

PLANT COMMUNITY DYNAMICS FOLLOWING WILDFIRE IN THE SOUTHERN
APPALACHIANS: CHANGES IN DIVERSITY AT MULTIPLE SPATIAL SCALES

by

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(Under the Direction of Michael C. Wimberly)

ABSTRACT

This study investigates changes in species richness and species turnover from the local to landscape scale after fire in the southern Appalachians. Results show that proportional increases in species richness of all plants are independent of scale up to 400 m², but a lack of immigration from outside local communities limits species richness of trees at larger scales. High rates of survival and low rates of extinction after fire maintain patterns of spatial structure in local communities. Despite large changes in species richness, beta diversity and species turnover of all plants across the landscape showed little change. The importance of the underlying gradients that structure vegetation and the distribution of frequency of occurrence were not altered by fire. Although immigration of wind dispersed species affects species richness, dispersal limitation in dominant tree species maintains the spatial structure of communities and overall heterogeneity across the landscape.

INDEX WORDS: Wildfire, Disturbance, Southern Appalachians, Linville Gorge, Species-area curves, Beta diversity, Species turnover

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INTRODUCTION

The role of fire has been well documented in the maintenance of pine-oak dominated communities of the southern Appalachians (Van Lear and Waldrup 1989, Barden and Woods 1976). Fire eliminates competing understory vegetation and prepares the seed bed for the germination and establishment of pine seedlings (Collins and Good 1987, Gibson and Good 1987) that will eventually dominate the canopy and define community structure. Ignition of fires by lightning in the region is infrequent (Barden and Woods 1973, Harmon 1982) and it is accepted that ignition of fires by Natives Americans and European settlers maintained fire as part of the historic disturbance regime of the region until the late 1930's (De Vivo 1991, Delcourt and Delcourt 1998, Harrod et al. 1998, Harrod and White 1999).

The results of past fires are reflected in the prevalence of many pine-oak dominated forests in the southern Appalachians today (Harmon 1982). These communities are associated with drier mid-elevation slopes and ridges (Whittaker 1956). Though conspicuous parts of current forest canopies, it appears that these pine-oak communities are currently in decline, apparently as a result of fire suppression and encroachment of more fire sensitive species (Abrams 1992, Barden and Woods 1976, Williams and Johnson 1990, Waterman et al. 1995, Williams 1998). The decline in these community types threatens landscape diversity and has prompted an interest in the reintroduction of fire to the disturbance regime of the region (Welch and Waldrop 2001).

While the results of previous studies have been enlightening on the regeneration and perpetuation of the dominant tree species, only a few have addressed the role of fire on

understory diversity in local communities (Arthur et al. 1998, Ducey et al. 1996, Elliott et al. 1999). Although maintaining pine and oak in the canopy is an important structural component of forest communities (Platt et al. 1987), it is the understory that accounts for the majority of species diversity in southern Appalachian forests. Although descriptive in terms of general patterns of diversity, previous studies have been limited due to sampling using small plots that quantify at diversity at a single scale. Whether or not these results are consistent at larger scales within local communities is unknown. In order to manage and preserve species diversity in these communities it is essential to understand not only the patterns of change in species diversity, but also the processes that maintain them. The potential for different processes to be occurring at different scales (Schmida and Wilson 1985) suggests that changes in species richness may be scale dependent as far as direction and magnitude of change. Sampling across a range of spatial scales allows a comparison of changes at different scales and the assessment of how the processes that determine diversity are affected by fire.

The southern Appalachians have long been recognized for their exceptionally rich flora (Bartram 1792, Whittaker 1956). Although the role of environmental variables such as elevation, moisture, and soil nutrients have been identified as major gradients determining the spatial distribution of mature forest communities across the landscape (Whittaker 1956, Newell and Peet 1998), those studies investigating beta diversity and species turnover in the landscape have been limited to sampling only undisturbed mature forest types (Harmon et al. 1983). A few authors have predicted that beta diversity and species turnover decrease during early successional stages (Werner and Platt 1977, Christensen and Peet 1984) but few if any ecological studies have explicitly examined the effects of disturbance using pre and post-disturbance data

The objective of this study is to examine the effects of a wildfire fire on different types of floral diversity at the local and landscape level in the forests of the southern Appalachians and the processes that drive these changes. Chapter I consists of a literature review regarding fire in the southern Appalachians and the role of disturbance on different types of species diversity. Chapter II focuses on the effects of wildfire on diversity within local forest communities. At the local community level, scale dependence of changes in species richness is examined using species-area curves. The relative contributions of community level processes including immigration, local extinction, and survivorship are quantified and related to variation in fire severity. These analyses are done for all plants together and trees only. Chapter III focuses on the effects of a wildfire on communities across the landscape. At the landscape level the effects of fire on the relative importance of underlying environmental gradients is assessed. Changes in rates of species turnover across the landscape and beta diversity are compared pre- and postfire for all plants as well as among different growth forms. Results are then interpreted and applied to infer how fire affects the spatial heterogeneity of forest community types across the southern Appalachians.

Literature Cited

- Abrams, M.D. 1992. Fire and the development of oak forests. *Bioscience* 42: 346-353.
- Bartram, W. 1792. *Travels through North and South Carolina, Georgia, east and west Florida*. 1973. Beehive Press, Savannah, Georgia, U.S.A.
- Christensen, N.L. and R.K. Peet. 1984. Convergence during secondary forest succession. *Journal of Ecology* 72: 25-36.
- Barden, L.S. and F.W. Woods. 1973. Characteristics of lightning fires in southern Appalachian forests. *Proc. Annual Tall Timbers Fire Ecology Conference No. 13*: 345-361.
- Barden, L.S. and F.W. Woods. 1976. Effects of fire on pine and pine-hardwood forests in the southern Appalachians. *Forest Science* 22: 399-403.
- Collins, S.L. and R.E. Good. 1987. The seedling regeneration niche: habitat structure of tree seedlings in an oak-pine forest. *Oikos* 48: 89-98.
- Delcourt, P.A. and H.R. Delcourt. 1998. The influence of prehistoric human-set fires on oak-chestnut forests in the southern Appalachians. *Castanea* 63(3): 337-345.
- DeVivo, M.S. 1991. Indian use of fire and land clearance in the southern Appalachians. In: Nodvin, S.C., and T.A. Waldrup (Eds.), *Fire and the Environment: Ecological and Cultural Perspectives*. USDA For. Serv. Gen. Tech. Rep. SE-69.
- Gibson, D.J. and R.E. Good. 1987. The seedling habitat of *Pinus echinata* and *Melapyrum lineare* in oak-pine forests of the New Jersey Pinelands. *Oikos* 49: 91-100.
- Harmon, M.E. 1982. Fire history of the westernmost portion of Great Smoky Mountains National Park. *Bulletin of the Torrey Botanical Society* 109: 74-79.

- Harmon, M.E., S.P. Bratton, and P.S. White. 1983. Disturbance and vegetation response to environmental gradients in the Great Smoky Mountains. *Vegetation* 55: 129-139.
- Harrod, J.C., P.S. White, and M.E. Harmon. 1998. Changes in xeric forests of western Great Smoky Mountain National Park, 1936-1995. *Castanea* 63: 346-360.
- Harrod, J.C. and R.D. White. 1999. Age structure and radial growth in xeric pine-oak forests in the western Great Smoky Mountains National Park. *Bulletin of the Torrey Botanical Society* 126(2): 139-146.
- Arthur, M.A., R.D. Paratley, and B.A. Blankenship. 1998. Single and repeated fires affect survival and regeneration of woody and herbaceous species in an oak-pine forest. *Journal of the Torrey Botanical Society* 125:225-236.
- Ducey, M.J., W.K. Moser, and M.S. Ashton. Effect of fire intensity on understory composition and diversity in a *Kalmia*-dominated oak forest, New England, USA. *Vegetatio* 123: 81-90.
- Elliott, K.J., R.L. Hendrick, A.E. Major, J.M. Vose, and W.T. Swank. 1999. Vegetation dynamics after a prescribed fire in the southern Appalachians. *Forest Ecology and Management* 114: 199-213.
- Platt, W.J., G.E. Evans, and S.J. Rathburn. 1987. The population dynamics of a long-lived conifer (*Pinus palustris*). *American Naturalist* 131: 491-525.
- Newell, C.L. and R.K. Peet. 1998. Vegetation of Linville Gorge Wilderness, North Carolina. *Castanea* 63(3): 275-322.
- Schmida, A. and M.V. Wilson. 1985. Biological determinants of species diversity. *Journal of Biogeography* 12:1-20.

- Van Lear, D.H. and T.A. Waldrop. 1989. History and uses of fire in the Appalachians. U.S.D.A. Forest Service, Southeastern Forest Experiment Station, Gen. Tech. Rep SE-54.
- Waterman J.R., A.R. Gillespie, J.M. Vose, and W.T. Swank. 1995. The influence of mountain laurel on regeneration in pitch pine canopy gaps of Cowheeta Basin, North Carolina, USA. *Canadian Journal of Forest Research* 25: 1756-1762.
- Welch, N.T. and T.A. Waldrop. 2001. Restoring table mountain pine (*Pinus pungens* Lamb.) communities with prescribed fire: an overview of current research. *Castanea* 66: 42-49.
- Werner, P.A., and W.J. Platt. 1976. Ecological relationships of co-occurring goldenrods (*Solidago*: Compositae). *The American Naturalist* 110:959-970.
- Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. *Ecological Monographs* 26: 1-80.
- Williams, C.E. and W.C. Johnson. 1990. Age structure and maintenance of *Pinus pungens* in pine-oak forests of southwestern Virginia. *American Midland Naturalist* 124: 130-141.
- Williams, C.E. 1998. History and status of table mountain pine-pitch pine forests of the southern Appalachian mountains. *Natural Areas Journal* 17: 81-90.

CHAPTER I

LITERATURE REVIEW

Introduction

The southern Appalachians have long been recognized for their exceptionally rich flora (Bartram 1792, Whittaker 1956). Environmental variables such as elevation, moisture, and soil nutrients have been identified as major factors in determining the spatial distribution of communities across this landscape (Whittaker 1956, Day and Monk 1974, Newell and Peet 1998). However, studies of the effects of disturbance on species diversity have been more limited in scope. Most studies of disturbance in southern Appalachian forest communities have examined the role of canopy gaps in mesic cove forests (Hicks 1980, Bratton 1976, Runkle 1981, Meier et al. 1995, Busing and White 1997), where disturbance is due mainly to wind throw (Runkle 1981) and canopy gaps create opportunities for regeneration of the more shade intolerant species. Investigations into the role of disturbance on community structure and diversity have been limited on more xeric sites (Arthur et al. 1997, Elliott et al. 1999) where fire has historically been the major disturbance. Although disturbance regimes differ across environmental gradients in the southern Appalachians (Harmon et al. 1983), the differential response of individual species to disturbance gradients and the cumulative effects on community structure have yet to be examined. Understanding the role of fire in these pine-oak communities is essential in formulating sound management practices and to maintain and restore floristic diversity in the region.

Fire in the southern Appalachian mountains has historically been most frequent on mid-elevation slopes and ridges (Barden and Woods 1976, Harmon 1981, Van Lear and Waldrup 1989). These communities are dominated by several species of pine and oak, with pine becoming increasingly important as topographic moisture decreases (Whittaker 1956, Racine 1966). Although natural ignition of fires by lightning does occur (Barden and Woods 1974, Harmon 1982, Newell 1998), anthropogenic ignition by Natives American and European settlers was the primary source of fire in the region (De Vivo 1991, Delcourt and Delcourt 1998, Harrod et al. 1998, Harrod and White 1999). This fire regime was altered in the 1930's when a policy of fire suppression was adopted. Humans are still the main source of ignition in the region, but fires today are less frequent and generally much smaller than those of the past. As a result it appears that these pine-oak communities are currently in decline because of the encroachment of more fire sensitive species and a lack of regeneration in canopy dominants (Abrams 1992, Barden and Woods 1976, Williams and Johnson 1990, Waterman et al. 1995, Williams 1998).

Although previous studies have examined the effects of fire on the regeneration and perpetuation of the dominant tree species, only a few have addressed the impacts of fire on understory diversity (Ducey et al. 1996, Arthur et al. 1998, Elliott et al. 1999). Although maintaining pine and oak in forest canopies is important, the understory accounts for the majority of species diversity in southern Appalachian pine communities. Past studies have described general patterns of species diversity, but have been limited to sampling vegetation in small, fixed-size plots. Although results have shown that species richness increases in the years immediately following fire, the processes that drive observed increases are largely unknown, especially at larger spatial scales. There is a need for a multi-scale approach because responses may vary in magnitude and even direction if different processes are occurring at different scales

(Schmida and Wilson 1985). In addition, the effect of fire on compositional turnover amongst communities (beta diversity) has yet to be investigated.

Historical and Ecological Role of Fire in the southern Appalachians

Historical accounts suggest that from 10,000 years before present until the arrival of Europeans, forests in the southern Appalachians were subject to recurrent fire (Devivo 1991, Van Lear and Waldrup 1989). Natives burned valleys near settlements to clear land for agriculture (DeVivo 1991). In the surrounding mountains, upper slopes and ridges were selectively burned, presumably to promote wildlife and mast production (Devivo 1991, Delcourt and Delcourt 1997). It has been hypothesized that effects of pre-Columbian burning increased landscape heterogeneity by maintaining a variety of community types across the region (Delcourt and Delcourt 1998).

Fire remained an important component of the disturbance regime after European settlement (Harmon 1982). Although natural fires have occurred, lightning frequency in the southern Appalachians is much lower than that of the rest of the southeastern U.S. (Barden and Woods 1973). It is most likely anthropogenic fire associated with the clearing of land for agriculture and slash burning by settlers maintained a frequent fire regime after the removal of Native Americans (Barden and Woods 1976, Van Lear and Waldrup 1989). For some parts of the southern Appalachians the fire return frequency between 1856 and 1940 is estimated at about thirteen years (Harmon 1982). Around 1940 a successful policy of fire suppression was adopted by the US Forest Service, decreasing the amount of fire in the southern Appalachians. This policy has left many forest communities in a degraded state due to the accumulation of fuels in the shrub layer and the encroachment of more fire sensitive species such as red maple (*Acer*

rubrum) and blackgum (*Nyssa sylvatica*) (Abrams 1992, Barden and Woods 1976, Williams and Johnson 1990, Waterman et al. 1995, Williams 1998). With a few exceptions, the fires that have occurred have been small (less than 7 ha) and low in severity with few crown fires. In 1925 a wildfire near Johnson City, TN burned approximately 20,000 ha and in 1952 another wildfire near Erwin, TN burned 10,000 ha (Barden and Woods 1973). Attempting to restore historical processes and conditions, land managers are now facing issues dealing with the high risk of current fuel conditions, an increase in household density in rural areas (Zhang unpublished manuscript), and questions about the ecological implications of wildfire suppression and the use of prescribed burns as a management tool in the southern Appalachians.

The dominance of pine and oak in the canopies of many mature forests in the southern Appalachians is a legacy of pre-suppression fire regimes (Abrams 1992, Barden and Woods 1976, Harmon et al 1983, Harrod and White 1999). These communities are most prevalent on the xeric end of the moisture gradient on mid-elevation slopes and ridges where the shift from oak to pine dominated communities occurs mostly along a gradient of decreasing topographic moisture (Whittaker 1956, Racine 1966). Although factors associated with soil nutrient status and pH often correlate strongly with the distribution of species (Newell 1998), these variables may also be strongly influenced by the species themselves. Topographic moisture is primarily the result of physical factors that are independent of the species present at a site such as slope, aspect, and topographic complexity.

Pine communities of the southern Appalachians are dominated by three species distributed along an elevation gradient (Whittaker 1956). At lower elevations from 600-900 m Virginia pine (*Pinus virginiana*) is dominant. Virginia pine is common throughout its range and its cones open after maturing each year. At middle and upper elevations from 900-1200 m pitch

pine (*Pinus rigida*) and table mountain pine (*Pinus pungens*) occur. Of the three species, pitch and table mountain pine are of most concern from the standpoint of conservation. Table mountain pine is endemic to the Appalachians and both species rely almost entirely on fire for regeneration (Barden and Woods 1976, Williams 1998). Seedling establishment is associated with shallow litter and open canopies (Ledig and Little 1979, Williams and Johnson 1992). Pitch pine has the ability to sprout epicormically and though its cones are serotinous in the northern part of its range, cones in southern Appalachian populations are usually not (Williams 1998). The cones of table mountain pine are predominantly serotinous and generally open only after fire (McIntyre 1929). These species commonly occur in even-aged stands in the southern Appalachians, and are currently in decline because of fire suppression over the last century and encroachment of hardwood and shrub species (Harmon 1982, Williams and Johnson 1990, Waterman et al. 1995, Harrod and White 1999).

Concern for the regeneration of table mountain and pitch pine has been a major force behind the recent reintroduction of fire to the southern Appalachians with prescribed burning (Elliott et al. 1999, Waldrop and Brose et al. 1999, Welch et al. 2000). Although it is generally thought that stand-replacing fires are necessary to regenerate table mountain and pitch pine, results from recent prescribed fires suggest that moderate severity fires are sufficient to promote regeneration (Waldrop and Brose 1999, Welch et al. 2000, Welch and Waldrop 2001). Abundant regeneration is associated with the removal of the canopy and shrub layers, but complete removal of litter and duff are not necessary for successful seedling establishment. Similar results were found in an experimental greenhouse study where shade and depth of duff were manipulated (Waldrop et al. 2002).

In addition to its importance for pine regeneration in the southern Appalachians, fire is also hypothesized to be necessary in maintaining dominance of oak species in canopies of many eastern forests (Abrams 1992). On drier slopes below 1100 m, forest canopies are dominated by scarlet oak (*Quercus coccinea*) and chestnut oak (*Quercus montana*) (Whittaker 1956). Above 1100 m Northern red oak (*Quercus rubra*) and white oak (*Quercus alba*) are dominant. A current lack of oak regeneration in these community types has been attributed to the encroachment of fire sensitive hardwood and shrub species such as red maple (*Acer rubrum*) and blackgum (*Nyssa sylvatica*), and mountain laurel (*Kalmia latifolia*) (Harrod and White 1999, Shumway et al. 1999). These fire sensitive species are prominent in oak understories where fires have been suppressed for long periods of time and have the ability to resprout vigorously in the years following fire (Arthur et al. 1998, Elliott et al. 1999). Low intensity fires may also reduce litter depth and provide suitable substrate thought to be sufficient for oak regeneration (Collins and Good 1987) in addition to eliminating faster growing, thinner barked species (Harmon 1984).

Disturbance and Community Diversity

Disturbance plays an important role in the maintenance of species diversity in plant communities (Huston 1979, Runkle 1981, Denslow 1980a, Christensen 1985, Pickett and White 1985, Schnitzer and Carson 2001). Common agents of disturbance in forested landscapes include fires, windstorms, pathogen outbreaks, and floods. These disturbances interact with landscape patterns and are frequently spatially correlated with specific types of vegetation and the underlying environmental gradients that structure them, contributing to the patchiness and overall spatial heterogeneity of a landscape (White 1979, Harmon et al. 1983). The temporal

variability of disturbances further contributes to heterogeneity within communities, by creating stands of different ages and successional stages (Wimberly et al. 2000).

In addition to different types of disturbance that constitute the disturbance regime of a landscape, frequency, size, and severity of disturbance are important parameters to consider in predicting the ensuing patterns of succession (Turner et al. 1998). Frequency refers to the mean return interval or time between disturbance events. Frequencies of different types of disturbances may vary, but are often fairly predictable for a single type of disturbance in a particular ecosystem. For instance, some ecosystems have evolved under relatively short and predictable return intervals and show long term stability in community composition until the disturbance regime is disrupted (Glitzenstein et al. 1995). The size of a disturbance may be particularly important in directing succession if the disturbance is large enough to create dispersal limitation for recolonizing species. In this case species composition may relate poorly to environmental variables and depend more on the presence of species with high dispersal capacity in the local species pool (del Moral 1999). Severity tends to be patchy across landscapes and directly effects the spatial distribution of post disturbance residuals (Turner et al. 1997, Putz and Sharitz 1991). In some cases these surviving residuals will influence post-disturbance successional pathways by supplying propagules or inhibiting local regeneration of other species (Peterson and Pickett 1995).

In landscapes where fire is a part of the disturbance regime, frequency, size and severity are often related to endogenous factors within a particular community. The accumulation of fuels during long intervals between fire events will promote high fire intensities (Agee and Huff 1987). Short intervals between fires tend to result in low intensity burns because fuels are consumed before they can accumulate. In landscapes where there is a high degree of

fragmentation of forest types, fires covering large spatial extents are unlikely due to a lack of connectivity in fuels (Turner and Romme 1994). However, despite the importance of these factors in predicting frequency, size and severity, fire behavior is also closely linked to short-term weather variation (Bessie and Johnson 1995). Larger scale climatic patterns influence inter-annual patterns of drought, precipitation, and temperature (Harrison and Meindl 2001, Kitzberger 2002, Beckage and Platt 2003), and extreme weather conditions can override the constraints of landscape pattern on fire regimes.

