.7	--	--	--	--
Muhlenbergia schreberi	Poaceae	G	N	--	--	--	--	--	--	--	--	--	--	0.7	--	--	--	--
Muhlenbergia tenuiflora	Poaceae	G	N	--	0.9	--	--	--	--	--	0.9	--	--	--	--	--	--	--
Nyssa sylvatica	Cornaceae	T	N	5.0	7.3	15.4	5.1	3.4	4.7	4.3	5.6	4.0	2.8	3.7	3.7	5.3	6.3	4.5
Oclemena acuminata	Asteraceae	F	N	--	--	--	2.2	--	--	--	1.7	3.6	--	--	--	1.9	1.4	1.4
Osmorhiza claytonii	Apiaceae	F	N	8.5	22.3	--	--	--	--	11.4	--	--	5.5	3.8	--	--	--	--
Osmunda cinnamomea	Osmundaceae	Fe	N	4.3	3.1	3.4	--	--	--	11.4	2.1	3.0	0.9	5.3	--	--	--	--
Osmunda claytoniana	Osmundaceae	Fe	N	8.5	22.3	4.8	--	--	--	11.4	--	--	5.5	3.8	5.8	--	--	--
Oxalis dillenii	Oxalidaceae	F	N	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0.5
Oxalis stricta	Oxalidaceae	F	N	--	--	--	--	--	--	--	--	--	--	--	--	--	0.7	1.3
Oxydendrum arboreum	Ericaceae	T	N	0.9	2.4	9.0	1.3	--	9.5	6.0	9.3	9.7	1.6	2.1	17.1	1.7	3.5	7.6
Oxypolis rigidior	Apiaceae	F	N	--	--	--	--	--	--	1.2	0.9	--	--	--	--	--	--	1.1
Panicum anceps	Poaceae	G	N	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0.5
Parthenocissus quinquefolia	Vitaceae	V	N	2.9	3.7	1.7	--	--	--	--	0.6	1.0	9.2	6.4	4.3	2.6	0.4	3.5
Phalaris arundinacea	Poaceae	G	N	--	--	--	--	--	--	--	--	--	--	--	--	--	2.0	--
Phegopteris hexagonoptera	Thelypteridaceae	Fe	N	--	--	--	--	1.6	--	--	--	--	--	--	--	--	--	--
Phytolacca americana	Phytolaccaceae	F	N	--	--	--	--	--	--	--	1.3	--	--	1.3	--	--	2.6	--
Pinus sp.	Pinaceae	T	N	--	--	--	--	--	1.7	--	--	--	--	--	--	--	--	--
Pinus rigida	Pinaceae	T	N	--	--	--	--	--	--	1.1	--	1.1	--	--	--	--	--	--
Pinus strobus	Pinaceae	T	N	--	--	--	1.3	--	0.8	3.1	6.2	5.1	2.4	--	--	--	--	--