Species Diversity

Whittaker (1960) discusses three types of species diversity to consider when investigating the diversity of a landscape. Alpha diversity is the number of species within a sample of a particular community and is most commonly referred to as species richness. Beta diversity is the rate of species turnover along a particular environmental gradient. The concept of beta diversity has more recently been extended to include species turnover with geographic distance (Condit et al. 2002). Alpha and beta diversity together comprise gamma diversity, or the total number of species in a landscape. Gamma diversity is almost impossible to measure due to physical limitations of sampling every habitat present and in most cases will be underestimated (Palmer 1990) due to the large number of rare species in a landscape. However, the concept itself has been applied to the total number of species in a collection of samples (Garcillan and Ezcurra 2003). To make accurate estimates of gamma diversity it is essential to know patterns of species richness at smaller scales where accurate samples can be feasibly attained, and the amount of turnover in species composition between samples. These metrics may be strongly influenced by

the frequency distributions of species and the spatial dispersion of conspecifics (Plotkin and Muller-Landau 2002).

Of the three, alpha diversity has received the majority of attention in the literature and is a major concern in conservation. The hypothesized mechanisms that promote and limit different levels of alpha diversity in plant communities are numerous and include niche partitioning through competition for limiting resources (Tilman 1982), dispersal limitation (Tilman 1994, Hurtt and Pacala 1995, Hubbell 1999) and large scale dynamics of immigration and extinction (MacArthur and Wilson 1967, Hubbell 2001). These hypotheses are not necessarily mutually exclusive and their relative importance depends on the spatial scale at which alpha diversity is observed (Schmida and Wilson 1985).

Species richness constitutes only one aspect of alpha diversity. In addition, species evenness takes into account the relative abundance of each species in a community. Evenness is often calculated using different equitability indices and can also be combined with richness into indices such as the Shannon-Weaver and Simpson diversity indices (Magurran 1988). The appropriateness of combining richness and evenness is subject to debate and it is often best to look at the two as separate measures (Peet 1974). Species richness and evenness can also be presented graphically in a dominance-diversity curves where species are ranked in decreasing order of abundance on the x-axis and plotted against abundance on the y-axis (Whittaker 1965).

Disturbance in natural communities promotes the coexistence of potentially competing species (Denslow 1985). Previous studies of the effects of fire on plant communities support this notion. In shrub-dominated communities, species richness (Keeley et al. 2003, Safford and Harrison 2004) and equitability (Christensen 1985) tend to be highest immediately after fire. Post-fire composition in these shrub communities is largely a reflection of resprouting vegetation

and species present in the seed bank (Christensen 1985, Moreno and Oechel 1991). Increases in species richness have also been observed after fire in forest communities (Ducey 1996, Arthur et al. 1998, Elliott et al. 1999, Keeley et al. 2003). In forest communities where fires are less frequent, species that maintain seed banks are less common and post-fire composition is largely reflective of those species that can resprout or disperse into burned areas (Turner et al. 1997). Changes in richness in the years following a fire are then a function of survival within and immigration from the periphery of an area. As a community reorganizes over time, there are also shifts in the presence and abundance of particular species and thus corresponding shifts in species richness and evenness (Shafi and Yarranton 1972, Denslow 1980b).

Although the causes of spatial variability in species richness are debatable, it has long been recognized that as grain of observation increases, the number of species encountered also increases (Rosenzweig 1995). This relationship between increasing species richness with increasing area is most easily seen by plotting a species-area curve with area on the x-axis and number of species on the y-axis. Although the species-area relationship may seem self-evident at first glance, its consistency in shape across different types of organisms all over the world is notable (Preston 1960, Cody 1975, Wright 1981).

The species-area relationship is most frequently fit to the power function, which in the southeastern United States provides a better fit than the often proposed Gleason function (Fridley et al. in press). This relationship was first proposed by Arrhenius (1921) and is as follows:

$$S=cA^z,$$

where S is the number of species in area A , and c and z are fitted constants. The relationship can be linearized by taking the natural log of both area and species richness. The constant z can then be interpreted as the slope of the relationship, or the rate of accumulation of species with

increasing area, and is thus important in controlling species richness at large scales. This slope parameter has been interpreted by some as a metric of beta-diversity (Caswell and Cohen 1993, Rosenzweig 1995, Hubbell 2001, Scheiner 2003). The constant c is the intercept of the line, or number of species per unit area. A standard biological interpretation of c has yet to be agreed upon though a few have been proposed. Rosenzweig (1995) demonstrates that c determines the rate of accumulation of species at fine scales below one unit of the area measure being used. Hubbell (2001) relates c to the density of individuals per unit of area by relating the power function to a species accumulation by individuals curve under the assumption that density is constant throughout all scales involved.

Despite its obvious importance in determining diversity at landscape scales, far less work has been done on understanding beta diversity than alpha diversity in natural communities. Since the inception of the idea by Robert Whittaker in 1960, beta diversity has received a relatively small amount of attention until recently (Tuomisto et al. 1995, Nekola and White 1999, Arita and Ridriguez 2002, Balvanera et al. 2002, Condit et al. 2002, Burnham 2004). Though several methods have been proposed for determining the rate of turnover of species (Velland 2001), a standardized method has not yet been agreed upon. The most recent studies on beta diversity have plotted community similarity versus environmental or geographic distance and interpreted beta diversity to be the slope of rate of decay in similarity (Nekola and White 1999, Cindut et al. 2002, Burnham 2004). In these cases increasing slope is indicative of higher species turnover and higher beta diversity.

Explanations of the causes of beta diversity have generally followed two lines of argument. Whittaker's original model of beta diversity was based upon the presence of strong environmental gradients that were the main underlying factors affecting the distribution of

species. The work of several other authors has confirmed the strong effect of environmental heterogeneity on beta diversity (Bratton 1975, Garcillan and Ezzcurra 2003), especially in tropical forests (Duivenvoorden 1995, Tuomisto 1995, Balanavera et al. 2002, Duivenvoorden et al. 2002, Potts et al. 2002). Other studies have investigated the decay in similarity among communities over geographic distance, drawing inferences on the role of dispersal in maintaining beta diversity (Nekola and White 1999, Condit et al. 2002, Potts et al. 2002).

Although space and environment are both important in structuring the distribution of species, these distributions are potentially very dynamic, especially in landscapes where large fires are part of the disturbance regime. The effects of disturbance on beta diversity have not been explicitly examined. Some authors have suggested that species in early successional communities show less of an affinity towards environmental conditions (Christensen and Peet 1984) and a higher degree of niche overlap (Werner and Platt 1976), potentially resulting in a decrease in beta diversity. However, if a disturbance was large and spatially heterogeneous due to variation in severity along environmental gradients, disturbance may reinforce the effects of environment and space on species distributions and increase beta diversity. The evidence behind either of these hypotheses remains to be seen.

Literature Cited

- Abrams, M.D. 1992. Fire and the development of oak forests. *Bioscience* 42: 346-353.
- Agee, J.K. and M.H. Huff. 1987. Fuel succession in a western Hemlock-Douglas fir forest. *Canadian Journal of Forest Research* 17: 697-704.
- Arita, H. and P. Rodriguez. 2002. Geographic range, turnover rate, and the scaling of species diversity. *Ecography* 25: 541-550.
- Arrhenius, O. 1923. Species and area. *Journal of Ecology* 9:95-99.
- Arthur, M.A., R.D. Paratley, and B.A. Blankenship. 1998. Single and repeated fires affect survival and regeneration of woody and herbaceous species in an oak-pine forest. *Journal of the Torrey Botanical Society* 125:225-236.
- Balvanera, P., E. Lott, G. Segura, C. Siebe, A. Islas. 2002. Patterns of beta diversity in a Mexican dry tropical forest. *Journal of Vegetation Science* 12: 145-158.
- Barden, L.S. and F.W. Woods. 1973. Characteristics of lightning fires in southern Appalachian forests. *Proc. Annual Tall Timbers Fire Ecology Conference No. 13*: 345-361.
- Barden, L.S. and F.W. Woods. 1976. Effects of fire on pine and pine-hardwood forests in the southern Appalachians. *Forest Science* 22: 399-403.
- Barden, L.S. 1977. Self-maintaining populations of *Pinus pungens* Lam. in the Southern Appalachian Mountains. *Castanea* 42: 316-323.
- Bartram, W. 1792. *Travels through North and South Carolina, Georgia, east and west Florida*. 1973. Beehive Press, Savannah, Georgia, U.S.A.
- Baskin, J.M. and C.C. Baskin. Endemism in rock outcrop plant communities of unglaciated eastern United States: an evaluation of the roles of edaphic, genetic, and light factors. *Journal of Biogeography* 15: 829-840.

- Beckage, B.B. and W.J. Platt. 2003. Predicting severe wildfire years in the Florida Everglades. *Frontiers in Ecology and the Environment* 1:235-239.
- Bessie, W.C. and E.A. Johnson. 1995. The relative importance of fuels and weather on fire behavior in subalpine forests. *Ecology* 76: 747-762.
- Bormann, F.H. and G.E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York, New York, USA.
- Bratton, S.P. 1975. A comparison of the beta diversity functions of the overstory and herbaceous understory of a deciduous forest. *Bulletin of the Torrey Botanical Club* 102: 55-60.
- Bratton, S.P. 1976. Resource division in an understory herb community: responses to temporal and microtopographic gradients. *The American Naturalist* 110(974): 679-693.
- Bray, J.R. and C.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27: 325-349.
- Brewer, J.S. and W.J. Platt. 1994. Effects of fire season and herbivory on reproductive succession a clonal forb, *Pityopsis graminifolia* (Mich.) Nutt. *Journal of Ecology* 82:665-675.
- Burnham, R.J. 2004. Alpha and beta diversity of lianas in Yasuni, Ecuador. *Forest Ecology and Management* 190: 43-55.
- Busing, R.T., and P.S. White 1997. Species diversity and small scale disturbance in an old-growth temperate forest: a consideration of gap partitioning concepts. *Oikos* 78:562-568.

- Caswell, H. and J.E. Cohen. 1993. Local and regional regulation of species area relations: a patch occupancy model. In *Species Diversity in Ecological Communities: historical and geographical perspectives*, ed. R. Ricklefs and D. Schluter, pp. 99-107. Chicago: University of Chicago Press.
- Christensen, N.L. and R.K. Peet. 1984. Convergence during secondary forest succession. *Journal of Ecology* 72: 25-36.
- Christensen, N.L. 1985. Shrubland fire regimes and their evolutionary consequences. In *The Ecology of Natural Disturbance and Patch Dynamics*, ed. S.T.A. Pickett and P.S. White, pp 85-100. Orlando, FL: Academic Press, Inc.
- Cody, M.L. 1975. Towards a theory of continental diversities: bird distributions over mediterranean habitat gradients. In *Ecology and Evolution of Communities*, ed. M.L. Cody and J.M. Diamond, pp. 214-257. Cambridge, MA: Belknap Press of Harvard University Press.
- Collins, S.L and R.E. Good. 1987. The seedling regeneration niche: habitat structure of tree seedlings in an oak-pine forest. *Oikos* 48: 89-98.
- Condit, R., N. Pitman, E.G. Leigh Jr., J. Chave, J. Terborgh, R.B. Foster, P. Nunez V., S. Aguilar, R. Valencia, G. Villa, H.C. Muller-Landau, E. Losos, and S.P. Hubbell. 2002. Beta-diversity in tropical forests. *Science* 295: 666-669.
- Davis, M.B. Old growth in the east: A survey. *Wild Earth*. Richmond, VT.
- Day, F.P. and C.D. Monk. 1974. Vegetation patterns on a southern Appalachian watershed. *Ecology* 55: 1064-1074.
- Delcourt, P.A. and H.R. Delcourt. 1997. Pre-Columbian Native American use of fire on southern Appalachian landscapes. *Conservation Biology* 11: 1010-1014.

- Delcourt, P.A. and H.R. Delcourt. 1998. The influence of prehistoric human-set fires on oak-chestnut forests in the southern Appalachians. *Castanea* 63(3): 337-345.
- del Moral, R. 1999. Plant succession on pumice at Mt. St. Helens. *American Midland Naturalist* 141: 101-114.
- Denslow, J.D. 1980a. Gap partitioning among tropical forest trees. *Biotropica* 12: 47-55.
- Denslow, J.D. 1980b. Patterns of species diversity during succession under different disturbance regimes. *Oecologia* 46: 18-21.
- Denslow, J.D. 1985. Disturbance-mediated coexistence of species. In *The Ecology of Natural Disturbance and Patch Dynamics*, ed. S.T.A. Pickett and P.S. White, pp 317-323. Orlando, FL: Academic Press, Inc.
- DeVivo, M.S. 1991. Indian use of fire and land clearance in the southern Appalachians. In: Nodvin, S.C., and T.A. Waldrup (Eds.), *Fire and the Environment: Ecological and Cultural Perspectives*. USDA For. Serv. Gen. Tech. Rep. SE-69.
- Ducey, M.J., W.K. Moser, and M.S. Ashton. Effect of fire intensity on understory composition and diversity in a *Kalmia*-dominated oak forest, New England, USA. *Vegetatio* 123: 81-90.
- Elliott, K.J., R.L. Hendrick, A.E. Major, J.M. Vose, and W.T. Swank. 1999. Vegetation dynamics after a prescribed fire in the southern Appalachians. *Forest Ecology and Management* 114: 199-213.
- Elliott, K.J., J.M. Vose, B.D. Clinton, and J.D. Knoepp. Effects of understory burning in a mesic mixed-oak forest of the southern Appalachians. *In Press*.
- Foster, D.R. 1982. The history and pattern of fire in the boreal forest of southeastern Labrador. *Canadian Journal of Botany*. 61: 2459-2471.

- Fridley, J.D., R.K. Peet, T.R. Wentworth, and P.S. White. 2004. Connecting fine-and broad-scale patterns of species diversity: species-area relationships of southeastern U.S. flora. *In press*.
- Garcillan, P.P. and E. Exequiel. 2003. Biogeographic regions and β -diversity of woody dryland legumes in the Baja California peninsula. *Journal of Vegetation Science* 14: 859-868.
- Gibson, D.J. and R.E. Good. 1987. The seedling habitat of *Pinus echinata* and *Melapyrum lineare* in oak-pine forests of the New Jersey Pinelands. *Oikos* 49: 91-100.
- Gilliam, F.S. and N.L. Christensen. 1986. Herb layer response to burning in pine flatwoods of the lower coastal plain of South Carolina. *Bulletin of the Torrey Botanical Club* 113: 42-45.
- Glitzenstein, J.S., W.J. Platt, and D.R. Streng. 1995. The effects of fire regime and habitat on tree dynamics in North Florida longleaf pine savannahs. *Ecological Monographs* 65: 441-476.
- Harmon, M.E. 1982. Fire history of the westernmost portion of Great Smoky Mountains National Park. *Bulletin of the Torrey Botanical Society* 109: 74-79.
- Harmon, M.E., S.P. Bratton, and P.S. White. 1983. Disturbance and vegetation response to environmental gradients in the Great Smoky Mountains. *Vegetation* 55: 129-139.
- Harmon, M.E. 1984. Survival of trees after low-intensity surface fires in Great Smoky Mountains National Park. *Ecology* 65: 796-802.

- Harrison, M. and C.F. Meindl. 2001. A statistical relationship between El-Niño Southern Oscillation and Florida wildfire occurrence. *Physical Geography* 22: 187-203.
- Harrod, J.C., P.S. White, and M.E. Harmon. 1998. Changes in xeric forests of western Great Smoky Mountain National Park, 1936-1995. *Castanea* 63: 346-360.
- Harrod, J.C. and R.D. White. 1999. Age structure and radial growth in xeric pine-oak forests in the western Great Smoky Mountains National Park. *Bulletin of the Torrey Botanical Society* 126(2): 139-146.
- Heinselman, M.L. 1973. Fire in the virgin forest of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research*. 3:329-382.
- Hicks, D.J. 1980. Intrastrand distribution patterns of southern Appalachian cove forest herbaceous species. *The American Midland Naturalist* 104(2): 209-223.
- Hiers, K.J., R. Wyatt, and R.J. Mitchell. 2000. The effects of fire regime on legume reproduction in longleaf pine savannahs: is a season selective? *Oecologia* 125: 521-530.
- Hubbell, S.P. 2001. *The Unified Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, New Jersey, USA
- Hurtt, G.C and S.W. Pacala. 1995. The consequences of recruitment limitation: Reconciling chance, history, and competitive differences between plants. *Journal of Theoretical Biology* 176: 1-12.
- Huston, M.A. 1979. A general hypothesis of species diversity. *American Naturalist* 113: 81-101.

- Kitzburger, T. 2002. ENSO as a forewarning tool of regional fire occurrence in northern Patagonia, Argentina. *International Journal of Wildfire* 11: 33-39.
- Ledig, F.T. and S. Little. 1979. Pitch pine (*Pinus rigida* Mill.): ecology, physiology, and genetics. Pp. 347-371 in R.T.T. Forman, ed., *Pine Barrens: Ecosystem and Landscape*. Academic Press, New York. 601 p.
- MacArthur, R.H. and Wilson, E.O. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey, USA
- Magurran, A.E. 1988. *Ecological Diversity and its Measurement*. Princeton University Press, Princeton, NJ.
- McIntire, A.C. 1929. A cone study of the mountain pine (*Pinus pungens* Lambert). *American Journal of Botany* 16: 402-406.
- Miller, T.E. 1982. Community diversity and interactions between size and frequency of disturbance. *American Naturalist* 120:533-536.
- Moreno, J.M. and W.C. Oechel. 1991. Fire intensity effects on germination of shrubs and herbs in southern California chaparral. *Ecology* 72: 1993-2004.
- Nekola, J.C. and P.S. White. 1999. The decay of similarity in biogeography and ecology. *Journal of Biogeography* 26: 867-878.
- Newell, C.L. 1997. Local and regional variation in the vegetation of the southern Appalachian Mountains. Ph.D. dissertation. Curriculum in Ecology, University of North Carolina at Chapel Hill. 1,008 p.
- Newell, C.L. and R.K. Peet. 1998. Vegetation of Linville Gorge Wilderness, North Carolina. *Castanea* 63(3): 275-322.

- Palmer, M. W. 1990. The estimation of species richness by extrapolation. *Ecology* 71: 1195-1198.
- Peet, R.K. 1974. The measurement of species diversity. *Annual Review of Ecological Systematics* 5: 285-307.
- Peet, R.K., T. R. Wentworth, and P.S. White. 1998. A flexible multipurpose method for recording vegetation composition and structure. *Castanea* 63: 262-274.
- Peterson, C.J. and S.T.A. Pickett. 1995. Forest reorganization: a case study in an old-growth forest catastrophic blowdown. *Ecology* 76: 763-774.
- Platt, W.J., G.E. Evans, and S.J. Rathburn. 1987. The population dynamics of a long-lived conifer (*Pinus palustris*). *American Naturalist* 131: 491-525.
- Plotkin, J.B. and H.C. Muller-Landau. 2002. Sampling the species composition of a landscape. *Ecology* 83(12): 3344-3356.
- Pickett, S.T.A. and P.S. White. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.
- Potts, M.D., P.S. Ashton, L.S. Kaufman, and J.B. Plotkin. 2002. Habitat patterns in tropical rain forests: a comparison of 105 plots in northwest Borneo. *Ecology* 83: 2782-2797.
- Putz, F.E. and R.R. Sharitz. 1991. Hurricane damage to old-growth forest in the Congaree Swamp National Monument, South Carolina, U.S.A. *Canadian Journal of Forest Research* 21:1765-1770.
- Racine, C.H. 1966. Pine communities and their site characteristics in the Blue Ridge Escarpment. *Journal of the Elisha Mitchell Society* 82: 172-181.

- Rosenzweig, M.L. *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, UK.
- Runkle, J.R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62: 1041-1051.
- Scheiner, S.A. 2003. Six types of species-area curves. *Global Ecology and Biogeography* 12: 441-447.
- Schmida, A. and M.V. Wilson. 1985. Biological determinants of species diversity. *Journal of Biogeography* 12:1-20.
- Schnitzer, S.A. and W.P. Carson. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* 82: 913-919.
- Shafi, M.I. and Yarranton, G.A. 1973. Diversity, floristic richness, and species evenness during a secondary (post-fire) succession. *Ecology* 54(4): 897-902.
- Shumway, D.L., M.D. Abrams, and C.M. Ruffner. 2001. A 400-year history of fire and oak recruitment in an old-growth forest western Maryland, U.S.A. *Canadian Journal of Forest Research* 31: 1437-1443.
- Tuomisto, H., K. Ruokolainen, R. Kalliola, A. Linna, W. Danjoy, and A. Rodriguez. 1995. Dissecting Amazonian biodiversity. *Science* 269: 63-66.
- Turner, M.G. and W.H. Romme. 1994. Landscape dynamics in crown fire ecosystems. *Landscape Ecology* 9: 59-77.
- Turner, M.G., W.L. Baker, C.J. Peterson, and R.K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems* 1: 511-523.

- Turner, M.G., W.H. Romme, and R.H. Gardner. 1999. Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. *International Journal of Wildland Fire* 9(1): 21-36.
- Van Lear, D.H. and T.A. Waldrop. 1989. History and uses of fire in the Appalachians. U.S.D.A. Forest Service, Southeastern Forest Experiment Station, Gen. Tech. Rep SE-54.
- Velland, M. 2001. Do commonly used indices of β -diversity measure species turnover? *Journal of Vegetation Science* 12: 545-552.
- Vose, J.M, W.T. Swank, B.D. Clinton, J.D. Knoepp, and L.W. Swift. 1999. Using stand replacement fires to restore southern Appalachian hardwood ecosystems: effects on mass, carbon, and nutrients. *Forest Ecology and Management* 114: 215-226.
- Waldrop, T.A. and P.H. Brose. 1999. A comparison of fire intensity levels for stand replacement of table mountain pine (*Pinus pungens* Lamb.). *Forest Ecology and Management* 113:155-166.
- Waldrop, T.A., P.H. Brose, N.C. Welch, H.H. Mohr, E.A. Gray, F.H. Tainter, and L.E. Ellis. 2002. High-intensity fires may be unnecessary for stand replacement of table mountain pine: an overview of current research. Pp. 137-142 in Outcalt, K.W., ED. 2002. Proceedings of the eleventh biennial southern silvicultural research conference. Gen. Tech. Rep SRS-48. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 622 p.

- Waterman J.R., A.R. Gillespie, J.M. Vose, and W.T. Swank. 1995. The influence of mountain laurel on regeneration in pitch pine canopy gaps of Cowheeta Basin, North Carolina, USA. *Canadian Journal of Forest Research* 25: 1756-1762.
- Welch, N.T., T.A. Waldrop, and E.R. Buckner. 2000. Response of southern Appalachian table mountain pine (*Pinus pungens*) and pitch pine (*P. rigida*) stands to prescribed burning. *Forest Ecology and Management* 136: 185-197.
- Welch, N.T. and T.A. Waldrop. 2001. Restoring table mountain pine (*Pinus pungens* Lamb.) communities with prescribed fire: an overview of current research. *Castanea* 66: 42-49.
- Werner, P.A. and W.J. Platt. 1976. Ecological relationships of co-occurring goldenrods (*Solidago*: Compositae). *The American Naturalist* 110: 959-971.
- White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. *Botanical Review* 45: 229-299.
- Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. *Ecological Monographs* 26: 1-80.
- Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30: 279-338.
- Whittaker, R.H. 1965. Dominance and diversity in land plant communities. *Science* 147: 250-260.
- Whittaker, R.H. 1972. Evolution and the measurement of species diversity. *Taxon* 21: 213-251.

- Williams, C.E. and W.C. Johnson. 1990. Age structure and maintenance of *Pinus pungens* in pine-oak forests of southwestern Virginia. *American Midland Naturalist* 124: 130-141.
- Williams, C.E. and W.C. Johnson. 1992. Factors affecting the recruitment of *Pinus pungens* in the southern Appalachian mountains. *Canadian Journal of Forest Research* 22: 878-887.
- Williams, C.E. 1998. History and status of table mountain pine-pitch pine forests of the southern Appalachian mountains. *Natural Areas Journal* 17: 81-90.
- Wimberly, M.C., T.A. Spies, C.J. Long, and C. Whitlock. 2000. Simulating historical variability in the amount of old forests in the Oregon Coast Range. *Conservation Biology* 14: 167-180.
- Wiser, S.K., R.K. Peet, and P.S. White. 1996. High-elevation rock outcrop vegetation of the southern Appalachian Mountains. *Journal of Vegetation Science* 7: 703-722.
- Wright, S.J. 1981. Intra-archipelago vertebrate distributions: the slope of the species-area relation. *American Naturalist* 118:726-748.
- Zobel, D.B. 1969. Factors affecting the distribution of *Pinus pungens*, and Appalachian endemic. *Ecological Monographs* 39: 303-333.

CHAPTER II

**WILDFIRE EFFECTS ON SPECIES RICHNESS AT MULTIPLE SPATIAL SCALES IN
FOREST COMMUNITIES OF THE SOUTHERN APPALACHIANS¹**

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Abstract

- 1.** We examined changes in the parameters of species-area curves fit to the power function to quantify changes in species richness of all plants together and trees only over five scales of magnitude (0.01 m² to 400 m²) after a wildfire in the Linville Gorge Wilderness Area, NC.
- 2.** Species richness of all plants increased at all scales after the fire, but increases were much greater in magnitude as scale increased. Despite these changes in absolute richness, a lack of change in the slopes (*z*-values) of species-area curves indicates that proportional changes were independent of scale of observation within the range of those included in our study.
- 3.** Increases in species richness of all plants at the 400 m² scale were driven by the immigration of herbaceous species coupled with high survival of tree and shrub species. Immigration was significantly related to fire severity, but neither survival nor local extinction of species present prefire was related to severity.
- 4.** Tree species richness increased at all spatial scales. However, proportional increases were smaller at larger scales and the slopes (*z*-values) of species-area curves decreased. Relatively low rates of immigration limited increases in richness at the 400 m² scale and were significantly related to severity. Survival was greater than local extinction but neither was related to severity.
- 5.** Although fire increases plant species richness within local communities, local recruitment of tree seedlings at small scales and immigration of herbaceous species at large scale maintain patterns of beta diversity and rates of spatial turnover. However, increases in tree species richness at small spatial scales and limited immigration at larger scales decreases beta diversity as there is more mixing of species in local forest communities.

Introduction

Disturbance plays a major role in structuring natural communities (Loucks 1970, Sousa 1984, Pickett and White 1985). Previous work in natural communities suggests that disturbance promotes the coexistence of species by reducing the dominance of strong competitors and allowing the establishment of less competitive species, increasing overall richness (Huston 1979, Denslow 1985). Although field studies of community response to natural disturbance generally support this prediction (e.g. Platt 1975, Connell 1978, Denslow 1980), most have been conducted at fairly small scales and few have examined whether results are consistent at larger scales. Those that have included observations at multiple scales show that results are frequently scale dependent (Schwilk et al. 1997, Glitzenstein et al. 2003, Keeley and Fotheringham 2003, Weiher and Howe 2003, Uys et al. 2004), but have only compared post-disturbance data from communities disturbed at different frequencies. A comparison of pre- and post-disturbance data enables one to examine the role of processes such as immigration, extinction, and survivorship that drive changes in species richness at the local community level (MacArthur and Wilson 1967).

A multiscale approach also provides insight into patterns manifest at one scale, but created by processes occurring at other scales (Levin 1992). Schmidha and Wilson (1985) provided one of the earliest conceptual models of how different processes determine species richness in plant communities at different spatial scales. At small scales ($< 1 \text{ m}^2$) competition and niche relations are major determinants of species richness. Provided that a more or less homogenous environment exists within an area, the importance of niche relations should not vary through space. At intermediate scales ($1\text{-}100 \text{ m}^2$) spatial heterogeneity is created by the presence of various microsites allowing for coexistence of species differing in resource requirements or

competitive abilities. This turnover, or differentiation diversity, is referred to by Schmid and Wilson as beta diversity following Whittaker (1960). Beta diversity will increase as competitive exclusion at small scales restricts species to sites where they are best suited. At larger scales ($>100 \text{ m}^2$), species richness is determined by mass effects (Schmid and Whittaker 1981). Mass effects occur when high propagule pressure from favorable source habitats results in the occurrence of species in sink habitats where they are unable to persist in the absence of immigration. The scale at which mass effects occur is determined by the dispersal abilities of species present in surrounding communities and the spatial distribution of species in relation to environmental heterogeneity across a landscape.

Multiple processes occurring simultaneously at different scales may result in scale-dependent patterns of change in species richness after disturbance. The magnitude and even direction of change may vary depending on the relative influences of the processes involved. At small scales ($<1 \text{ m}^2$) disturbance weakens the intensity of competition, and thus the importance of niche relationships. Platt (1975) found that localized disturbances approximately $0.2\text{-}0.3 \text{ m}^2$ created by digging badgers reduced direct competition and enabled coexistence in a guild of fugitive prairie plant species. At intermediate spatial scales ($1\text{-}100 \text{ m}^2$), species richness is constrained by habitat heterogeneity and the resulting patterns of beta diversity. Denslow (1980) suggested heterogeneous light resources in tropical forest gaps are partitioned among different species depending on their requirements for light. The relative importance of habitat heterogeneity after disturbance depends on the spatial pattern of the disturbance and the resulting changes in the physical environment. At scales where mass effects may be occurring ($>100 \text{ m}^2$) the effects of disturbance on the net changes in species richness will be dictated by how much extinction and immigration occurs within the local community. Mass effects are likely to be

prominent if there are many species in the surrounding landscape capable of dispersing large distances.

The use of species-area curves to assess the impacts of disturbance has proved to be a novel application of one of ecology's longest recognized patterns (Rosenzweig 1995) that has altered the interpretation of the role of disturbance in the maintenance of species diversity (Denslow 1995, Busing and White 1997, Hubbell et al. 1999). Species-area curves allow not only a comparison of species richness at multiple spatial scales before and after a disturbance, but also an assessment of change in the rate at which species richness increases with area. Although changes in species richness at a single scale have preoccupied past studies of disturbance, it is really the slope of the species-area relationship that determines species richness at larger scales. The most widely accepted equation used to fit species-area curves is the Arrhenius power function where:

$$S = cA^z$$

and S =the number of species, A = area, and the two fitted parameters, c and z are constants where c = species richness at one unit of area (α diversity) and z = the rate at which the number of species increases with area (β diversity) (Rosenzweig 1995, Hubbell 2001, Scheiner 2003). Assuming that disturbance will increase c (richness at small scales), there are three possible outcomes of changes in species richness at larger scales. If z increases, changes in richness will be positive at all scales, but the magnitude of increase will be greater at larger scales. If z decreases and a large enough range of scales has been sampled, then changes in richness will be equal at some intermediate scale and negative at large scales. If z remains the same, then increases will be proportionally equal across scales. Thus, an interpretation of how both c and z change after a disturbance will allow the prediction of both the direction and magnitude of

change in species richness, revealing insights into how processes occurring at different scales are affected by disturbance.

The objective of this study was to use species-area curves to determine if changes in plant species richness are consistent across scales after fire in southern Appalachian forests, and to infer how processes occurring at different spatial scales are affected by disturbance. The flora of the southern Appalachians has long drawn the attention of botanists and ecologists (Bartram 1792, Whittaker 1956, Runkle 1981). In the xeric pine and oak forests that cover the mid-elevation slopes and ridge tops of this region, fire has historically been the dominant disturbance, recurring every ten to twelve years during the 1800's (Barden and Woods 1973, Harmon 1984). Since the late 1930's most wildfires have been suppressed. Previous studies on the effects of fire on species richness have documented increases at single scales (Arthur et al. 1998, Elliott et al. 1999), but the roles of community level processes such as immigration and local extinction that are potentially driving observed patterns are largely unknown. One of the largest wildfires the region has experienced in last fifty years recently occurred in the Linville Gorge Wilderness, located in western North Carolina. The existence of a network of nested permanent plots ranging from 0.01 m² to 400 m² (Newell and Peet 1998) presents a unique opportunity to examine the role of natural disturbance in changes in species richness across five scales of magnitude.

We address three questions: 1) Are changes in species richness after fire at small scales consistent at larger scales? Increases in species richness at small scales can occur from recruitment of species present in the local community, but increases in richness at larger scale will depend on immigration of species from outside the local community. 2) What is the effect of fire severity on immigration, survival, and extinction in local communities? The relationship between these processes that drive changes in species richness and severity will be determined

by the number of species in the landscape with high capacity for dispersal and the degree of resilience exhibited by species in the pre-disturbance community. 3) Are patterns of change in trees the same as those for all species? Trees differ from other plants in their longevity, size, and capacity for dispersal and therefore are likely to show different postfire patterns of species richness than all plants together.

Methods

Study Site

Linville Gorge is a 4,390 ha federally designated wilderness area located in the Pisgah National Forest in Burke County, NC. Elevation ranges from 1250 m on upper ridges to 820 m at the bottom of the gorge. Upper and lower slopes are separated by prominent bluffs that bisect both sides of the gorge. As a result of downcutting from the Linville River, several types of parent material have been exposed. The plots chosen for this study were restricted to upper slopes occurring on the lower quartzite formation which is exposed by the bluffs and extends above to the ridge. Soils on the lower quartzite are generally thin and coarse, consisting primarily of Typhic or Lithic Dystrochep. Annual precipitation ranges from 1,250 to 1,625 mm and is highest in the summer months, occurring mostly as rain.

Because of the steep slopes and inaccessibility of the gorge, the vast majority of the landscape is old-growth and thought to be representative of pre-settlement forests (Davis 1996). Ridges and bluffs are dominated by *Pinus pungens*, *P. rigida*, and *P. virginia*. Slopes are dominated by *Quercus coccinea* and *Q. montana* with *Acer rubrum*, *Nyssa sylvatica*, and *Oxydendrum arboreum* in variable amounts. A thick layer of ericaceous shrubs including *Kalmia latifolia* and *Vaccinium* spp. is present throughout the slopes, ridges, and bluffs.

Sheltered moist coves and slopes are dominated by large *Tsuga canadensis* in the overstory and dense *Rhododendron maximum* in the shrub layer. See Newell and Peet (1998) for a detailed account of prefire vegetation. Evidence from fire scars and tree cores suggests that in the last 150 years Linville Gorge has been subject to several fires, varying in intensity and extent (C. Frost, unpublished data). Catastrophic crown fires occurred in 1860 and 1915. Several low intensity surface fires also occurred, but their extent and frequency of occurrence are unknown. Prior to 2000, the last widespread surface fire occurred in the 1950's. No subsequent fires occurred until November 2000 when an unattended campfire ignited a wildfire that burned over 2,000 ha within the wilderness boundaries.

Data Collection

A series of permanent plots was established and sampled in Linville Gorge in the summer of 1992 as part of a regional vegetation classification (Newell 1997, Newell and Peet 1998). Twenty-five of these plots were relocated and resampled during the summer of 2003. Twenty of the resampled plots burned in 2000 while the remaining five did not. The five unburned plots served as a control for any major changes in vegetation since the original sampling that may have been due to factors other than the fire. A preliminary analysis showed little or no change in species richness and composition in the unburned plots (M. Reilly, unpublished data). Thus, we concluded that the observed community dynamics in burned plots were attributable to fire effects and not to other changes occurring between 1992 and 2000. Subsequent analyses were focused on the 20 burned plots.

All plots were set up following the Carolina Vegetation Survey protocol (Peet et al. 1998), with nomenclature following Kartesz (1994). Each of the plots consisted of a set of 10 x 10 m² adjacent modules (Figure 2.1). Of the burned plots, seventeen consisted of four modules

(400 m²) and three consisted of two modules (200 m²). In each module two corners were sampled for the presence of all vascular plant species in a series of four nested quadrats increasing in size from 0.01 m² to 10 m². The rest of the 100 m² module was then searched for additional species. Canopy cover was estimated with a moosehorn densiometer in the four corners and center of each module and put into one of the following cover classes: trace, 0-1 %, 1-2 %, 2-5 %, 5-10 %, 10-25 %, 25-50 %, 50-75 %, 75-95 %, 95-100 %.

All trees, shrubs, and lianas taller than 1.4 m were measured and put into diameter at breast height (dbh) size classes (0-1 cm, 1-2.5 cm, 2.5-5 cm, 5-10 cm, 10-15 cm, ... 35-40 cm, >40 cm). Trees >40 cm dbh were measured to the nearest centimeter. Postfire tree sampling included measurement of both live and dead stems (standing and on the ground) to account for all stems found in 1992. These data were used to construct pre-fire basal area, providing a more accurate estimate of severity than using the prefire basal area because there was considerable growth in some plots between 1992 and 2003.

Data Analysis

Plots were classified into communities based on 1992 basal area using PC ORD. Basal areas were relativized by plot totals to account for the three smaller plots in the data set. The flexible beta group linkage method (beta=-.25) and Bray-Curtis distance measure were used in the cluster analysis. The dendrogram was cut at 2.2848, resulting in four groups corresponding with the classification of Newell and Peet (1998). These groups were then used as community classifications in subsequent analyses. A Kruskal-Wallis test was used to compare differences in reduction in basal area since data failed the equal variance test. Dunn's Test was then used for multiple pairwise comparisons of reduction in basal area among community types. A one way analysis of variance was used to compare levels canopy cover amongst the four community

types. Tukey's Test was then used for multiple pairwise comparisons of canopy cover among community types. All statistical analyses were carried out using SigmaStat 3.0

Pre- and postfire species-area curves were created for all plants and for trees only using nonlinear curve fitting in SigmaPlot 2000. For each plot, the mean number of species at each spatial scale (0.01 m², 0.1 m², 1.0 m², 10 m², 100 m², 400 m²) was fit to the power function:

$$S=cA^z$$

where S= # of species, A=area, and *c* and *z* are fitted constants. Plots were also grouped and pre- and postfire species-area curves were fit for each of the four community type.

We used paired *t*-tests to assess changes plot-level changes in *c* and *z* following fire, and linear regression to correlate changes in these parameters with fire severity. Fire severity was estimated as the percent reduction in basal area after the fire. To assess how heterogeneity in light levels was related to the accumulation of species with area, the standard deviation of the 20 canopy cover measurements from each plot was correlated with postfire *z* values using linear regression for all plants together and trees only. All species present in a plot pre- and postfire were separated into the number of survivors (species present pre- and postfire), immigrants (species present only postfire), and local extinctions (species present only prefire). We then used linear regression to investigate how the number of species that immigrated, survived, and went extinct locally was correlated with fire severity.

Results

Community Composition and Severity

Four community types were distinguished from the cluster analysis. Thermic pine forests (n=8) were dominated by varying amounts of *Pinus pungens*, *P. rigida*, and *P. virginia* in the

overstory. The midstory was dominated by *Kalmia latifolia* usually with the presence of some hardwood species including *Quercus coccinea*, *Acer rubrum*, and *Nyssa sylvatica*. Thermic oak forests (n=5) consisted of varying amounts of *Q. coccinea*, *Q. montana*, and *Q. alba*. *K. latifolia* was abundant in the midstory along with *Acer rubrum*, *P. strobus*, and *Oxydendrum arboreum*. Acidic slope forests (n=5) were dominated by *Q. montana*, *A. rubrum*, and *P. strobus*. The midstories were mixed, often with the presence of *K. latifolia*, *Rhododendron maximum*, and *Tsuga canadensis*. Acidic cove forests (n=2) were dominated by *Tsuga canadensis* in the overstory with a thick midstory of *Rhododendron maximum*.

The mean and standard deviation of reduction in basal area and canopy openness followed very similar patterns across communities (Figure 2.2). Both were highest in thermic pine and acidic cove communities. These two community types showed relatively little variability in severity and canopy openness. Acidic slopes had the third highest mean reduction in basal area and levels of canopy openness but had a high degree of variability. Thermic oak plots had the lowest reduction in basal area and the lowest amount of canopy openness. Significant differences among community types were found for reduction of basal area ($p=0.028$) and canopy openness ($p=0.001$). The only significant pairwise differences ($p<0.05$) in reduction in basal area and canopy cover existed only between thermic pine and thermic oak forest types. The reduction of basal area will be used synonymously with fire severity from here on because it is based on a comparison of pre- and post-disturbance conditions and is representative of the decrease in overstory dominance within a local community.

Changes in the Species-Area Relationship for All Plants

Community level species-area curves fit to the power function for all plant species showed that absolute changes in species richness at all scales were positive and increase in

magnitude with increasing scale (Figure 2.3). On a log-log scale, species area curves showed that although absolute increases in species richness were greatest at large scales, proportional increase were approximately equal across all scales (Figure 2.3). Changes were greatest in acidic cove and thermic pine communities where mean severity was high. Changes were smallest in the thermic oak communities where severity was generally low. Increases in species richness in acidic slope communities were intermediate in magnitude and showed a large amount of variability. Community level pre- and postfire comparisons of the fitted parameters c and z indicated that values of c increased but values of z changed very little (Table 2.1).

Pairwise t -tests between pre- and postfire values of c and z showed statistically significant increases in c ($p < 0.0001$) but no significant change in z values ($p = 0.11$). Changes in c were significantly and positively correlated with severity ($p < 0.001$, $r^2 = 0.46$) whereas no significant relationship was found between changes in z and severity ($p = 0.7572$, $r^2 = 0.005$) (Figure 2.4). There was also no statistically significant relationship between variability in canopy cover within a plot and postfire z values ($r^2 = 0.016$, $p = 0.5945$).