Plantago rugelii	Plantaginaceae	F	N	--	--	--	--	--	--	--	--	--	--	--	--	--	0.5	--
Platanthera orbiculata	Orchidaceae	F	N	1.6	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Poa compressa	Poaceae	G	Int	--	--	--	--	--	--	--	--	--	--	--	--	--	0.4	--
Poa cuspidata	Poaceae	G	N	--	--	--	--	--	--	--	0.6	--	--	--	--	--	1.3	0.8
Poa pratensis	Poaceae	G	Int	--	--	--	--	--	--	--	--	--	--	--	--	--	4.6	--
Polygonatum biflorum	Liliaceae	F	N	2.1	2.0	1.5	3.6	3.8	2.5	1.9	1.1	1.1	3.0	1.2	1.8	3.1	1.1	1.1
Polystichum acrostichoides	Dryopteridaceae	F	N	10.0	--	3.7	27.9	18.0	17.3	--	--	--	4.3	--	1.5	--	--	0.8
Populus grandidentata	Salicaceae	T	N	--	--	--	--	--	--	--	0.6	--	--	--	--	--	--	--
Potentilla canadensis	Rosaceae	F	N	--	5.7	2.4	--	1.8	1.0	--	1.0	--	--	1.0	1.1	--	7.2	2.2

Species	Family																	
Potentilla simplex	Rosaceae	F	N	2.8	--	--	4.0	1.9	1.7	0.9	--	1.0	4.1	1.0	1.3	5.0	2.0	4.5
Prenanthes sp.	Asteraceae	F	N	2.1	2.9	2.0	6.7	4.0	4.6	3.0	1.7	--	3.7	2.2	1.2	4.9	2.0	2.4
Prosartes lanuginosa	Liliaceae	F	N	--	--	--	4.3	4.7	1.2	--	--	--	--	--	--	--	--	--
Prunus pensylvanica	Rosaceae	T	N	8.7	--	--	--	--	--	--	6.0	1.2	--	1.7	--	--	7.6	5.8
Prunus serotina	Rosaceae	T	N	6.1	5.6	5.2	4.7	2.5	2.6	5.8	4.3	5.0	3.2	1.9	2.4	2.9	3.1	3.2
Pseudognaphalium obtusifolium	Asteraceae	F	N	--	--	--	--	--	--	--	--	--	--	--	--	--	0.4	--
Pteridium aquilinum	Dennstaedtiaceae	Fe	N	1.0	0.9	--	2.1	4.7	6.1	2.9	1.6	1.4	2.7	2.7	1.4	--	1.7	1.2
Pycnanthemum sp.	Lamiaceae	F	N	--	--	--	--	--	--	--	--	--	--	--	0.6	--	--	--
Pycnanthemum incanum	Lamiaceae	F	N	--	--	--	--	--	--	--	--	--	--	0.5	--	--	--	--
Pyrola americana	Pyrolaceae	F	N	--	--	--	--	--	--	--	--	--	--	--	0.6	--	--	--