Changes in the Species-Area Relationship for Trees Only

Species-area curves for trees showed that absolute changes in species richness were positive at all scales (Figure 2.5). Although absolute increases in species richness were highest at large scales, log-log scale species-area curves showed that proportional increases were highest at small scales and decreased in magnitude with increasing scale (Figure 2.5). Changes were greatest in acidic cove and thermic pine forests where mean severity was high. Changes were smallest in the thermic oak communities where severity was generally low. Increases in species richness in acidic slopes were intermediate in magnitude and showed a great deal of variability. A comparison of the fitted parameters c and z from pre- and postfire species area curves for trees

indicated that values of c increased but values of z decreased (Table 2.1). Pairwise t -tests between pre- and postfire values of c and z showed statistically significant increases in c ($p < 0.0001$) and statistically significant decreases in z values ($p < 0.0001$). Changes in c were significantly and positively correlated with severity ($p = 0.0038$, $r^2 = 0.38$) whereas no significant relationship ($p = 0.1961$, $r^2 = 0.09$) was found between changes in z and severity (Figure 2.6). There was no relationship between variability in canopy cover within a plot and postfire z values ($r^2 = 0.033$, $p = 0.4421$).

Immigration, Survivorship, and Local Extinction

The number of local extinctions of all plants was low with a mean and standard deviation of 7.0 ± 3.9 species per plot. Tree extinction was also low at 2.25 ± 1.72 species per plot. Mean survivorship of all plants was higher than extinction at 20.5 ± 6.8 species per plot. Mean survivorship of trees was 8.75 ± 2.36 species per plot. Mean immigration of all plants was by far the greatest with a mean of 35.6 ± 19.5 species per plot. Immigration of trees was low with a mean and standard deviation of 7.4 ± 3.36 species per plot. Results of linear regression (Figure 2.7) indicated that for all plants immigration was positively and significantly related to severity ($p = 0.001$, $r^2 = 0.44$), whereas there was no relationship between severity and local extinction ($p = 0.95$, $r^2 = 0.016$) or survivorship ($p = 0.59$, $r^2 = 0.0003$). Immigration of trees was positively and significantly related to severity ($p = 0.001$, $r^2 = 0.46$), whereas there was no relationship between severity and local extinction ($p = 0.51$, $r^2 = 0.02$) or survivorship ($p = 0.32$, $r^2 = 0.05$) of trees (Figure 2.7).

Changes in diversity were driven mostly by herbaceous species, which comprised 66% of all immigrants. The family Asteraceae dominated forb immigration. The forb species with the highest rates of immigration were *Erechtites hieracifolia*, *Eupatorium rugosum*, *Solidago*

altissima, *Lactuca canadensis*, *Erigeron canadensis*, and *Erigeron canadensis* var. *pusilla*.

Graminoid immigration was dominated by *Andropogon virginicus* and several species of the genus *Dicanthelium*. *Dennstaedtia punctilobula* was the fern species with the highest rate of immigration. Tree species comprised 23 % of all immigrants with *Liriodendron tulipifera*, *Paulownia tomentosa*, *Betula lenta*, *Robinia pseudoacacia*, *Sassafras albidum*, and *Ilex montana* accounting for more than half of the trees. Shrubs and woody vines composed 11 % of all immigration. *Vitis aestivalis*, *Rubus argutus*, *Vaccinium corymbosum*, *Rubus alleghaniensis*, and *Robinia hispida* together composed over half of all the immigration of shrub species.

Most local extinctions were infrequent species that occurred in only a few plots. The one frequent species with a notable rate of local extinction was *Pinus strobus*. The only tree species that were lost from the whole sample were *Fagus grandifolia* and *Cornus florida*. The only shrub species that was lost from the whole sample was *Castanea dentata*, whose prefire presence was presumably due to stump sprouts. There were several herbaceous species that went locally extinct after the fire, but only a few were lost from the entire sample. Those that were lost from the sample and occurred in more than three plots included *Arisaema triphyllum* and *Maianthemum racemosum*.

Discussion

Effects of Fire on Species-Area Curves of all Plants

Changes in species richness of all plants are consistent across scales up to 400 m² after fire in the southern Appalachians. Despite considerable variation in severity and increases in absolute species richness ranging from just a few species to over 60 species, proportional changes were constant across five orders of magnitude as indicated by the lack of changes in the

slopes (z -values) of the species area curves. Our results suggest that it is equally important to include both z and c when examining the species area relationship (Rosenzweig 1995), and that although severity is important in predicting fire impacts on community diversity, these changes are generally independent of the scale of observation. Thus, fire in the southern Appalachians increases alpha diversity depending on severity, but has little effect on beta diversity and species accumulation rates at scales from 0.01 m² to 400 m².

The notion that spatial aggregation of conspecifics resulting from limited dispersal determines the rate of species turnover within local communities (Hubbell 1979, Condit et al. 2000) is supported by both theoretical models (He and Legendre 2002) and empirical data (Plotkin et al. 2000). The more clumped the distributions of species become, the steeper the slope of the species-area curve. As the degree of species mixing in space increases, the slope of the species-area curve decreases because most species will be found at smaller scales and few are added with more area. Though we did not map species distributions within plots, the lack of change in z supports the idea that the fire did not alter the spatial pattern and degree of species mixing as a whole. Hughes and Fahey (1991) similarly found that overstory removal in a northern hardwood forest had little effect on the spatial pattern of understory species, and that the location of predecessors before disturbance was a strong predictor of the spatial distribution of species after canopy removal. One possible explanation for a lack of changes in spatial distribution after disturbance lies in the patterns of survivorship, local extinction, and immigration.

The low rates of extinction in local communities indicated that most of those species present before the fire were also present afterward as surviving stems or resprouts, thus maintaining the prefire spatial distribution of individual species. Community composition

prefire was largely comprised of woody species, many of which are fire adapted. In thermic oak and acidic slope communities fire severity was mostly low to moderate. Several species which dominate these deciduous communities (*Quercus sp.*, *Acer rubrum*, *Nyssa sylvatica*, *Kalmia latifolia*, *Vaccinium sp.*) can survive low severity fire by resprouting from surviving underground root systems. Though fire severity and stem mortality in thermic pine forests was very high, postfire dominance of yellow pine species (*Pinus pungens*, *P. rigida*, and *P. virginiana*) was maintained by abundant seedling establishment from the canopy seed banks of either serotinous or persistent cones. In acidic cove forests where severity was high and prefire species richness was extremely low, the two dominant species, *Tsuga canadensis* and *Rhododendron maximum*, suffered very high mortality. The loss of these species, both ubiquitous and evenly distributed within the acidic cove plots, had little effect on turnover and the value of z .

Patterns of survivorship and mortality may account for the lack of change in z , but recruitment of local species at small scales (particularly trees) and immigration are primarily responsible for the change in c and increase in species richness at each scale. Most studies of species-area curves have focused little attention on c . It has generally been interpreted as the number of species at the scale of one unit at which the study is being conducted (α diversity) and there have been few biological interpretations of it. Rosenzweig (1995) suggests that c is more than just a coefficient, but is important in determining the initial rate at which species accumulate at fine scales before reaching one unit of area (1 m^2 in this study). A second biological interpretation of c relates the parameter specifically to the density of individuals. Hubbell (2001) relates species-individual curves to species-area curves under the assumption that the relationship between area and individuals increases linearly and density is constant. Starting with the power function $S=cA^z$, c is replaced with ρ , where ρ =the density of individuals and

$J=pA$, where J =the number of individuals. In this case the species-individual curve is predicted with the formula $S=J^c$. This allows for a density independent comparison the accumulation of species.

The two interpretations of c are not mutually exclusive, and to some extent actually support each other. If c increases because of higher richness at small scales, the effect can be attributed to an increase in density of individuals. Denslow (1995) suggested using the density hypothesis as a null model for looking at the effects of canopy gaps on diversity where species-accumulation curves are created by plotting number of species against number of individuals and comparing the slope with a species-area curve from the same data. Evidence that the density hypothesis explains increases in richness has been found in both temperate and tropical rain forest trees (Busing and White 1997, Hubbell et al. 1999), but additional analyses have shown that it generally only holds true for shade tolerant species and not for intolerants (Busing and White 1997, Schnitzer and Carson 2001).

Though counting individuals is practical in studies of trees ≥ 10 cm dbh, accurate estimates of density were impossible in our study because of the large number of clonal species present in the herbaceous and shrub layer. Photographs taken pre- and postfire at each plot attest that increases in density have occurred, especially in high severity plots, but an accurate quantitative estimate is not available. Our best estimate of changes in density can be made using presence of species at the smallest scale (0.01 m²). At such fine scales it has been suggested that richness is fundamentally constrained by density (Preston 1960, Fridley et al. in Review). Williams (1996) suggests that at fine scales mean species richness is actually more of a measure of the probability of finding an organism, thus it may serve as a rough estimate of density. Using mean species richness for all plots together at the 0.01 m² scale, our data suggest that on average

density has doubled from 0.24 species to 0.49 species and we cannot rule out the possibility that increases in richness are due to the increase in number of individuals.

Effects of Fire on Species-Area Curves of Trees

Changes in tree species richness after the fire were not consistent across all scales. Increases in the value of c postfire indicate increases in alpha diversity at fine scales, but decreases in z values indicate decreases in the rate of species accumulation with area. Interpreting changes in both c and z together indicates that proportional increases in richness after the fire actually decreased in magnitude with increasing spatial scale. Despite increasing alpha diversity, fire in the southern Appalachians decreases beta diversity in tree communities at scales from 0.01 m² to 400 m².

The changes in z values for trees did not reflect those changes observed in all plants together. This inconsistency results from differences in immigration rates at larger scales. Most trees in the southern Appalachians are dispersal limited, with the majority of seeds of most species generally falling within 50 meters of trees (Clark et al. 1998). Lack of long distance dispersal in trees limits immigration at larger scales. Seedling recruitment of species present in the local community increases tree diversity at fine scales, but does nothing to increase diversity at the plot level. Therefore, more species are found at smaller scales as seedlings and there is a steeper initial accumulation of species with increasing area. At the 400 m² scale increases in richness are limited by the number of tree species in the immediate vicinity of the plot and the number of species in the landscape that are capable of long distance dispersal. Though seed banks play a major role in some Mediterranean systems where fire is a major part of the disturbance regime (Keely and Fotheringham 2003), there is little evidence to suggest that many trees in the southern Appalachians have seeds that remain dormant in the soil for prolonged

amounts of time (USDA 1974). The two species in our plots that do maintain a seed bank are bird dispersed (*Prunus pennsylvanica*) and wind dispersed (*Liriodendron tulipifera*), and presumably have greater capacity for long distance dispersal than most other species in the area.

Directional changes in c were positive for both all plants and trees, but the magnitude of proportional change was smaller in trees. These results still support the interpretation of c by both Rosenzweig (1995) and Hubbell (2001). The removal of recruitment limitation by fire allows for a higher density of tree seedling establishment, resulting in a faster initial rate of accumulation of tree species. At larger scales (100-400 m²), species richness of trees is limited by immigration of new species into the plot. Despite the likely increases in density which would occur at all scales, increases in species richness occurred only at smaller scales. Those occurring at larger scales are likely due to germination of those species previously mentioned from the seed bank and immigration of species capable of infrequent, long distance dispersal by either wind (*Betula lenta*) or birds (*Amelanchier arborea*, *Ilex montana*, *Magnolia fraseri*).

Effects of fire on processes occurring at different scales

At the smallest scales (≤ 1 m²), inferences about fire effects on competition come from an interpretation of changes in c . Though our data show that species richness increases at small scales, the likely increases in density after the fire suggest that levels of competition should be higher. The conflict then lies in the idea that competitive effects are enhanced by increased density, not relaxed. This conflict can potentially be reconciled in two ways. First, if light is the limiting resource that plants are competing for after a disturbance, then the removal of canopy cover and resultant increase in light levels would lead to more abundant resources that can be partitioned by more individuals. This increase in resource levels would then negate the idea that density dependent effects on competition would actually decrease species richness. In addition,

the large competitive asymmetries between different growth forms (i.e. trees and herbs) due to size have been reduced where tree and shrub cover was removed. Thus, disturbance has actually relaxed competition, allowing smaller, light demanding species to co-occur.

At intermediate scales, an interpretation of changes in the z -values from species-area curves provides a logical means to assess how habitat heterogeneity promotes species coexistence. If the rate of species accumulation with area is related to habitat heterogeneity, then the lack of change in z in all plants suggests that the way species respond to this heterogeneity hasn't changed. The lack of correlation between the variation in canopy cover and postfire z values also suggests that habitat heterogeneity has little influence species turnover at these scales. In fact, the plots with the highest number of species were those where severity was uniformly high. The role of habitat heterogeneity in maintaining species diversity may be more apparent at larger scales where differences in severity across landscape gradients maintain landscape heterogeneity.

At scales where mass effects are most important in determining species richness ($>100 \text{ m}^2$) we are limited to interpreting changes in species richness at the 400 m^2 scale and changes in the total species pool from our sample. Increases in richness of all plants at these scales were driven by the immigration of species from outside the plots. Although recruitment of species from dormant seeds present in the soil is possible, only a few new species found in our plots are reported to be capable of long term dormancy. Instead, the majority of immigration was composed of shade-intolerant herbs capable of long distance dispersal, particularly those in the Asteraceae family. Presence of these fugitive species in plots prefire was likely restricted by recruitment limitation created by closed canopies and thick layers of organic matter, both of which were reduced by the fire. Although many of these species were observed reaching

reproductive stature postfire, their presence is likely fleeting and limited by the rate of litter accumulation and canopy closure.

Despite the increased influence of mass effects in determining species richness of all plants, the importance of mass effects in determining species richness as larger scales in trees is far less apparent. Proportional increases in the tree species richness at the 400 m² scale and in all plots together were smaller than those of all plants, indicative of dispersal limitation for most tree species in the region (Clark et al. 1998). Although mass effects may be responsible for the few shade intolerant species (*Salix nigra*, *Liquidambar styraciflua*) that frequently immigrated postfire, the role of mass effects has probably not been altered for the more shade tolerant species present in the area.

Conclusions

The relative importance of ecological processes occurring at different scales is altered by fire in Southern Appalachian forest communities. Although competition may be important in determining species richness at small scales in mature forest communities, our results indicate that competition is less important in communities recently disturbed by fire where light availability has increased and size asymmetries between growth forms have been reduced. Our results do not support the hypothesis that increases in species richness postfire are related to increased habitat heterogeneity at the local community level. However, an increase in habitat heterogeneity created by variation in severity across the landscape may promote the co-occurrence of more species at scales greater than those addressed in our study. The importance of mass effects is increased by the opening of the forest canopy, which allows for the coexistence of highly vagile, light demanding species that can immigrate over large distances and those mature forest species that can survive fire. This increases species richness at all scales within

local communities but does not affect the rate of species accumulation with area. For guilds of species that are generally dispersal limited such as trees, species richness increases at smaller scales, but mass effects are not important and species richness at large scales is limited by the number of species present in the surrounding landscape that can disperse in. The effects of fire on species richness must be considered in terms of the severity of disturbance, the spatial grain of observation, and the capacity for dispersal of the species present in the surrounding landscape.

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Literature Cited

- Arthur, M.A., R.D. Paratley, and B.A. Blankenship. 1998. Single and repeated fires affect survival and regeneration of woody and herbaceous species in an oak-pine forest. *Journal of the Torrey Botanical Society* 125:225-236.
- Barden, L.S. and F.W. Woods. 1973. Characteristics of lightning fires in the southern Appalachian forests. *Proc. Ann. Tall Timbers Fire Ecology Conference*. 13: 345-361.
- Bartram, W. 1792. *Travels through North and South Carolina, Georgia, east and west Florida*. 1973. Beehive Press, Savannah, Georgia, U.S.A.
- Busing, R.T., and P.S. White 1997. Species diversity and small scale disturbance in an old-growth temperate forest: a consideration of gap partitioning concepts. *Oikos* 78:562-568.
- Clark, J.S., E. Macklin, and L.Wood. 1998. Stages and spatial scales of recruitment limitation in southern Appalachian Forests. *Ecological Monographs* 68: 213-235.
- Condit, R., P.S. Ashton, P. Baker, S. Bunyavejchewin, S. Gunatilleke, N. Gunatilleke, S.P. Hubbell, R.B. Foster, L. Hua Seng, A. Itoh, J.V. LaFrankie, E. Losos, N. Manokaran, R. Sukumar, and T. Yamakura. 2000. Spatial patterns in the distribution of common and rare tropical tree species: a test from large plots in six different forests. *Science* 288: 1414-1418.
- Connell, J.H. 1978. Diversity in tropical rainforests and coral reefs. *Science* 199: 1302-1310.
- Davis, M.B. 1996. *Old growth in the east: A survey*. Wild Earth. Richmond, VT, USA.

- Denslow, J.S. 1980. Gap partitioning among tropical rainforest trees. *Biotropica* 12: 47-55.
- Denslow, J.S. 1985. Disturbance-mediated coexistence of species. Pages 307-323 *in* S.T.A. Pickett and P.S. White, editors. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, London, UK.
- Denslow, J.S. 1995. Disturbance and diversity in tropical rain forests: the density effect. *Ecological Application* 5: 962-968.
- Elliott, K.J., R.L. Hendrick, A.E. Major, J.M. Vose, and W.T. Swank. 1999. Vegetation dynamics after a prescribed fire in the southern Appalachians. *Forest Ecology and Management* 114: 199-213.
- Fridley, J.D., R.K. Peet, T.R. Wentworth, and P.S. White. Connecting fine- and broad-scale patterns of species diversity: species-area relationships of the Southeastern U.S. flora. In revision, *Ecology*.
- Glitzenstein, J.S., D.R. Streng, and D.D. Wade. 2003. Fire frequency effects on longleaf pine (*Pinus palustris* P. Miller) vegetation in South Carolina and Northeast Florida, USA. *Natural Areas Journal* 23: 22-37.
- Harmon, M.E. 1984. Survival of trees after low-intensity surface fires in Great Smoky Mountains National Park. *Ecology* 65: 796-802.
- He, F. and Legendre, P. 2002. Species diversity patterns derived from species-area models. *Ecology* 83:1185-1198
- Hubbell, S.P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* 203: 1299-1309.

- Hubbell, S.P., R.B. Foster, S.T. O'Brien, K.E. Harms, R. Condit, B. Wechsler, S.J. Wright, and S. Loo de Lao. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283: 554-557.
- Hubbell, S.P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Hughes, J.W. and T.J. Fahey. 1992. Colonization dynamics of herbs and shrubs in a disturbed northern hardwood forest. *Journal of Ecology* 79: 605-616.
- Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist* 113: 81-101.
- Kartesz, J.T. 1994. *A synonymized checklist of the vascular flora of the United States, Canada, and Greenland. Volume 1-Checklist*. Timber Press, Portland, Oregon.
- Keeley, J.E. and C.J. Fotheringham. 2003. Species-area relationships in Mediterranean-climate plant communities. *Journal of Biogeography* 30:1629-1657.
- Levin. S.A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology* 73: 1943-1967.
- Loucks, O.L. 1970. Evolution of diversity, efficiency, and community stability. *American Zoologist* 10: 17-25.
- MacArthur, R.H. and E.O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Newell, C.L. 1997. Local and regional variation in the vegetation of the southern Appalachian Mountains. Ph.D. dissertation. Curriculum in Ecology, University of North Carolina at Chapel Hill. 1,008 p.

- Newell, C.L. and R.K. Peet. 1998. Vegetation of Linville Gorge Wilderness, North Carolina. *Castanea* 63(3): 275-322.
- Sousa, W.P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics*. 15: 353-391.
- Pickett, S.T.A. and P.S. White. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.
- Platt, W.J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. *Ecological Monographs* 45: 285-305.
- Plotkin, J.B. and H.C. Muller-Landau. 2002. Sampling the species composition of a landscape. *Ecology* 83(12): 3344-3356.
- Preston, F.W. 1960. Time and space and the variation of species. *Ecology* 41: 611-627.
- Rosenzweig, M.L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, UK.
- Runkle, J.R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62: 1041-1051.
- Scheiner, S.A. 2003. Six types of species-area curves. *Global Ecology and Biogeography* 12: 441-447.
- Schnitzer, S.A. and W.P. Carson. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* 82:913-919.
- Schmida, A. and M.V. Wilson. 1985. Biological determinants of species diversity. *Journal of Biogeography* 12:1-20.

- Schmida, A. and R.H. Whittaker. 1981. Pattern and biological microsite effects in two shrub communities, southern California. *Ecology* 62: 234-251.
- Schwilk, D.W., J.E. Keeley, and W.J. Bond. 1997. The intermediate disturbance hypothesis does not explain fire and diversity pattern in fynbos. *Plant Ecology* 132: 77-84.
- U.S. Department of Agriculture, Forest Service. 1974. Seeds of woody plants in the United States. U.S. Dep. Agric., Agric. Handb. 450.
- Uys, R.G., W.J. Bond, and T.M. Everson. 2004. The effect of different fire regimes on plant diversity in southern African grasslands. *Biological Conservation* 118: 489-499.
- Weier, E. and A. Howe. 2003. Scale-dependence of environmental effects on species richness in oak savannas. *Journal of Vegetation Science* 14: 917-920.
- Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. *Ecological Monographs* 26: 1-80.
- Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30: 279-338.
- Williams, M.R. 1996. Species-area curves: the need to include zeroes. *Global Ecology and Biogeography Letters* 5: 91-93.

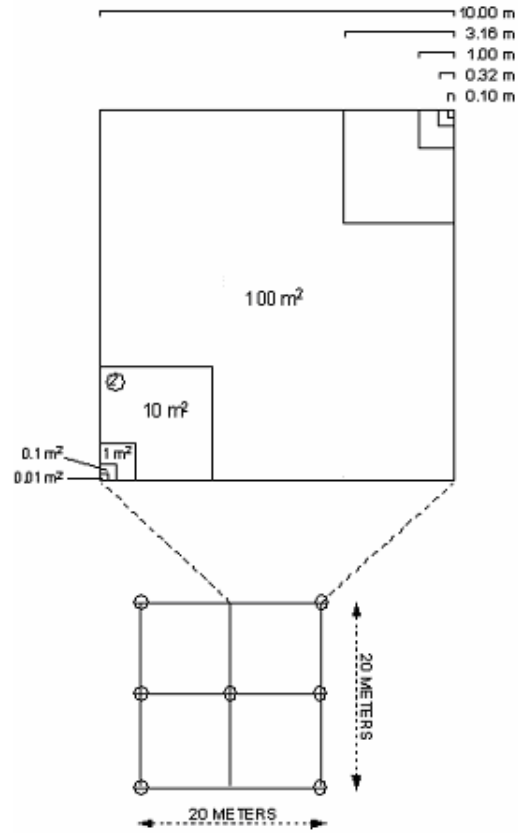


Figure 2.1. Modified setup of Carolina Vegetation Survey Plots (adapted from Peet et al. 1998).

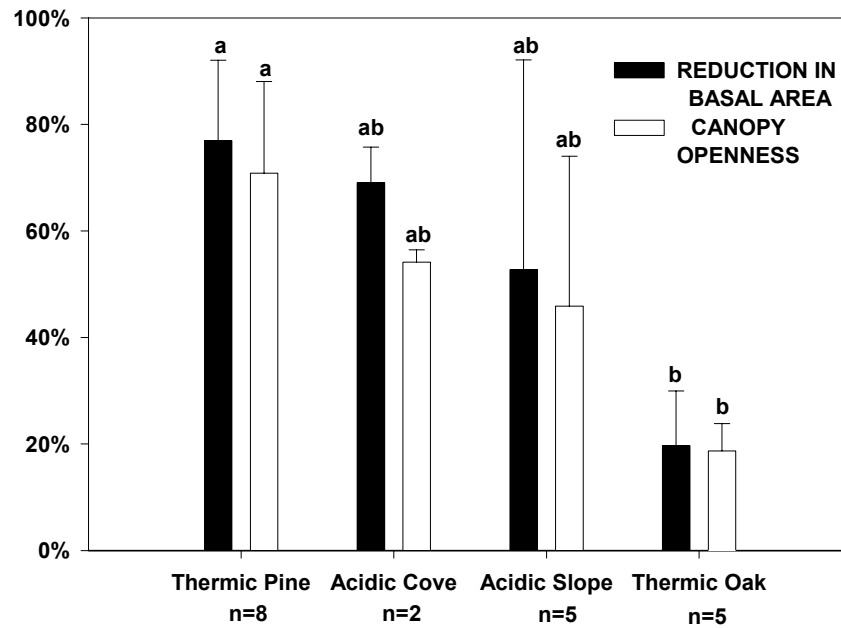


Figure 2.2. Fire severity estimated as the mean percent decrease in basal area, and the mean postfire percent canopy openness across four community types. Community means with the same letters are not significantly different at $p \leq 0.05$. Bars represent standard deviations.

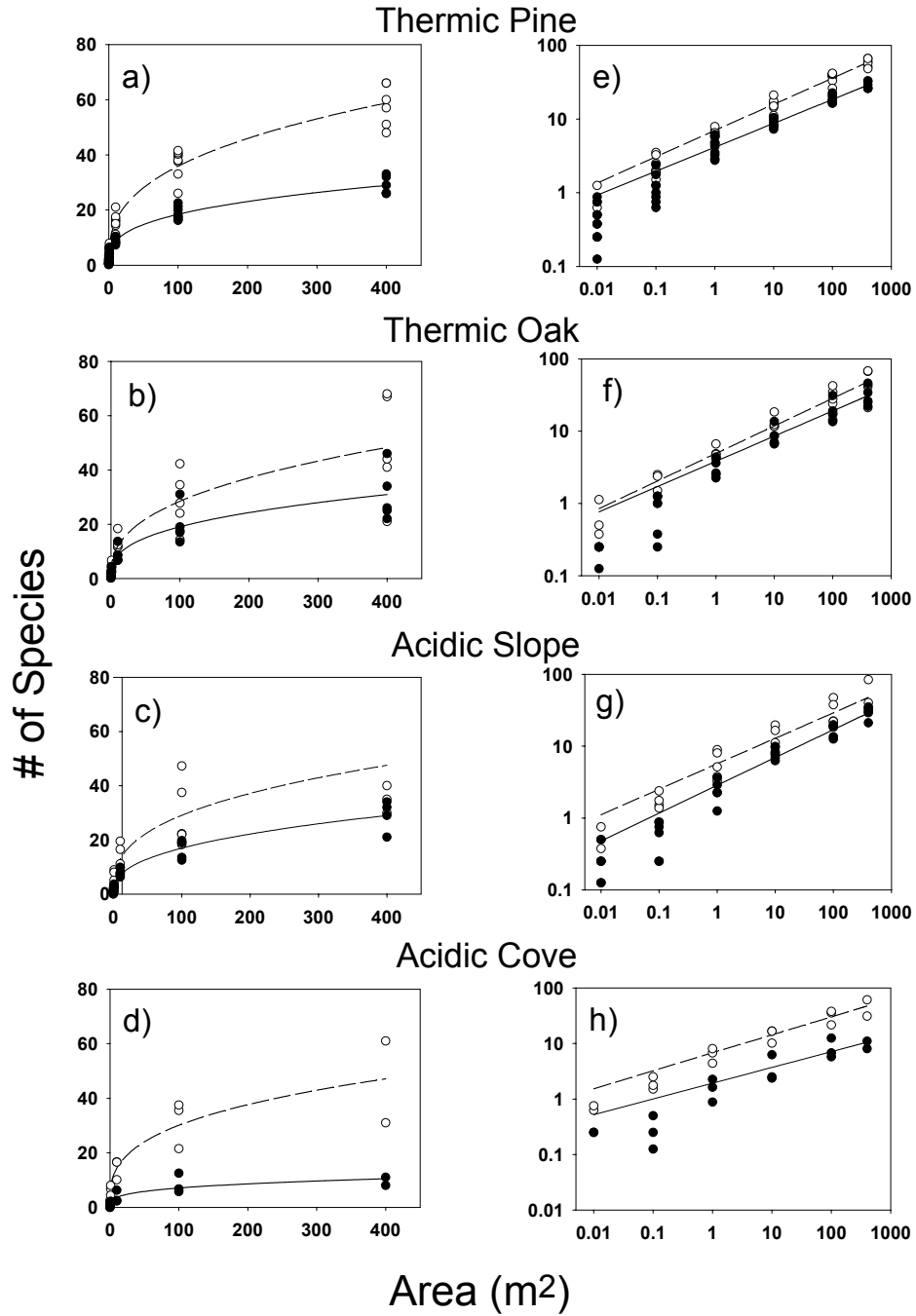


Figure 2.3. Pre- and postfire species-area curves displayed on arithmetic (a-d) and logarithmic (e-h) scales for all plants in four community types. Prefire data are represented by closed circles and solid lines. Postfire data are represented by open circles and dashed lines. Data points are the mean number of species at each spatial scale from each plot. Values of zero are not represented on the logarithmic plots.

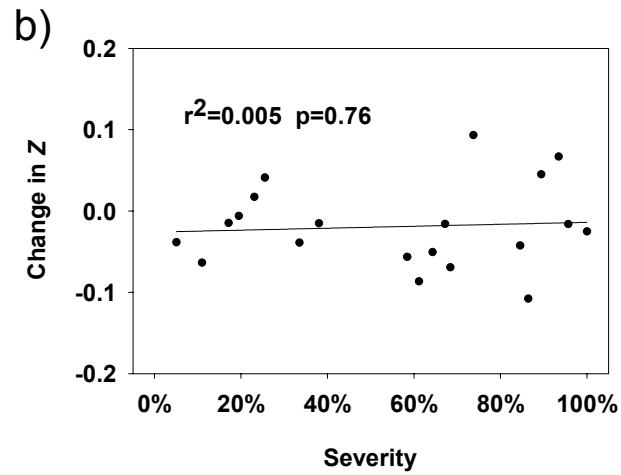
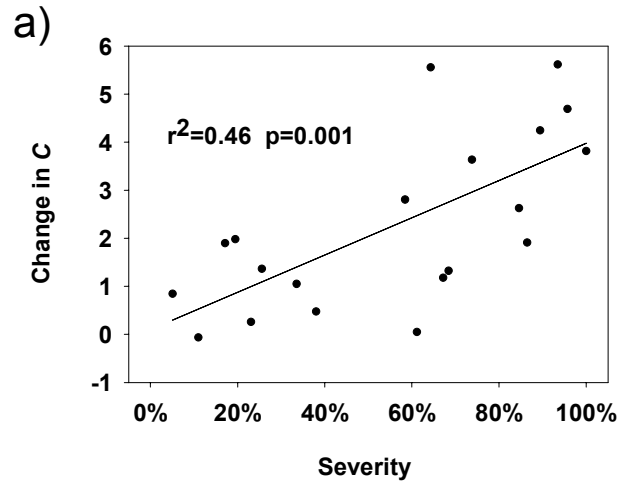


Figure 2.4. Linear regression results for the relationship between severity (% reduction in basal area) and a) change in *c* and b) change in *z* all plants.

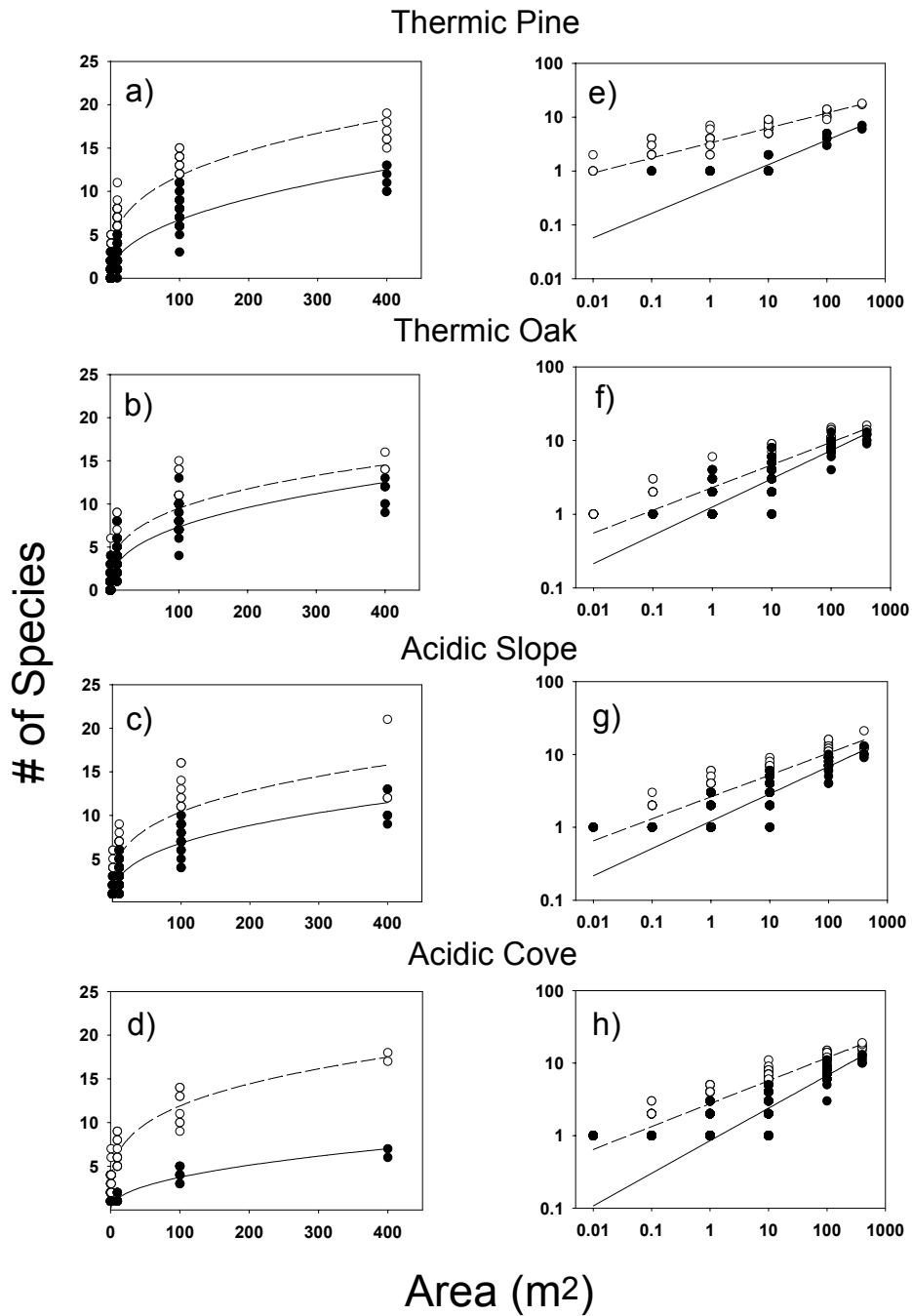


Figure 2.5. Pre- and postfire species-area curves displayed on arithmetic (a-d) and logarithmic (e-h) scales for trees in four community types. Prefire data are represented by closed circles and solid lines. Postfire data are represented by open circles and dashed lines. Data points are the mean number of tree species at each spatial scale from each plot. Values of zero are not represented on the logarithmic plots.

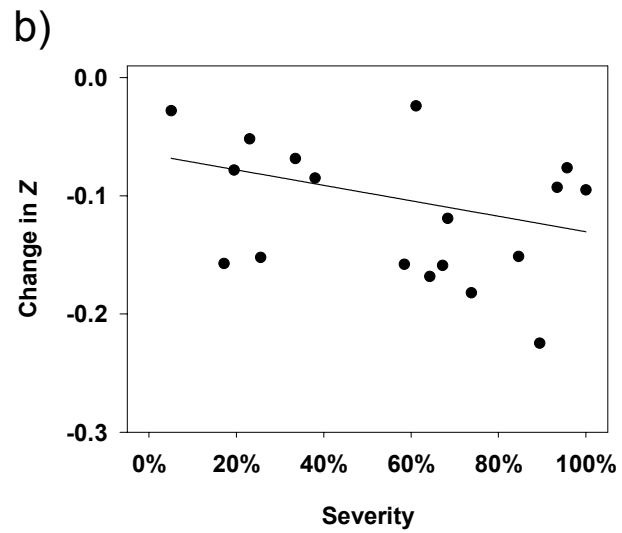
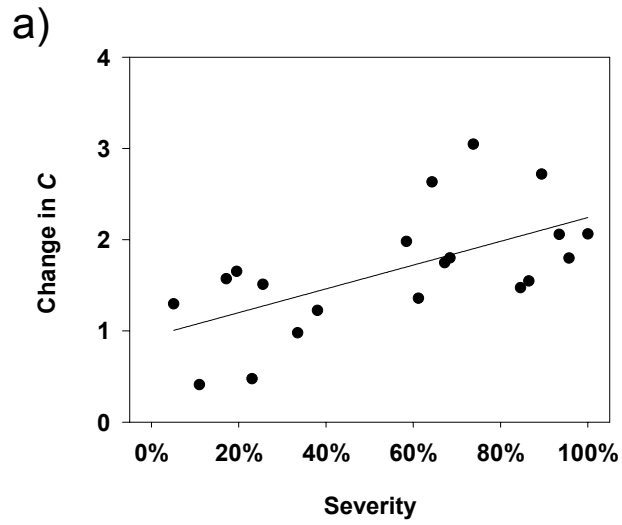


Figure 2.6. Linear regression results for the relationship between severity (% reduction in basal area) and a) change in c and b) change in z trees.

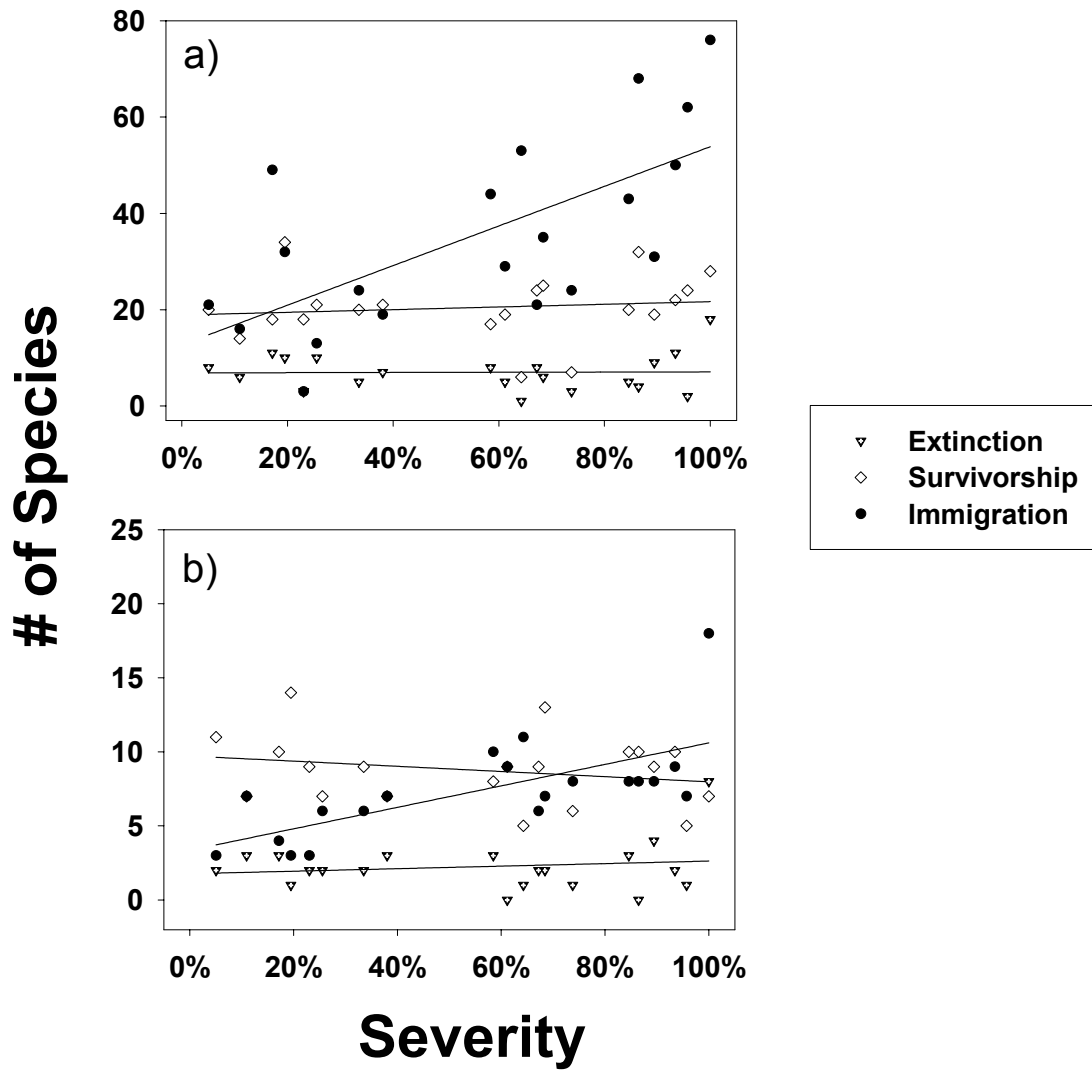


Figure 2.7. Linear regression results for the relationships between severity (% reduction in basal area) and immigration, extinction, and survivorship of species in local forest communities (400m²) for a) all plants and b) trees.

Table 2.1. Slope (z) and coefficient (c) values by community type for pre- and postfire species-area curves all plants.