Quercus alba	Fagaceae	T	N	7.5	4.0	7.7	5.6	5.2	7.8	4.8	2.3	2.8	10.3	5.7	9.3	5.6	4.8	7.9
Quercus coccinea	Fagaceae	T	N	7.3	12.4	9.6	9.2	12.2	7.1	9.6	8.4	7.4	6.9	12.4	10.6	6.8	7.9	13.6
Quercus prinus	Fagaceae	T	N	6.6	4.9	14.3	9.8	8.3	13.5	10.3	5.9	10.5	21.7	11.0	11.5	7.6	3.0	8.0
Quercus rubra	Fagaceae	T	N	11.8	13.2	6.2	9.5	8.8	7.0	5.8	4.6	10.1	4.9	8.3	6.2	8.4	5.5	4.6
Quercus stellata	Fagaceae	T	N	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1.1
Quercus velutina	Fagaceae	T	N	3.5	4.3	4.8	11.8	9.9	5.9	9.3	5.4	11.8	7.3	2.5	5.4	4.7	4.0	9.3
Ranunculus recurvatus	Ranunculaceae	F	N	--	--	--	--	--	--	--	--	--	--	--	--	--	0.4	--
Rhododendron calendulaceum	Ericaceae	S	N	--	4.0	5.4	1.6	5.0	3.0	--	4.4	3.4	--	5.3	1.9	--	5.1	1.3
Rhododendron periclymenoides	Ericaceae	S	N	--	2.5	8.2	--	9.5	3.3	--	1.9	6.3	--	0.7	2.7	--	0.5	4.7
Rhus typhina	Anacardiaceae	T	N	--	--	--	--	--	--	--	1.0	--	--	--	--	--	--	--
Robinia pseudoacacia	Fabaceae	T	N	--	--	--	1.8	1.9	0.8	--	1.0	1.1	0.8	1.1	2.0	--	1.7	4.1
Rosa carolina	Rosaceae	S	N	--	2.7	1.2	--	6.4	3.3	--	0.6	1.1	--	1.6	0.9	--	0.4	1.5
Rosa multiflora	Rosaceae	S	Int	--	--	--	--	--	--	--	--	--	1.3	--	--	--	--	--
Rubus sp.	Rosaceae	S	Unk	--	--	--	--	--	1.3	--	--	1.5	--	--	6.9	--	--	2.6
Rubus allegheniensis	Rosaceae	S	N	--	3.7	--	--	1.1	--	2.4	4.7	1.6	--	5.0	1.9	--	5.6	2.7
Rubus canadensis	Rosaceae	S	N	--	--	--	--	1.6	4.6	14.1	25.3	13.8	--	17.3	8.1	1.9	29.8	24.8
Rubus flagellaris	Rosaceae	S	N	--	1.1	--	--	2.1	--	--	1.5	--	--	15.7	2.9	--	7.3	2.6
Rubus occidentalis	Rosaceae	S	N	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1.5