	PREFIRE		r^2	POSTFIRE		r^2
	z	c		z	c	
Thermic Pine	0.32	4.12	0.97	0.36	7.06	0.97
Thermic Oak	0.35	3.83	0.85	0.38	4.91	0.81
Acidic Slope	0.39	2.73	0.92	0.36	5.78	0.76
Acidic Cove	0.29	1.99	0.79	0.33	6.88	0.87

Table 2.2. Slope (z) and coefficient (c) values by community type for pre- and postfire species-area curves trees.

	PREFIRE		r^2	POSTFIRE		r^2
	z	c		z	c	
Thermic Pine	0.45	0.85	0.89	0.32	2.75	0.91
Thermic Oak	0.38	1.25	0.86	0.31	2.30	0.84
Acidic Slope	0.37	1.21	0.87	0.30	2.61	0.85
Acidic Cove	0.45	0.46	0.89	0.28	3.31	0.89

CHAPTER III

**WILDFIRE EFFECTS ON BETA DIVERSITY AND SPECIES TURNOVER IN A
SOUTHERN APPALACHIAN FOREST LANDSCAPE¹**

¹Reilly, M.J., M.C. Wimberly, and C. L. Newell. To be submitted to the *Journal of Vegetation Science*.

Abstract

Although the effects of disturbance on alpha diversity (species richness) are commonly studied, insights into the effects of disturbance on beta diversity are limited to predictions of how the species overlap changes during succession. To gain a better understanding of how disturbance affects community structure along spatial and environmental gradients, we examined changes in beta diversity and species turnover after a wildfire in Linville Gorge, NC. We quantified the effects of fire on relationships between community composition, environment and fire severity, species frequency distributions, Whittaker's beta diversity metric (β_w), and the decay in similarity over a topographic moisture gradient and geographic distance. Our results indicate that fire does little to change beta diversity and species turnover in the southern Appalachians because of a lack of change in the relationship between environment and species composition, limited exchange of common species between communities, and high rates of immigration of locally rare wind dispersed species from the surrounding landscape. Despite a large increase in the mean species richness in local communities from high rates of immigration after the fire, there was little change in the degree of species overlap between samples. When all species were separated into trees, shrubs, and herbs there were inconsistencies in the results compared with all species analyzed together. We propose that effects of fire on species overlap in a landscape is limited by the number of species that are capable of dispersing and immigrating in large numbers to exploit the reduction in the relative importance of competition.

Introduction

Although the idea of beta diversity was introduced over four decades ago (Whittaker 1960), ecologists have only recently revisited the role of different processes in maintaining patterns of turnover in plant species over landscapes and regions (Tuomisto et al. 1995, Ohmann and Spies 1998, Nekola and White 1999, Pitman et al. 2001, Condit et al. 2002, Duivenvoorden et al. 2002, Potts et al. 2002, Tuomisto 2003). The resurgence of interest in beta diversity has been facilitated by at least two factors: the accumulation of data sets spanning large areas (Chave and Leigh 2002), and the emergence of techniques that explicitly incorporate measures of similarity over environmental and spatial gradients (Nekola and White 1999). Although no predominant theory behind what controls beta diversity has arisen, previous studies have clearly documented that species turnover results from spatial processes such as dispersal limitation and niche partitioning along environmental gradients.

Despite the attention that the effects of disturbance on alpha diversity have received in the literature (see Denslow 1985 for review) there have been few or no investigations into the effects of natural disturbance on beta diversity. Species turnover along environmental gradients and geographic distance determines species richness at landscape scales (Whittaker 1970, Plotkin and Muller-Landau 2002), yet previous studies of beta diversity have mostly been limited to documenting static patterns of turnover. This is somewhat surprising given the documentation of large changes in alpha diversity after disturbance (Connell 1978, Platt 1975, Denslow 1980, Elliott et al. 1999, Schnitzer and Carson 2001) and the awareness that ecological processes at large scales have a critical impact on the preservation of biodiversity (Franklin 1993, Hobbs 1997).

Although previous work on beta diversity has identified the factors controlling turnover patterns and developed quantitative methods of measuring turnover, the effects of disturbance on beta diversity have not yet been explicitly examined. Ecological theory from past studies on succession suggests that beta diversity in early-successional forests is lower than in mature forests. After disturbance competition is generally relaxed, and the relative importance of dispersal and mass effects increases. It has been suggested that these changes promote more overlap of species and decrease beta diversity during early-successional stages following disturbance (Werner and Platt 1976, Christensen and Peet 1984). However, if many species are dispersal limited and disturbance is highly correlated with environment and community type, underlying gradients and site history would be reinforced, thus increasing beta diversity. In this situation species overlap would decrease and the distribution of species would be more closely linked to their ecological optima. We suggest that alternative outcomes are possible depending on the effects of disturbance on species richness, the distribution of relative abundances within local communities, the amount of species exchange between local communities, and the amount of immigration from the surrounding landscape from which the sample is drawn.

Spatial variation in species composition has been measured in many ways, but methods generally fall into one of two categories (Velland 2001). Those in the first category measure among-sample variation by incorporating total species richness in all samples (γ diversity) and the average species richness in each sample (α diversity). Most of these are related to Whittaker's original β_w (Whittaker 1960), where $\beta_w = \gamma/\alpha$. These indices are useful in measuring the amount of among-sample variability, but do not take into consideration the spatial or environmental context of the samples. Measures in the second category incorporate compositional similarity and the spatial or environmental distance between samples, providing a

more quantitative analysis of beta diversity. Ordination techniques enable an investigator to identify and quantify the importance of underlying gradients that structure vegetation. Once these gradients have been identified, the rate of decay in similarity over space or environmental distance can be quantified and interpreted as the rate of species turnover and the amount of beta diversity.

The objective of this study is to assess how a large-scale natural disturbance affects beta diversity in a forested landscape of the southern Appalachians. These forests have a diverse flora where the role of environmental gradients, particularly topographic moisture and elevation, has long been recognized (Whittaker 1956, Day and Monk 1974, Newell 1998). Although small scale disturbance created by individual-tree mortality is an important part of the disturbance regime (Runkle 1981), it has also been suggested that historic anthropogenic fires maintained landscape heterogeneity before European colonization (Delcourt and Delcourt 1998). Fire remained an important component of the disturbance regime with an estimated return frequency of about thirteen years up until the late 1930's when a policy of fire suppression was adopted (Harmon 1982). This period of suppression has left many pine and oak forests of the region in a degraded state due to the encroachment of fire-sensitive species (Barden and Woods 1976, Harmon 1982, Williams 1998). Although others have investigated the effects of fire in this region on small-scale species richness (Arthur 1998, Elliott et al. 1999), a better understanding of the effects of disturbance on species turnover at the landscape scale is necessary for managing large areas.

We address three main questions in this study. First, how does the relationship between community composition and environment change after wildfire? If immigrants are dispersed at random then it is likely that the role of environmental gradients will decrease. However, if

severity is highly correlated with a particular environmental gradient, then we would expect the relative importance of that gradient to increase. Second, how do different measures of beta diversity and species turnover change after the fire? If species show less fidelity to specific sites, then beta diversity should decrease. However, if fire is correlated with environmental gradients it may act to reinforce them and increase beta diversity. Third, how do results of the first two questions change when pre- and postfire communities are separated into trees, shrubs, and herbs? Trees, shrubs, and herbs differ in many of their ecological characteristics. Differences in life-history traits, particularly the capacity for dispersal, suggest that changes in beta diversity are likely to differ among different growth forms.

Methods

Study Site

Linville Gorge is a 4,390 ha federally designated wilderness area located in Burke County, NC in the Pisgah National Forest. Elevation ranges from 1250 m on upper ridges to 820 m at the bottom of the gorge. Upper and lower slopes are separated by prominent cliff-like bluffs that bisect both sides of the gorge. As a result of downcutting from the Linville River, several types of parent material have been exposed in the gorge. The plots chosen for this study were restricted to upper slopes occurring on the lower quartzite formation, which is exposed by the bluffs and extends above to the ridge. Soils on the lower quartzite are generally thin and coarse, consisting primarily of Typhic or Lithic Dystrochep soils. Annual precipitation ranges from 1,250 to 1,625 mm and is highest in the summer months, occurring mostly as rain.

Because of the steep slopes and inaccessibility of the gorge, the vast majority of the landscape is old growth and thought to be representative of pre-settlement forests (Davis 1996).

Ridges and bluffs are dominated by *Pinus pungens*, *P. rigida*, and *P. virginia*. Slopes are dominated by *Quercus coccinea* and *Q. montana* with *Acer rubrum*, *Nyssa sylvatica*, and *Oxydendron arboreum* in variable amounts. A thick layer of ericaceous shrubs including *Kalmia latifolia* and *Vaccinium* spp. is present throughout the slopes, ridges, and bluffs. More sheltered moist coves and slopes are dominated by large *Tsuga canadensis* in the overstory and dense *Rhododendron maximum* in the shrub layer. See Newell and Peet (1998) for a detailed account of the vegetation present prefire. Evidence from fire scars and tree cores suggest that in the last 150 years Linville Gorge has been subject to several fires, varying in intensity and extent (C. Frost, unpublished data). Catastrophic crown fires occurred in 1860 and 1915. In between these large fires several low intensity surface fires occurred, but their extent and frequency of occurrence are unknown. Prior to 2000, the last widespread surface fire occurred in the 1950's. Fires were suppressed until November 2000 when an unattended campfire ignited a wildfire that burned over 2,000 ha within the wilderness boundaries.

Data Collection

A series of permanent plots were established and sampled in Linville Gorge in the summer of 1992 as part of a regional vegetation classification (Newell 1997, Newell and Peet 1998). Twenty-five plots of these plots were relocated and resampled during the summer of 2003. Twenty of the resampled plots burned in 2000 while the remaining five did not. The five unburned plots served as a control for any major changes in vegetation since the original sampling that may have been due to factors other than the fire. A preliminary analysis showed little or no change in species richness and composition in the unburned plots (M. Reilly, unpublished data). Thus, we concluded that the observed community dynamics in burned plots

were attributable to fire effects and not to other changes occurring between 1992 and 2000. Subsequent analyses were focused on the 20 burned plots.

All plots were set up following the Carolina Vegetation Survey protocol (Peet et al. 1998) and nomenclature follows Kartesz (1994). Each of the plots consisted of a series of 10 x 10 m² adjacent modules (Figure 3.1). Of the burned plots, seventeen consisted of four modules (400 m²) and three consisted of two modules (200 m²). In each module two corners were sampled for the presence of all vascular plant species in a series of four nested quadrats increasing in size from 0.01 m² to 10 m². The rest of the module was then searched for additional species. Abundance of each species at the plot level was estimated by using the average spatial scale, or depth, where it was first encountered in each module (0.01 m²=5, 0.1 m²=4, 1.0 m²=3, 10 m²=2, 100 m²=1). The depth estimate of abundance was used because of the large size asymmetries between different growth forms. Assuming the most abundant species will be found at the smallest scales, the resulting estimate is a log-scaled frequency estimate of abundance. All trees, shrubs, and lianas taller than 1.4 m were measured and put into diameter at breast height (dbh) size classes (0-1 cm, 1-2.5 cm, 2.5-5 cm, 5-10 cm, 10-15 cm, ..., 35-40 cm, >40 cm). Trees >40 cm dbh were measured to the nearest centimeter. Post-fire tree sampling included measurement of both live and dead stems (standing and on the ground) to account for all stems found in 1992. These data were used to construct pre-fire basal area. This reconstruction gave a more accurate estimate of severity than using the prefire basal area because there was considerable growth in some plots between 1992 and 2003.

The program SOLARFLUX (Hetrick et al. 1993, Hetrick, Rich, and Weiss 1993) was used to calculate elevation, topographic moisture, and potential solar radiation from a digital elevation model in ArcInfo. Potential solar radiation (PSR) predicts local levels of insolation in

the context of the surrounding landscape. A modified version of Parker's (1982) topographic relative moisture index was used to calculate a topographic moisture index (TMI). TMI incorporates relative slope position, curvature, and solar radiation, which are all rescaled and summed to produce an index where higher values correspond to higher potential site moisture. Fire history was based on the presence of evidence of past fire observed during the 1992 sampling. Plots with no evidence of fire received 0, plots with a dark layer in the soil possibly indicating past fire received a 1, plots with small amounts of charcoal in the soil received a 2, and plots with abundant charcoal in the soil or the presence of charred stumps received a 3. Fire severity in 2000 was estimated based on the percent reduction in basal area after the fire. UTM coordinates were used to construct a matrix of geographic distances for all pairs of plots.

Data Analysis

Plots were characterized into communities based on 1992 basal area using PC ORD. Basal areas were relativized by plot totals to account for the three smaller plots in the data set. The flexible beta group linkage method ($\beta = -.25$) and Bray-Curtis distance measure were used in the cluster analysis. The dendrogram was cut at 2.2848 in order to give a workable number of groupings and to correspond with those groupings of Newell and Peet 1998. The resulting groups were then used as community classifications in the analyses that followed.

Dominance-diversity curves were created using the pre- and postfire log based frequency estimates of abundance on the y-axis and rank in abundance on the x-axis (Whittaker 1965). These abundance estimates were relativized by total abundance to show how levels of relative dominance changed on a per plot basis after the fire. We fit the logarithmic function to these curves for each plot using nonlinear curve fitting in SigmaPlot and used the slope of the fitted curve as an estimate of dominance, where steeper curves corresponded to greater levels of

dominance. We tested for changes in dominance between pre- and postfire slopes of rank abundance curves using a Wilcoxon Rank Sign test. Changes in the slopes of the curves were correlated with severity using linear regression in SigmaPlot.

We examined changes in frequency to investigate how fire changed the degree of species overlap. Frequency is a rough estimate of the niche breadth of a particular species and forms the basis for measures suggested and used by others in the past (McNaughton and Wolf 1970, Werner and Platt 1976, Christensen and Peet 1984, ter Braak and Verdonschot 1995). A Mann-Whitney rank sum test was used to test for a difference in pre- and postfire median frequency of all species present either pre- or postfire. To examine how frequency changed independent of losses and gains of species, we look at differences in pre- and postfire frequencies of only those species that were present both pre- and postfire using a Wilcoxon signed rank test. We plotted prefire versus postfire frequency for each species to illustrate how frequencies changed. A chi-square goodness-of-fit test was used to determine whether or not the frequency distribution changed after the fire. The presence of several classes with fewer than five occurrences in the higher frequency classes required us to group frequencies into the following five classes: 1-20 %, 21-40 %, 41-60 %, 61-80 %, and 81-100 %. All analyses were done in SigmaStat 3.0.

Non-Metric Multidimensional Scaling (NMS) based on a quantitative Jaccard similarity index was used to examine how the relationship between environment and community composition was affected by the fire. All ordination were carried using PC-ORD software (McCune and Mefford 1999). NMS is an indirect ordination technique that determines gradient structure based on species composition alone, and does not constrain axes to secondary variables. (Økland 1996). We used an indirect ordination technique to provide an unbiased representation of community structure both pre- and postfire because we cannot be certain that all relevant

environmental and disturbance variables were measured. Preliminary NMS runs recommended a two-axis solution as the addition of more axes did little to reduce final stress. We used a two-dimensional Bray-Curtis ordination based on a Jaccard index to get a starting configuration for NMS. The slow and thorough defaults in PC-ORD were used for the remaining parameters and a Monte Carlo test with 999 runs was used to test whether NMS was extracting stronger axes than expected by chance. Biplots were created and axes were manually rotated such that TMI correlated strongest with Axis 1, following Whittaker's model of vegetation in the Great Smoky Mountains (Whittaker 1956).

Pre- and postfire beta diversities were compared based on among-plot variation in species composition and decay in similarity along spatial and environmental gradients. To investigate the change in among-plot variation, Whittaker's β_w was calculated as

$$\beta_w = \gamma / \alpha$$

where γ = the number of species in all plots, and α = the mean number of species per plot.

The decay in similarity over environmental and geographic gradients was compared by calculating the slope of the simple linear regression of Jaccard similarity against environmental and geographic distance. The Jaccard Similarity index (Magurran 1988) is defined as:

$$J_s = a / (a + b + c),$$

where a = the total abundance of shared species, b = the abundance of species only occurring in sample 1, and c = the abundance of species only occurring in sample 2. We chose a quantitative index as opposed to one based on presence-absence because species abundance data is more sensitive to the environmental gradients and disturbance we were trying to capture (Nekola and White 1999). Mantel tests were used to determine the strength of the relationship between each gradient and community composition. Similarities between all possible pairwise pre-and postfire

plot combinations (n=190) were compared using a pairwise *t*-test in SigmaPlot to see if the degree of similarity between plots had changed after the fire. These analyses were repeated for trees, shrubs, and herbs alone.

Results

Four community types were distinguished from the cluster analysis of prefire trees. Thermic pine forests (n=8) were dominated by varying amounts of *Pinus pungens*, *P. rigida*, and *P. virginiana* in the overstory. The midstory was dominated by *Kalmia latifolia* usually with the presence of some hardwood species including *Quercus coccinea*, *Acer rubrum*, and *Nyssa sylvatica*. Thermic oak forests (n=5) communities consisted of varying amounts of *Q. coccinea*, *Q. montana*, and *Q. alba*. *K. latifolia* was abundant in the midstory along with *Acer rubrum*, *P. strobus*, and *Oxydendrum arboreum*. Acidic slope forests (n=5) were dominated by *Q. montana*, *A. rubrum*, and *P. strobus*. The midstories were mixed, often with the presence of *K. latifolia*, *Rhododendron maximum*, and *Tsuga canadensis*. Acidic cove forests (n=2) were dominated by *Tsuga canadensis* in the overstory with a thick midstory of *Rhododendron maximum*.

The total number of species (γ) was 107 prefire and 200 postfire. Mean species richness in all plots (α) was 25.7 (stdev=8.6) prefire and 49.6 (stdev=14.1) postfire. Despite the large changes in γ and α after the fire, β_w changed very little. Prefire β_w was 4.33 and postfire β_w was 4.14. The total number of trees increased from 27 to 35. The increase in shrubs was also small, from 25 to 32. The number of herb species increased the most from 55 to 133.

Results of a Wilcoxon Signed Rank test between pre- and postfire dominance estimates (slopes of the rank abundance curves) indicated that dominance at the plot level was significantly reduced postfire ($p < 0.001$). Change in the slope of the dominance diversity curves was

significantly and positively correlated with severity ($r^2=0.42$, $p=0.0019$). When measured across the whole sample, relative abundance was also more even after the fire. Abundance in the first thirty ranked classes was lower postfire. The large difference in the number of species across the whole sample resulted from the long tail of rare species present postfire (Figure 3.2).

Results of a Mann-Whitney rank sum test indicated that there was no significant difference between frequency of all species pre- and postfire ($p=0.386$). Results of the Wilcoxon Rank Sum Test indicated that the frequency of species present both pre- and postfire was significantly higher postfire ($p<0.001$). A total of 40 species increased in frequency, 21 did not change in frequency, and 20 decreased in frequency (Figure 3.3). There was no significant difference in the distribution of frequency of occurrence between pre- and postfire (Chi-square=20, d.f.=16, $p=0.220$) (Figure 3.4).

The NMS ordinations indicated that similar gradients structure community composition pre- and postfire (Figure 3.5, Table 3.1), although the strength of some gradients changed. Final stress was less than 13 in both the pre- and postfire ordinations, and all axes were significant ($p\leq 0.01$). Axis 1 was strongly related moisture availability both pre- and postfire. Axis 2 was weakly correlated with fire history and PSR in the prefire landscape. Elevation was not strongly correlated with community structure in the prefire ordination. Axis 2 was strongly correlated with elevation and fire severity postfire. The most notable changes in the ordination were the increase in correlation of elevation with axis 2, the increase in correlation of PSR with axis 1, and the strong correlation of fire severity with axis 2. Thermic oak and thermic pine plots exhibited greater separation along axis 2 in the postfire than in the prefire ordination. Acidic slope and acidic cove plots show less separation along axis 1.

There were statistically significant relationships ($p \leq 0.05$), but weak correlations between Jaccard similarity and both topographic moisture and geographic distance pre- and postfire for all plants, trees, shrubs, and prefire herbs (Table 3.2). The slope of decay in similarity over topographic moisture decreased by a small amount, but there was no change for the relationship with geographic distance (Figure 3.6). The results of the pairwise *t*-test indicate that similarity among pairs of plots was higher postfire ($p=0.005$).

Changes in the decay in community similarity over environmental and geographic distance of trees, shrubs, and herbs were not always consistent with the changes in all species (Table 3.2, Figure 3.7). For trees, the rate of decay in similarity over both environmental and geographical distance in trees increased slightly postfire, and the pairwise similarity of plots was greater postfire ($p < 0.0001$). For shrubs, the rate of decay in similarity over both environmental and geographic distance decreased postfire, and there was no significant difference between pairwise similarities pre- and postfire ($p=0.645$). For herbs, the rate of decay in similarity over environmental or geographic distances decreased to zero postfire, and the pairwise similarity of plots decreased postfire ($p < 0.0001$).

Discussion

Although this study and others have found large changes in alpha diversity after fire in the southern Appalachians (Arthur et al. 1998, Elliott et al. 1999), our results show that fire had relatively little effect on species turnover in Linville Gorge. Lack of change in the amount of among-plot variation (β_w), the relative strength of different environmental gradients, and the decay in similarity consistently showed that there was little change in beta diversity after the fire. Although a decrease in dominance at the local and landscape levels suggests a decrease in the

relative importance of competitive interactions, the degree of species overlap has not changed. These results contrast with the predictions and findings of others who have hypothesized that beta diversity would decrease because of increases in the niche breadth of individual species, leading to more species overlap (Werner and Platt 1976, Christensen and Peet 1984). We suggest that the lack of change in beta diversity can be attributed to the strong constraints imposed by topographic moisture gradients both pre and postfire, the lack of change in the frequency distribution of species amongst plots, and the unexpectedly high rates of immigration of infrequent herbaceous species not present prefire.

Our results are consistent with other studies which have determined that a combination of factors underlie species turnover in the southern Appalachians (Whittaker 1956, Newell 1998) as well as in other forested landscapes (Ohmann and Spies 1998, Wimberly and Spies 2001, Condit et al. 2002, Duivenvoorden et al. 2002, Tuomisto 2003). Although Whittaker has been criticized for sampling only mature vegetation with no evidence of recent disturbance (Harmon et al. 1983), our results suggest that these relationships hold true even at early successional stages after disturbance. Variables affecting site moisture availability (PSR and TMI) are among the most important variables in the old-growth prefire forests, supporting Whittaker's original model of vegetation in the southern Appalachians. The weak relationship between elevation and community structure prefire may have occurred because of the relatively narrow range of elevations among the plots (approximately 1,500 m). Although elevation is correlated with postfire vegetation, fire severity is strongly correlated with the same gradient, suggesting that elevation had an indirect on vegetation through its effects on fire severity.

Beta diversity in the context of among plot variability (β_w) is dependent on the mean frequency of species (Routledge 1977, Schutler and Ricklefs 1993, Vellend 2001). Thus, the lack

of change in β_w reflects the lack of change in mean frequency after the fire. These results are in contrast with the prediction that frequencies should generally increase following a disturbance (Platt and Werner 1976, Christensen and Peet 1984). However, once the species that were lost through extinction or gained through immigration as a result of the fire were removed from the analysis, postfire frequency was indeed greater, especially in the case of the more common species. The exclusion of immigration and extinction from the analyses generally removes only rare, infrequent species. Of the 117 species that immigrated, 84 occurred in less than 25% of the plots. All of the 25 species that went extinct in our sample were in less than 15% of the plots. It is this influx that maintains the presence of infrequent species after the fire.

Fire had very little effect on the rate of decay in similarity over either environmental or geographic distance in Linville Gorge. In addition, there was little change in the strength of the relationship between decay and distance. However, regardless of the distance variable, or the actual distance, pairwise comparisons of plots consistently had higher similarity postfire, indicating a higher degree of homogeneity after the disturbance. The average change was even across environmental and geographical distance, and again results from the large degree of immigration of rare species. Since we used Jaccard similarity as a quantitative index, the shared abundances of common species are weighted much more than species with low abundances in computing the degree of dissimilarity.

Rates of decay in similarity of trees, shrubs, and herbs were not the same as those of all species together. These results are consistent with the findings of Nekola and White (1999) who suggest that differences in dispersal abilities and niche widths among growth forms result in different patterns of decay. The slight increases in the decay of similarity over both environmental and geographic distances suggest that rates species turnover in trees has

increased. Past studies have shown that tree species of this region have different levels of tolerance to fire at different sizes due to variation in bark thickness (Harmon 1984), thus dominant overstory species such as oaks (*Quercus* spp.) suffered less mortality from the fire than species typically present as small saplings in the shrub layer such as *Tsuga canadensis*, *Acer rubrum*, and *Nyssa sylvatica*. In addition, tree species of this region are generally dispersal limited (Clark et al. 1998), suggesting that dispersal limitation is preventing the immigration of many new tree species and limiting the potential for more overlap in frequency.

Shrub community structure changed very little along geographic and environmental gradients after the fire. This lack of change probably reflects the high resilience of most shrub species, which tended to resprout vigorously after the fire. Herbs in Linville Gorge represent a variety of dispersal types, but the increase in number of highly vagile, wind dispersed species suggests an increased role of dispersal in patterns of species turnover after the fire. As a result, there were relatively weak relationships between environmental and geographic distance and community similarity. Herbs were generally low in local abundance and therefore their overall measure of similarity was more sensitive to the change in number of unique species since even shared species are not especially abundant. The greater sensitivity of the Jaccard index to unique herbaceous species resulted in a decrease in overall similarity between plots and a decrease in species turnover after the fire.

Conclusions

Although fire results in large increases in alpha diversity in the southern Appalachians, there is little to no effect of fire on beta diversity and species turnover across the landscape. The lack of change in beta diversity is likely due to a combination of the effects of strong constraints created by underlying environmental gradients and dispersal limitation in dominant species.

Immigration of ruderal species may increase alpha diversity, but because individual species of immigrants are generally infrequent or occur at low levels of abundance, they do not affect commonly used metrics of beta diversity and species turnover. Although beta diversity of all species appears insensitive to the effects of fire in Linville Gorge, inconsistencies in patterns of species turnover among different growth forms and all species combined indicate that different outcomes are possible depending on the differences in species' dispersal abilities. As the number of species that are dispersal limited increases (as in trees), it is likely that fire will increase beta diversity at the landscape scale even if competition and dominance are reduced at local scales. However, if most species are not dispersal limited (as in herbs), beta diversity and species turnover will decrease. Our results suggest that fire reinforces underlying gradients in the southern Appalachians and is important in maintaining landscape heterogeneity.

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Literature Cited

- Arthur, M.A., R.D. Paratley, and B.A. Blankenship. 1998. Single and repeated fires affect survival and regeneration of woody and herbaceous species in an oak-pine forest. *Journal of the Torrey Botanical Society* 125:225-236.
- Barden, L.S. and F.W. Woods. 1976. Effects of fire on pine and pine-hardwood forests in the southern Appalachians. *Forest Science* 22: 399-403.
- Christensen, N.L. and R.K. Peet. 1984. Convergence during secondary forest succession. *Journal of Ecology* 72: 25-36.
- Clark, J.S., E. Macklin, and L. Wood. 1998. Stages and spatial scales of recruitment limitation in southern Appalachian Forests. *Ecological Monographs* 68: 213-235.
- Condit, R., N. Pitman, E.G. Leigh Jr., J. Chave, J. Terborgh, R.B. Foster, P. Nunez V., S. Aguilar, R. Valencia, G. Villa, H.C. Muller-Landau, E. Losos, and S.P. Hubbell. 2002. Beta-diversity in tropical forests. *Science* 295: 666-669.
- Connell, J.H. 1978. Diversity in tropical rainforests and coral reefs. *Science* 199: 1302-1310.
- Davis, M.B. Old growth in the east: A survey. Wild Earth. Richmond, VT, USA.
- Day, F.P. and C.D. Monk. 1974. Vegetation patterns on a southern Appalachian watershed. *Ecology* 55: 1064-1074.
- Delcourt, P.A. and H.R. Delcourt. 1998. The influence of prehistoric human-set fires on oak-chestnut forests in the southern Appalachians. *Castanea* 63(3): 337-345.
- Denslow, J.D. 1980. Gap partitioning among tropical forest trees. *Biotropica* 12:47-55.

- Denslow, J.D. 1985. Disturbance-mediated coexistence of species. In *The Ecology of Natural Disturbance and Patch Dynamics*, ed. S.T.A. Pickett and P.S. White, pp 317-323. Orlando, FL: Academic Press, Inc.
- Elliott, K.J., R.L. Hendrick, A.E. Major, J.M. Vose, and W.T. Swank. 1999. Vegetation dynamics after a prescribed fire in the southern Appalachians. *Forest Ecology and Management* 114: 199-213.
- Franklin, J. F. 1993. Preserving biodiversity: species, ecosystems or landscapes? *Ecological Applications* 3(2):202-205.
- Harmon, M.E. 1982. Fire history of the westernmost portion of Great Smoky Mountains National Park. *Bulletin of the Torrey Botanical Society* 109: 74-79.
- Harmon, M.E., S.P. Bratton, and P.S. White. 1983. Disturbance and vegetation response to environmental gradients in the Great Smoky Mountains. *Vegetation* 55: 129-139.
- Harmon, M.E. 1984. Survival of trees after low-intensity surface fires in Great Smoky Mountains National Park. *Ecology* 65: 796-802.
- Hetrick, W.A., P.M. Rich, F.J. Barnes, and S.B. Weiss. 1993. GIS-based solar radiation flux models. *Proc. ASPRS-ACSM Annual Convention*. (Bethesda, MD: ASPRS) 3:132-143.
- Hetrick, W.A., P.M. Rich, and S.B. Weiss. 1993. Modeling insolation on complex surfaces. *Proceedings of the 13th Annual ESRI Users Conference*. (Redlands:ESRI) 2: 447-458.
- Hobbs, R. 1997. Future landscapes and the future of landscape ecology. *Landscape and Urban Planning* 37:1-9.

- Kartesz, J.T. 1994. A synonymized checklist of the vascular flora of the United States, Canada, and Greenland. Volume 1-Checklist. Timber Press, Portland, Oregon.
- Magurran, A.E. 1988. Ecological Diversity and its Measurement. Princeton University Press, Princeton, NJ.
- McCune, B. and M.J. Mefford. 1999. PC-ORD. Multivariate Analysis of Ecological Data, Version 4. MjM Software Design, Glenden Beach, Oregon, USA.
- McNaughton, S.J. and L.L. Wolf. 1970. Dominance and niche in ecological systems. Science 167: 131-139.
- Nekola, J.C. and P.S. White. 1999. The decay of similarity in biogeography and ecology. Journal of Biogeography 26: 867-878.
- Newell, C.L. 1997. Local and regional variation in the vegetation of the southern Appalachian Mountains. Ph.D. dissertation. Curriculum in Ecology, University of North Carolina at Chapel Hill. 1,008 p.
- Newell, C.L. and R.K. Peet. 1998. Vegetation of Linville Gorge Wilderness, North Carolina. Castanea 63(3): 275-322.
- Ohmann, J.H., and T.A. Spies. Regional gradient analysis and spatial patterns of woody plant communities of Oregon forests. Ecological Monographs 68: 151-182.
- Okland, R.H. 1996. Are ordination and constrained ordination alternative or complementary strategies in general ecological studies? Journal of Vegetation Science 7: 289-292.
- Parker, A.J. 1982. The topographic relative moisture index: an approach to soil-moisture assessment in mountain terrain. Physical Geography 3: 60-168.

- Platt, W.J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. *Ecological Monographs* 45: 285-305.
- Plotkin, J.B. and H.C. Muller-Landau. 2002. Sampling the species composition of a landscape. *Ecology* 83(12): 3344-3356.
- Potts, M.D., P.S. Ashton, L.S. Kaufman, and J.B. Plotkin. 2002. Habitat patterns in tropical rain forests: a comparison of 105 plots in northwest Borneo. *Ecology* 83: 2782-2797.
- Routledge, R.D. 1977. On Whittaker's components of diversity. *Ecology* 58: 1120-1127.
- Runkle, J.R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62: 1041-1051.
- Schutler, D. and R.E. Ricklefs. 1993. Species diversity: an introduction to the problem. In: Ricklefs, R.E. and D. Schutler (eds.) *Species diversity in ecological communities: historical and geographical perspectives*, pp. 1-10. University of Chicago Press, Chicago, IL.
- Schnitzer, S.A. and W.P. Carson. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* 82:913-919.
- Tuomisto, H., K. Ruokolainen, R. Kalliola, A. Linna, W. Danjoy, and A. Rodriguez. 1996. Dissecting Amazonian biodiversity. *Science* 269: 63-66.
- Tuomisto, H., K. Ruokolainen, and M. Yli-Halla. 2003. Dispersal, environment, and floristic variation of western Amazonian forests. *Science* 299: 241-244.

- Velland, M. 2001. Do commonly used indices of β -diversity measure species turnover?
Journal of Vegetation Science 12: 545-552.
- Werner, P.A., and W.J. Platt. 1976. Ecological relationships of co-occurring goldenrods
(*Solidago*: Compositae). The American Naturalist 110:959-970.
- Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecological
Monographs 26: 1-80.
- Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California.
Ecological Monographs 30: 279-338.
- Whittaker, R.H. 1965. Dominance and diversity in land plant communities. Science
147: 250-260
- Whittaker, R.H. 1970. Communities and Ecosystems. MacMillan, NY.
- Williams, C.E. 1998. History and status of table mountain pine-pitch pine forests of the
southern Appalachian mountains. Natural Areas Journal 17: 81-90.
- Wimberly, M.C. and T.A. Spies. 2001. Influences of environment and disturbance on
forest patterns in coastal Oregon watersheds. Ecology 82: 1443-1459.
- Wiser, S.K., R.K. Peet, and P.S. White. 1996. High-elevation rock outcrop vegetation of
the southern Appalachian Mountains. Journal of Vegetation Science 7: 703-722.

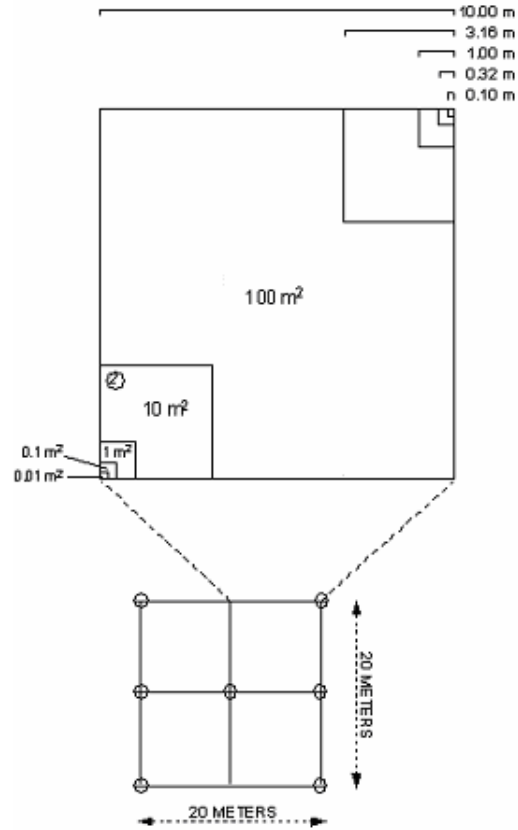


Figure 3.1. Modified setup of Carolina Vegetation Survey Plots (adapted from Peet et al. 1998).

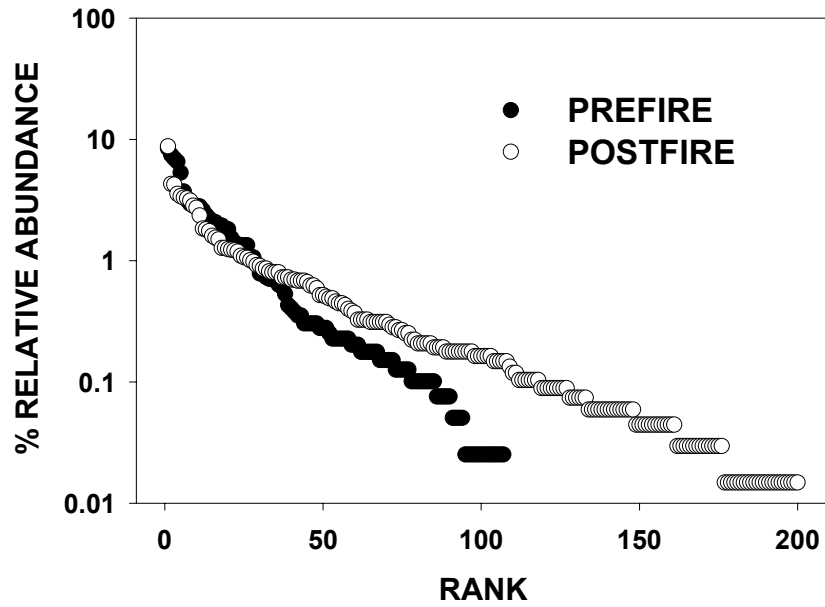


Figure 3.2. Pre- and postfire dominance-diversity curves for all plots.

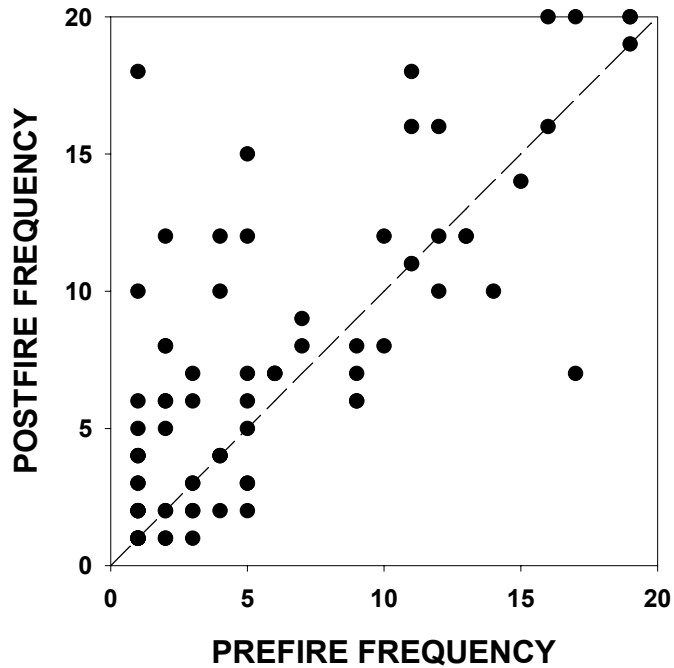


Figure 3.3. A comparison of pre- and postfire frequencies of species present at both sampling periods. Not all points are visible because of overlap of species with the same amount of change.

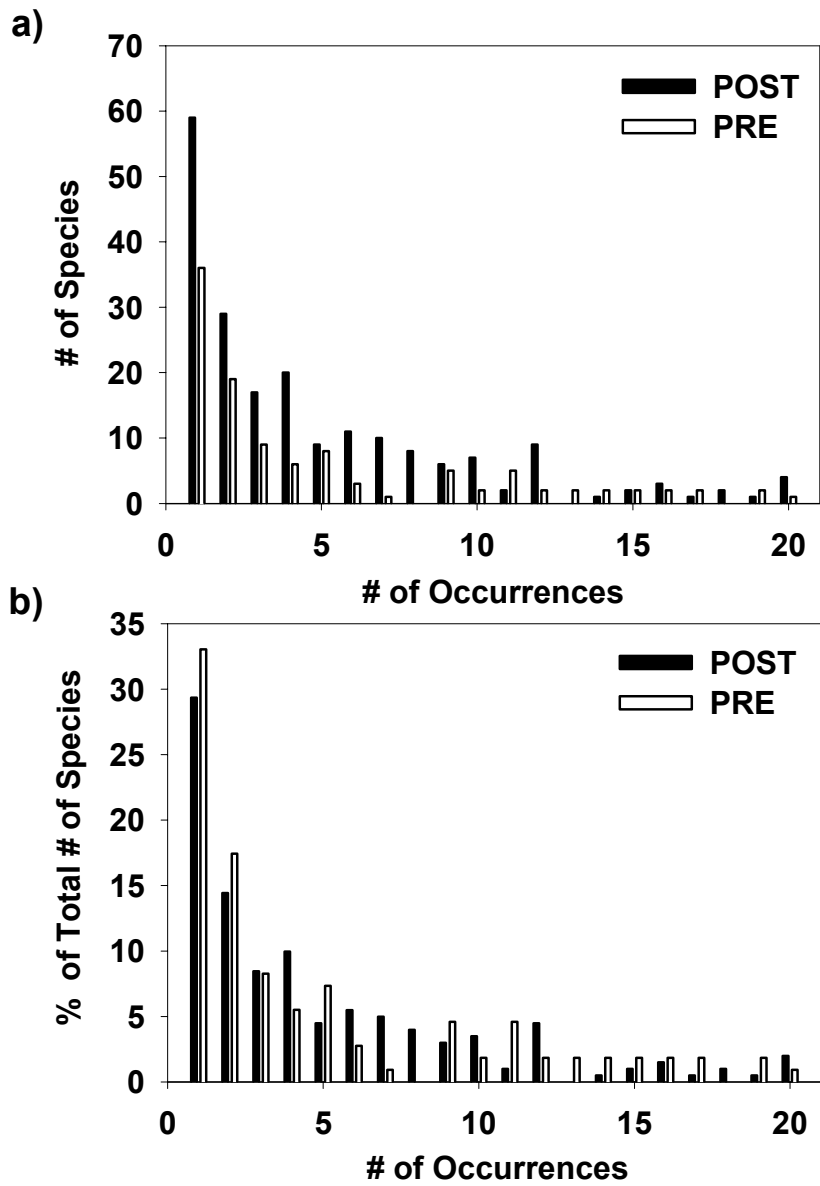


Figure 3.4. Pre- and postfire distributions of a) absolute and b) relative frequency.