Rubus pensilvanicus	Rosaceae	S	N	--	--	--	--	--	--	--	--	--	--	--	--	--	--	3.0
Rumex acetosella	Polygonaceae	F	Int	--	--	--	--	--	--	--	--	--	--	--	--	--	0.6	--
Salix nigra	Salicaceae	T	N	--	--	--	--	--	--	--	--	--	--	--	--	--	--	4.5
Sassafras albidum	Lauraceae	T	N	14.9	10.7	5.4	15.8	13.3	12.7	11.8	10.7	12.8	9.7	12.4	11.4	12.2	7.8	5.8
Schedonorus phoenix	Poaceae	G	Int	--	--	--	--	--	--	--	0.6	--	--	2.6	0.6	--	6.3	0.5
Schizachyrium scoparium	Poaceae	G	N	--	--	--	--	--	--	--	--	1.1	--	--	--	--	--	--
Scutellaria elliptica	Lamiaceae	F	N	--	--	1.2	--	--	--	--	--	--	--	1.4	0.6	--	1.2	1.7
Sibbaldiopsis tridentata	Rosaceae	F	N	--	--	--	1.3	--	--	--	--	--	--	--	--	--	--	--
Smilax glauca	Smilacaceae	V	N	7.3	6.2	7.9	4.1	2.6	2.9	10.3	8.4	7.0	6.8	4.4	5.3	7.4	3.6	3.4

Species	Family																		
Smilax herbacea	Smilacaceae	F	N	1.5	1.3	1.1	--	1.7	1.4	1.2	1.1	0.9	0.8	1.4	0.9	2.7	1.1	1.3
Smilax rotundifolia	Smilacaceae	V	N	30.3	44.6	40.9	9.4	13.7	16.9	30.8	27.0	22.0	11.8	9.7	9.4	28.8	16.8	18.1
Solidago sp.	Asteraceae	F	N	--	--	2.1	--	--	--	--	--	1.1	--	--	0.6	--	--	1.1
Solidago altissima	Asteraceae	F	N	--	--	--	--	--	--	--	--	--	--	--	--	--	0.4	--
Solidago arguta	Asteraceae	F	N	--	1.0	1.2	--	--	--	--	--	--	--	--	1.7	--	0.4	2.0
Solidago bicolor	Asteraceae	F	N	--	--	--	--	--	0.8	--	--	--	--	--	--	--	--	0.5
Solidago caesia	Asteraceae	F	N	--	--	--	--	0.9	--	--	--	--	--	--	--	--	--	1.6
Solidago curtisii	Asteraceae	F	N	--	--	--	--	4.7	3.6	2.4	0.6	2.1	--	1.1	6.6	1.9	0.7	2.9
Solidago roanensis	Asteraceae	F	N	--	--	--	--	--	1.4	--	--	0.9	--	--	0.8	--	--	1.9
Stellaria pubera	Caryophyllaceae	F	N	1.8	1.9	1.2	4.1	6.3	2.4	2.1	--	--	5.6	2.4	1.4	1.1	0.5	--
Symphyotrichum lanceolatum	Asteraceae	F	N	--	1.0	--	--	--	--	--	--	--	--	--	--	--	--	--
Symphyotrichum pilosum	Asteraceae	F	N	--	--	--	--	--	--	--	--	--	--	--	--	--	0.4	--
Symphyotrichum undulatum	Asteraceae	F	N	--	1.0	--	--	--	0.8	--	--	--	--	--	0.6	--	1.2	0.5
Taenidia integerrima	Apiaceae	F	N	--	--	--	--	--	--	--	--	--	--	--	--	--	0.4	--
Taraxacum officinale	Asteraceae	F	Int	--	--	--	--	--	--	--	--	--	--	--	--	--	1.0	--
Thalictrum sp.	Ranunculaceae	F	N	--	--	--	--	--	--	--	--	--	1.0	0.5	1.1	--	--	--
Thelypteris noveboracensis	Thelypteridaceae	Fe	N	48.8	23.7	20.6	39.4	29.9	22.1	20.3	7.7	7.6	31.1	24.5	24.1	28.6	17.7	14.6
Toxicodendron radicans	Anacardiaceae	V	N	--	--	--	--	--	--	--	--	--	1.0	0.5	--	--	--	--
Trifolium campestre	Fabaceae	F	Int	--	--	--	--	--	--	--	--	--	--	--	--	--	0.4	--
Trifolium pratense	Fabaceae	F	Int	--	--	--	--	--	--	--	--	--	--	--	--	--	0.7	--
Trifolium repens	Fabaceae	F	Int	--	--	--	--	--	--	--	--	--	--	0.5	--	--	0.8	--
Trillium erectum	Liliaceae	F	N	--	--	--	--	--	--	--	--	--	--	0.6	--	--	--	--
Trillium undulatum	Liliaceae	F	N	10.6	6.1	2.9	--	1.9	0.7	2.4	1.5	1.1	4.3	0.5	0.8	1.9	0.6	1.0
Uvularia perfoliata	Liliaceae	F	N	3.5	3.7	--	--	--	--	--	--	--	6.1	2.4	3.3	1.8	--	0.5
Uvularia puberula	Liliaceae	F	N	3.7	2.7	3.1	3.5	2.8	2.1	4.7	2.8	1.8	2.7	1.3	1.1	3.0	1.5	1.7
Uvularia sessilifolia	Liliaceae	F	N	1.0	--	--	--	--	--	--	--	--	4.0	--	--	--	--	--
Vaccinium pallidum	Ericaceae	S	N	17.0	18.5	13.9	17.9	17.5	20.9	17.3	16.1	13.6	12.9	13.2	8.7	20.2	16.0	13.5
Vaccinium simulatum	Ericaceae	S	N	6.7	20.2	3.6	6.0	2.8	3.1	9.9	7.5	20.7	2.4	8.3	7.5	4.0	4.0	5.8