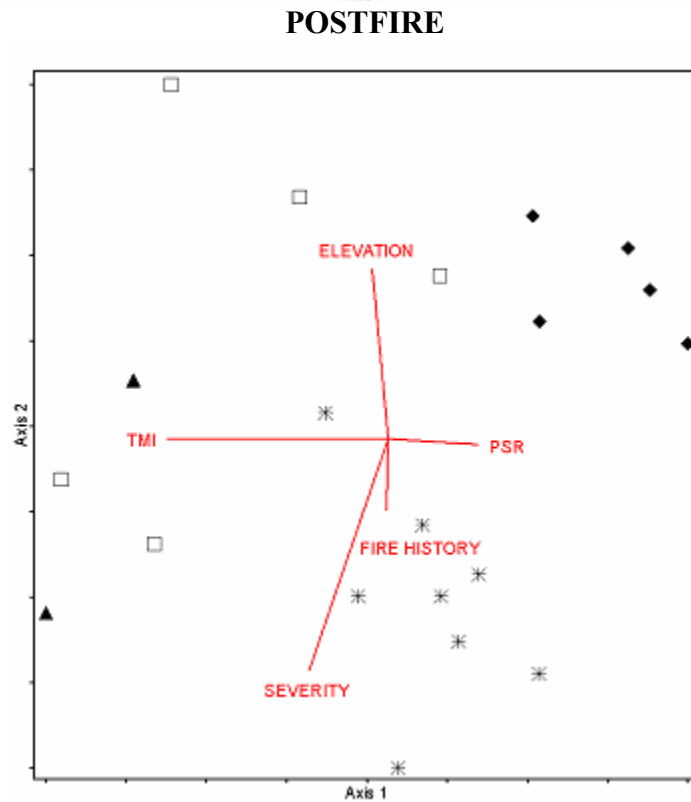
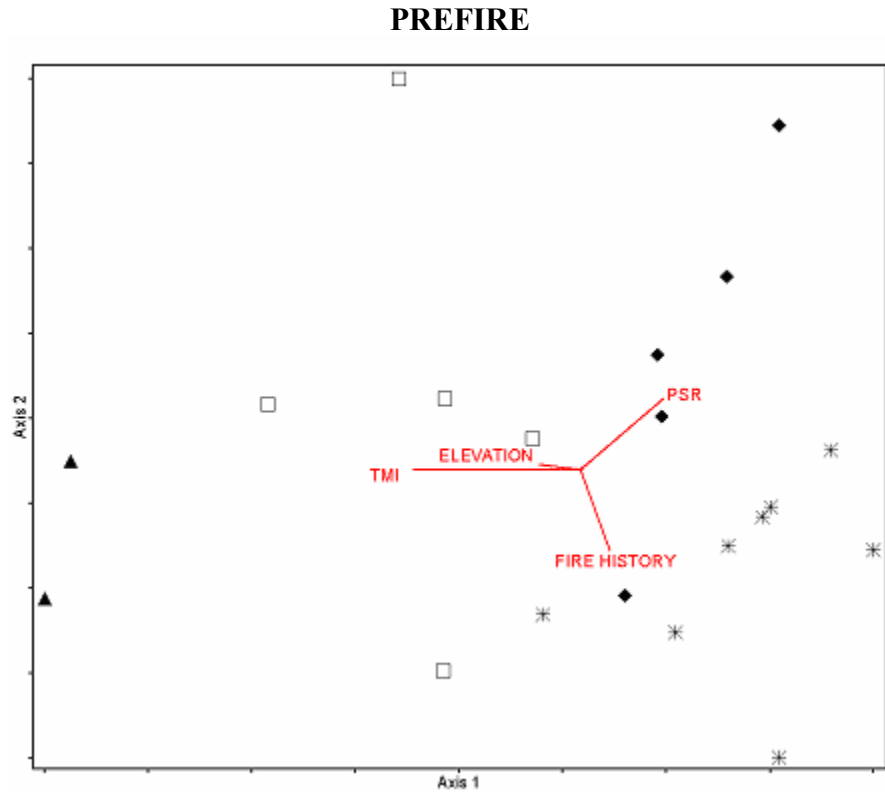


Figure 3.5. Biplots with samples overlain on pre- and postfire NMS ordinations. Thermic pine plots are represented by stars, thermic oak plots by closed diamonds, acidic slope plots by open squares, and acidic cove plots by closed triangles.

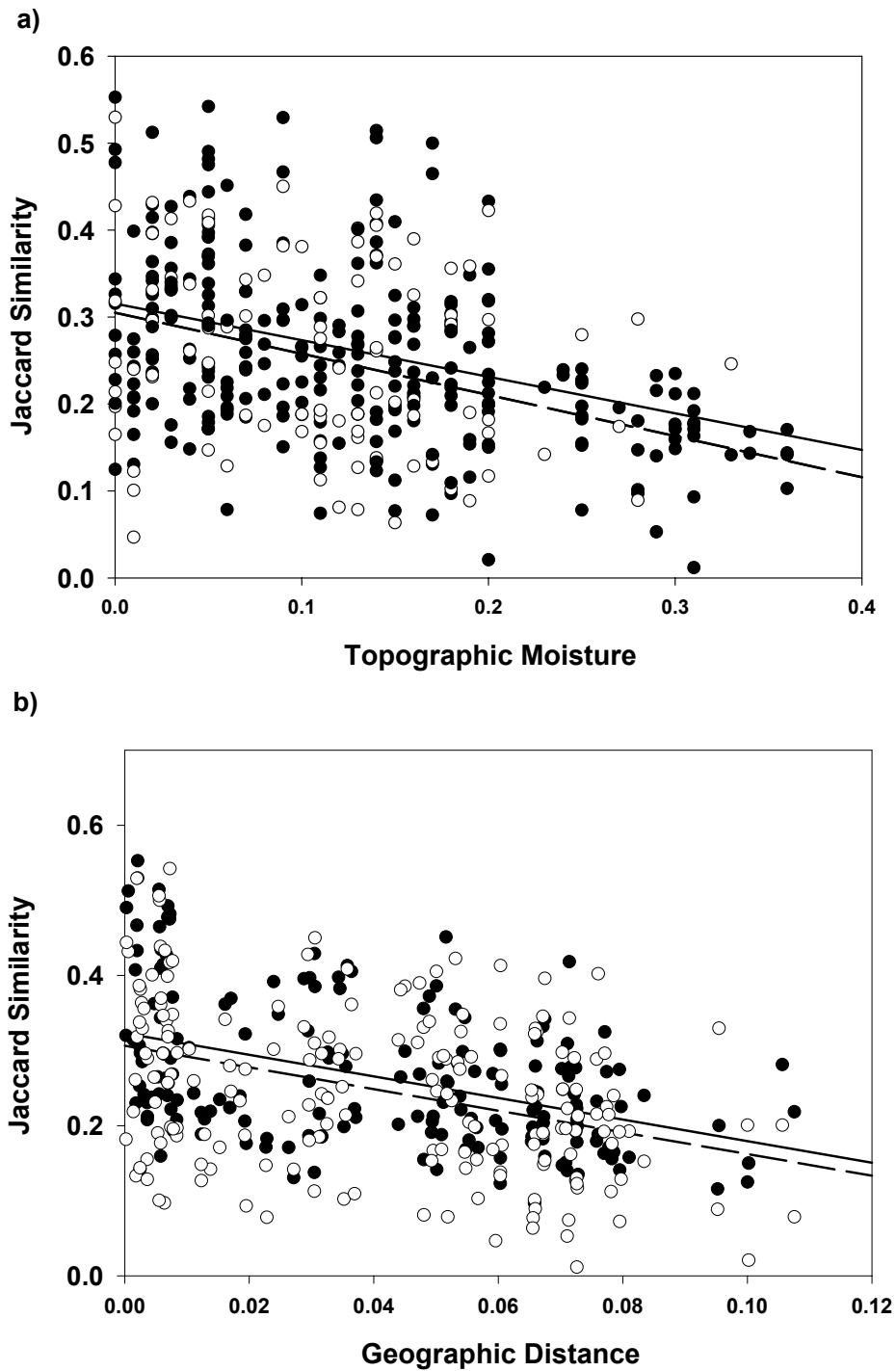


Figure 3.6. Pre- and post-fire decay in similarity over a) geographic distance and b) topographic moisture distance. Open circles and dashed lines are for prefire and closed circles and solid lines are for postfire.

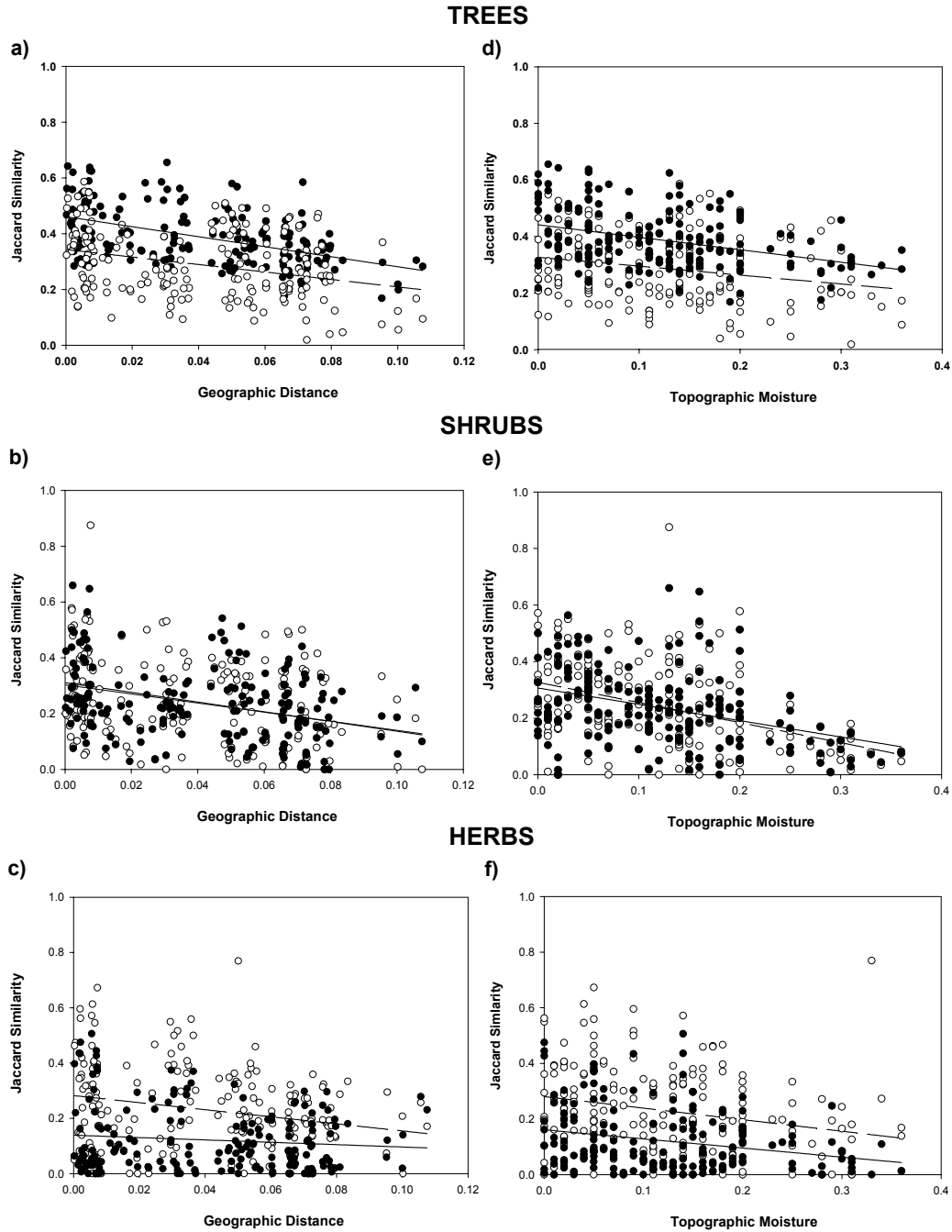


Figure 3.7. Decay in similarity over geographic (a-c) and environmental (d-f) and distance for trees (a,d), shrubs (b,e), and herbs (c,f). Open circles and dashed lines are for prefire and closed circles and solid lines are for postfire.

Table 3.1. Pre- and postfire correlation of first two axes with environmental variables from NMS.

	Prefire		Postfire	
	Axis 1 (p=0.002)	Axis 2 (p=0.001)	Axis 1 (p=0.003)	Axis 2 (p=0.001)
r^2	0.560	0.287	0.386	0.411
	r	r	r	r
TMI	-0.634	0.021	-0.803	-0.020
Potential Solar Radiation	0.450	0.414	0.511	-0.126
Elevation	-0.315	0.111	-0.216	0.703
Fire History	0.266	-0.443	-0.062	-0.457
Severity	-	-	-0.481	-0.822

Table 3.2. Decay in similarity over geographic distance and difference in topographic moisture amongst all plants, trees, shrubs, and herbs.

Distance	Prefire	Post	TMI	Prefire	Post
All	y=0.31-1.44x r=0.38 p<0.001	y=0.32-1.44x r=0.44 p<0.001	All	y =0.30-0.47x r=0.38 p<0.0001	y=0.32-0.42x r=0.39 p<0.0001
Trees	y=0.34-1.34x r=0.32 p=0.001	y=0.46-1.79x r=0.50 p=0.001	Trees	y=0.33-0.32x r=0.23 p=0.035	y=0.44-0.44x r=0.38 p=0.0001
Shrubs	y=0.31-1.74x r=0.32 p=0.001	y=0.30-1.63x r=0.35 p=0.002	Shrubs	y=0.33-0.71x r=0.40 p=0.001	y=0.31-0.58x r=0.38 p=0.003
Herbs	y=0.28-1.28x r=0.24 p=0.007	y=0.139-0.43x r=0.11 p=0.104	Herbs	y=0.28-0.42x r=0.23 p=0.032	y=0.16-0.33x r=0.25 p=0.016

CONCLUSIONS

Although the role of fire in the southern Appalachians has drawn the attention of ecologists since the 1970's (Barden and Woods 1976), there have been few, if any, large scale fires in the last fifty years from which to draw inferences about the ecological role of fire at the landscape scale. Most fires have been small, and extensive prefire has only been available for prescribed fires. Although prescribed fires are a means of reintroducing fire back into the disturbance regime, it is likely that many historical fires burned during times of prolonged drought and resulted in much greater variation in fire severity than might occur under the limited burning conditions for prescribed fires. The occurrence of a large wildfire in Linville Gorge following a prolonged period of drought at the end of the 1990's offered a unique chance to examine the effects of fire at the scale on where fire has most likely operated historically.

Delcourt and Delcourt (1998) hypothesized that prior to European settlement fire maintained landscape heterogeneity across the region by increasing the contrast between plant communities, thus increasing landscape biodiversity. Although Native Americans settled in river valleys, they used fire as a tool to promote hardwood mast along upper slopes and ridges. Fire spread may be rapid on slopes and ridges and capable of covering large areas if not suppressed, but fires usually do not spread into adjacent coves and stream valleys (Bratton and Meier 1995). The effect of the topographic-edaphic gradient on fire severity (Harmon et al. 1983) thus reinforces the underlying moisture gradient that others have found to influence forest community composition (Whittaker 1956).

One major hypothesis in the long term successional patterns of southern Appalachian forests is that the elimination of fire has resulted in an increase in the abundance of fire sensitive species whose presence may have historically been limited to mesic sites (Abrams 1992, Barden and Woods 1976, Harmon 1982). The lack of fire over the last century has allowed fire sensitive species to expand their environmental ranges into more xeric sites, where they now dominate in the understory and midstory of forests. In the continued absence of fire it appears that much of the current dominance of oak (*Quercus*) and pine (*Pinus*) species will be lost. Although the historical role of fire in the dominance of oak species is debatable (Clark and Royal 1996, Abrams and Seischab 1997), it is certainly necessary for the regeneration of pine species (Barden and Woods 1976, Williams 1998, Welch and Walrop 2001). Evidence from these studies clearly suggests that the removal of fire from the disturbance regime of the southern Appalachians will inevitably decrease landscape heterogeneity and overall diversity.

The results of this research offer the first investigation of the effects of fire on changes in plant diversity in the southern Appalachians from the local community to landscape scale. Although there were increases in species richness across all scales after the fire, there was little to no effect on beta diversity and the rate of species turnover along environmental or spatial gradients. These results can be attributed to the high immigration rate of herbaceous species that were represented by few individuals at both the local and landscape level. Though rare in our study relative to the abundance and frequency of other species present prefire, most species that immigrated are ruderal and common in the surrounding “cultural landscape.” Thus, although fire increased species richness dramatically in Linville Gorge, within the surrounding context of the Blue Ridge Escarpment, there was likely no effect of the fire on species richness. At some threshold spatial scale, the effects of the 2000 fire will do little more than result in the shuffling

of species abundances and the slope of the postfire species-area curve must level off and intersect with that of prefire. This effect is evident in trees where dispersal limitation essentially constrains the maximum number of species that can coexist in a small area to the number of species that can disperse in over long distances.

Although fire decreases competitive asymmetries and allows smaller stature species to coexist temporarily with species found temporarily in mature forests, it did little to affect turnover rates or beta diversity of all plant species. However, there was a decrease in the rate of turnover of tree species across Linville Gorge, suggesting that fire increases beta diversity of trees at the landscape scale. This finding supports the idea that in addition to environmental gradients, fire could have been a major factor in the maintenance of forest community diversity. In addition to reinforcing underlying environmental gradients, it limits the abundance of fire-sensitive species moving across the moisture gradient into more xeric sites. Fire also potentially enhances the effects of dispersal limitation by maintaining those populations of species in the understory as sink populations, whereas in the absence of fire these species may grow to reproductive stature and become source populations.

The separation of the role of environmental gradients and disturbance in the southern Appalachians is not possible in the current thesis. What may potentially be useful in future work is to include sampling of as many unburned plots as burned. Though much of Linville Gorge was burned in the fire of 2000 there is still a large portion of the pine and oak dominated forest that did not burn. While comparing pre- and postfire data has revealed insights into the effects of fire across the landscape on alpha and beta diversity, sampling unburned forests would provide a control to investigate the fate of different types of species diversity in the absence of fire. Pine dominance has already been decreased in unburned forest due to an outbreak of the southern pine

beetle during the drought of the late 1990's. As dominant overstory trees in unburned thermic pine and oak forests senesce, succession may be accelerated and allowing sink populations of more mesic species present in the understory to become sources (Abrams and Scott 1989). Over the next decade it is likely that those unburned pine and oak forests will reach thresholds past which the possibility of restoring and maintaining fire dependent communities is eliminated, decreasing overall landscape diversity and heterogeneity in Linville Gorge.

Literature Cited

- Abrams, M.D. and M.L. Scott. 1989. Disturbance-mediated accelerated succession in two Michigan forest types. *Forest Science* 35:42-49.
- Abrams, M.D. & Seischab, F.K. (1997) Does the absence of sediment charcoal provide substantial evidence against the fire and oak hypothesis? *Journal of Ecology* 85: 373-375.
- Barden, L.S. and F.W. Woods. 1976. Effects of fire on pine and pine-hardwood forests in the southern Appalachians. *Forest Science* 22: 399-403.
- Bratton, S.P. and A.J. Meier. 1995. The natural disturbance history of the Chattooga watershed: written records. United States Forest Service, Chattooga River Demonstration Project, Clemson, South Carolina.
- Clark, J.S. and P.D. Royall. 1996. Local and regional charcoal evidence for fire regimes in presettlement north-eastern North America. *Journal of Ecology* 84: 365-382.
- Delcourt, H.R. and P.A. Delcourt. 1997. Pre-Columbian Native American use of fire on southern Appalachian landscapes. *Conservation Biology* 11: 1010-1014.
- Harmon, M.E. 1982. Fire history of the westernmost portion of Great Smoky Mountains National Park. *Bulletin of the Torrey Botanical Society* 109: 74-79.
- Harmon, M.E., S.P. Bratton, and P.S. White. 1983. Disturbance and vegetation response to environmental gradients in the Great Smoky Mountains. *Vegetation* 55: 129-139.
- Welch, N.T. and T.A. Waldrop. 2001. Restoring table mountain pine (*Pinus pungens* Lamb.) communities with prescribed fire: an overview of current research. *Castanea* 66: 42-49.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecological
Monographs 26: 1-80.

Williams, C.E. 1998. History and status of table mountain pine-pitch pine forests of the
southern Appalachian mountains. Natural Areas Journal 17: 81-90.