Vaccinium stamineum	Ericaceae	S	N	10.7	18.9	6.2	7.9	18.2	24.5	5.8	7.5	7.3	3.3	2.4	3.9	4.2	8.0	5.1
Verbascum thapsus	Scrophulariaceae	F	Int	--	--	--	--	--	--	--	--	--	--	--	--	--	0.4	0.8
Veronica arvensis	Scrophulariaceae	F	Int	--	--	--	--	--	--	--	--	--	--	--	--	--	0.8	--
Veronica officinalis	Scrophulariaceae	F	Int	--	--	--	--	--	--	--	--	--	--	--	--	--	3.2	1.0
Viburnum acerifolium	Caprifoliaceae	S	N	2.2	1.4	1.3	3.8	1.9	2.9	2.4	0.6	1.0	2.2	5.1	3.0	6.2	1.2	4.2
Viburnum prunifolium	Caprifoliaceae	S	N	--	--	--	--	0.9	--	--	--	--	--	3.1	--	3.7	1.2	2.4
Vicia caroliniana	Fabaceae	F	N	--	--	--	--	--	--	--	--	--	--	--	--	--	0.4	0.5
Viola sp.	Violaceae	F	N	--	--	1.5	--	--	1.1	--	--	1.1	--	--	2.2	--	--	1.6
Viola affinis	Violaceae	F	N	--	--	--	--	--	--	--	--	1.4	--	--	--	--	--	--

Species	Family																	
Viola blanda	Violaceae	F	N	--	--	--	2.2	2.0	3.9	--	1.7	4.3	--	2.5	2.4	--	4.3	4.2
Viola cucullata	Violaceae	F	N	--	--	--	--	--	--	4.7	--	--	--	--	--	--	--	--
Viola hastata	Violaceae	F	N	4.4	6.4	9.2	2.0	8.5	9.2	1.1	4.0	4.5	1.0	4.2	6.2	4.5	6.2	8.1
Viola hirsutula	Violaceae	F	N	--	1.0	1.2	--	1.9	0.8	2.4	--	--	--	2.4	2.2	9.5	5.1	2.4
Viola macloskeyi	Violaceae	F	N	--	--	--	--	--	--	--	--	1.2	--	--	1.4	--	--	--
Viola pedata	Violaceae	F	N	--	--	--	--	--	--	5.4	--	--	--	--	--	--	--	--
Viola rotundifolia	Violaceae	F	N	3.6	1.7	1.7	0.9	1.6	5.9	3.9	1.2	--	3.1	0.5	2.7	7.6	1.7	3.2
Viola sororia	Violaceae	F	N	--	4.7	0.9	--	8.1	1.1	1.2	2.9	2.2	--	3.2	3.1	--	1.9	1.5
Viola triloba	Violaceae	F	N	--	--	--	2.1	--	--	--	--	--	--	--	--	2.5	--	--
Vitis aestivalis	Vitaceae	V	N	6.9	2.5	--	4.3	2.6	2.1	2.3	4.0	4.7	4.4	8.2	3.8	1.8	4.8	2.9
Zizia aurea	Apiaceae	F	N	--	--	--	--	--	0.8	--	--	--	--	--	--	--	--	--
Zizia trifoliata	Apiaceae	F	N	--	0.8	--	1.6	1.9	--	--	--	--	--	0.5	--	--	--	--

APPENDIX E. RESISTANCE –RESILIENCE RELATIONSHIPS
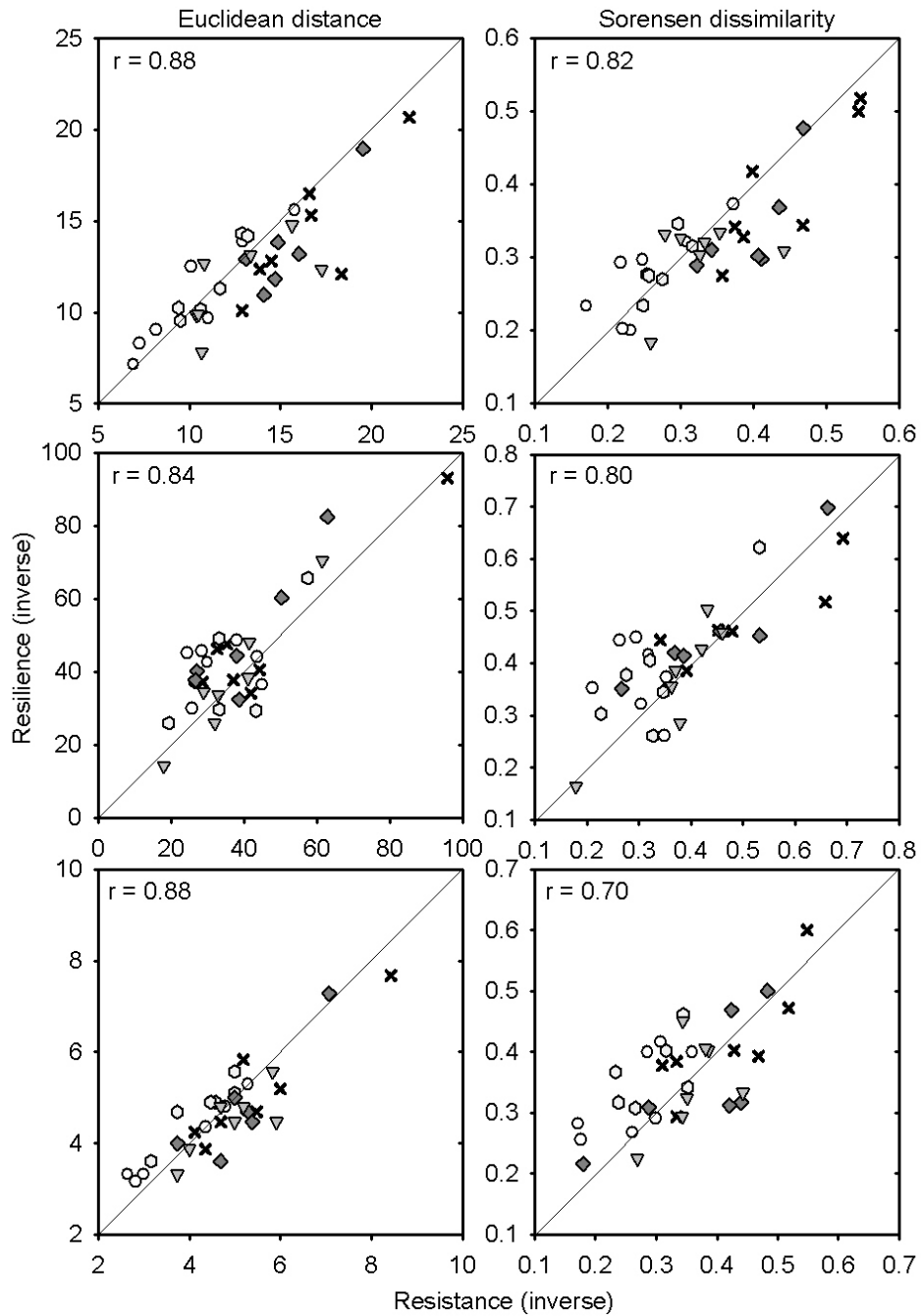
Appendix E. Relationship between resistance and resilience values of plots (top) and subplots using abundance (middle) or presence (bottom) with one-to-one line superimposed on figure. R-values are Pearson correlation coefficients, which were all significant ($P < 0.01$). Symbols are the same as described in Figure 5.3.

**APPENDIX F. RICHNESS, CHANGE IN EVENESS, AND RESISTANCE**

Appendix F. Relationship between pre-disturbance richness and change in evenness of subplots (1 m^2) following disturbance treatment application (top); change in evenness and resistance based on Euclidean distance (bottom left) and Sorensen dissimilarity index (bottom right). Dashed line is included to highlight subplots that increased or decreased in evenness. Species composition changed more as evenness decreased based on correlations between negative evenness values and ED (r = -0.70, p < 0.01) or SD (r = -0.64, p = 0.01) (bottom figures).
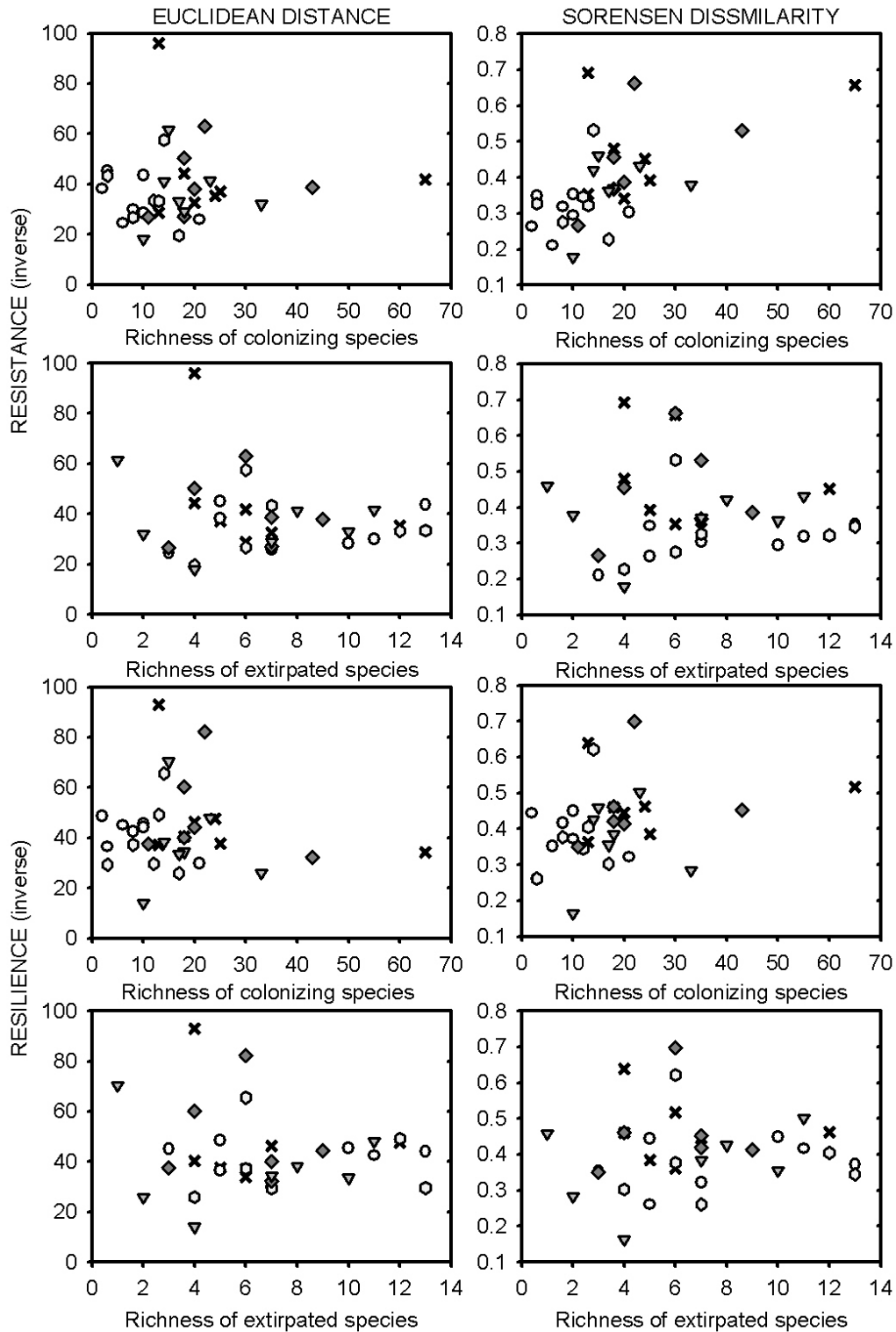
APPENDIX G. CORRELATIONS BETWEEN COLONIZATION, EXTIRPATION, AND STABILITY

Appendix G1. Spearman correlation coefficients relating the number of initial extirpated and colonized species (total and functional groups) one year after disturbance to resistance and resilience of community composition at 2 spatial scales as estimated by Euclidean distances (ED) and Sorensen dissimilarity index (SD). Bold values indicate significant correlations ($P < 0.05$). Plots showing relationships between all colonizers and extirpated species and resistance and resilience are in Appendix E1; subplot data are in Appendix E2.

		Plots (576 m^2)				Subplots (1 m^2)			
		Resistance		Resilience		Resistance		Resilience	
		ED	SD	ED	SD	ED	SD	ED	SD
Extirpated	All	-0.10	-0.13	0.07	-0.13	-0.02	0.00	0.02	0.08
	Trees	0.13	0.06	**0.46**	0.20	-0.02	-0.14	0.02	-0.08
	Shrubs	-0.18	**-0.35**	-0.11	-0.23	0.05	0.16	0.01	0.10
	Forbs	-0.23	-0.16	-0.23	-0.22	-0.04	-0.01	0.03	0.08
	Graminoids	-0.05	-0.17	0.24	-0.11	0.08	0.13	0.19	0.26
	Vines	0.10	0.20	0.02	0.13	-0.07	0.13	-0.18	0.04
	Ferns	0.00	-0.10	-0.13	-0.27	0.07	-0.17	0.10	0.03
Colonized	All	**0.91**	**0.83**	**0.72**	**0.71**	0.15	**0.63**	-0.02	**0.39**
	Trees	**0.46**	**0.60**	0.31	**0.61**	0.11	**0.45**	0.02	0.17
	Shrubs	**0.58**	**0.52**	**0.43**	**0.44**	**-0.47**	-0.02	-0.25	0.02
	Forbs	**0.89**	**0.75**	**0.80**	**0.74**	0.11	**0.52**	-0.02	0.34
	Graminoids	**0.82**	**0.86**	**0.44**	**0.45**	0.17	**0.56**	-0.04	0.33
	Vines	0.07	0.09	0.11	0.13	0.06	-0.03	-0.08	-0.12
	Ferns	**0.39**	**0.38**	0.17	0.19	0.22	0.28	0.25	0.24
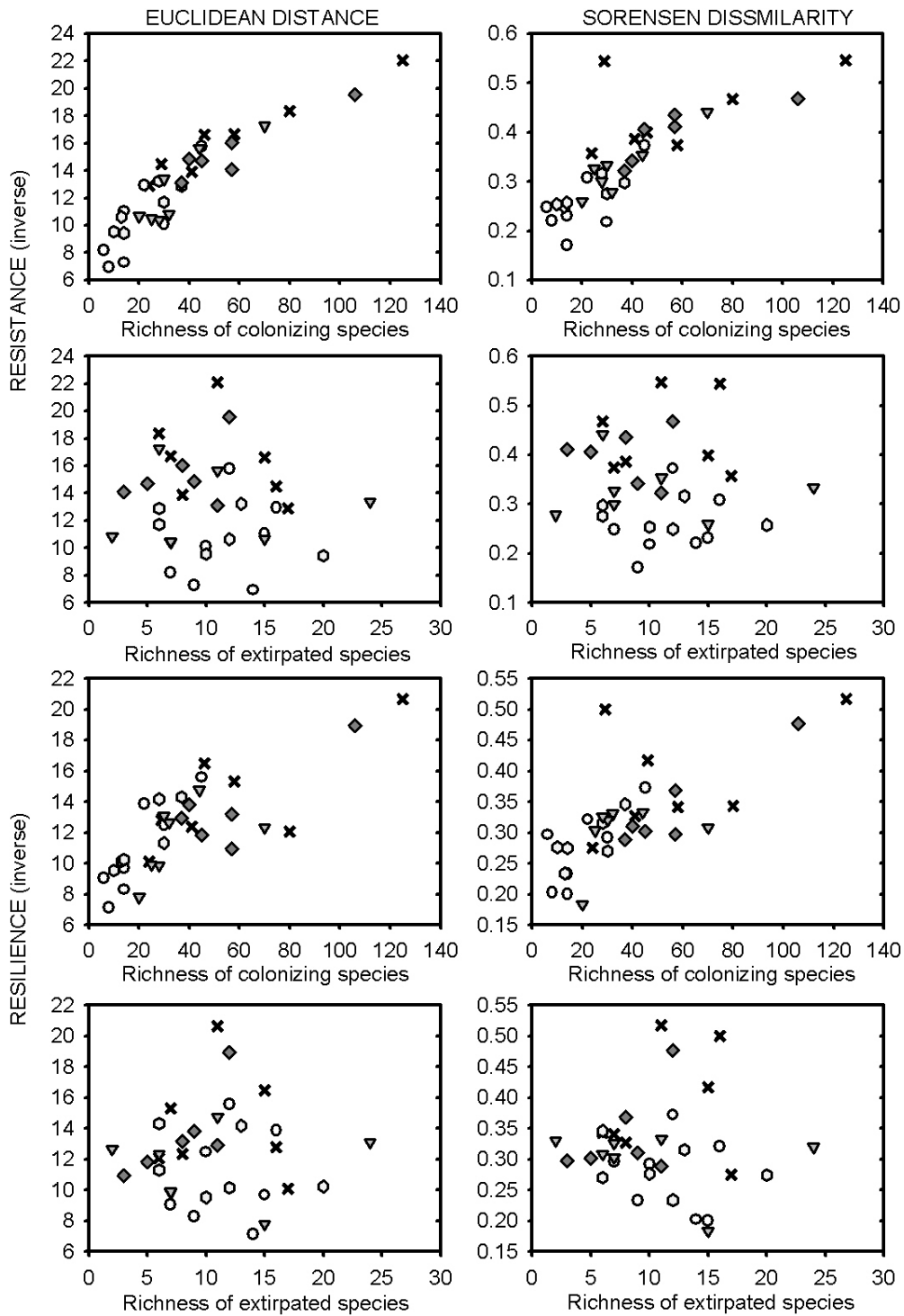
Appendix G2. Relationship between initial (i.e., 1 year) colonizing and extirpated species richness and resistance or resilience based on Euclidean distances or Sorensen dissimilarity index at the plot scale.

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Appendix G3. Relationship between initial (i.e., 1 year) colonizing and extirpated species

richness and resistance or resilience based on Euclidean distances or Sorensen dissimilarity index

at the subplot scale.