RECOVERY AND RESILIENCE OF APPALACHIAN HERBS

By

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# TABLE OF CONTENTS

ACKNOWLEDGEMENTS ........................................................................................................ ii  

LIST OF TABLES ........................................................................................................ vi  

LIST OF FIGURES ....................................................................................................... v  

CHAPTER I

Introduction ................................................................................................................ 1  

CHAPTER II

Century-old logging legacy on spatial and temporal patterns among herbaceous species within Southern Appalachian cove forests

ABSTRACT ................................................................................................................. 27  

INTRODUCTION ....................................................................................................... 28  

MATERIALS AND METHODS .................................................................................. 31  

RESULTS ............................................................................................................... 37  

DISCUSSION ............................................................................................................ 40  

LITERATURE CITED ............................................................................................... 46  

CHAPTER III

Decoupling of herbaceous layer composition from the abiotic environment after long term recovery from large-scale disturbance

ABSTRACT ................................................................................................................. 73  

INTRODUCTION ....................................................................................................... 75  

MATERIALS AND METHODS .................................................................................. 78  

RESULTS ............................................................................................................... 84  

iv
<table>
<thead>
<tr>
<th>Chapter IV</th>
<th>Fine-scale spatial patterns in an understory Appalachian herb community</th>
</tr>
</thead>
<tbody>
<tr>
<td>ABSTRACT</td>
<td>.............................................................................................115</td>
</tr>
<tr>
<td>INTRODUCTION</td>
<td>..........................................................................................116</td>
</tr>
<tr>
<td>MATERIALS AND METHODS</td>
<td>.................................................................120</td>
</tr>
<tr>
<td>RESULTS</td>
<td>.............................................................................................123</td>
</tr>
<tr>
<td>DISCUSSION</td>
<td>.............................................................................................127</td>
</tr>
<tr>
<td>LITERATURE CITED</td>
<td>..................................................................................131</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Chapter V</th>
<th>A trait based analysis of coexistence mechanisms in the understory herb layer of rich cove forests</th>
</tr>
</thead>
<tbody>
<tr>
<td>ABSTRACT</td>
<td>.............................................................................................156</td>
</tr>
<tr>
<td>INTRODUCTION</td>
<td>..........................................................................................158</td>
</tr>
<tr>
<td>MATERIALS AND METHODS</td>
<td>.................................................................162</td>
</tr>
<tr>
<td>RESULTS</td>
<td>.............................................................................................167</td>
</tr>
<tr>
<td>DISCUSSION</td>
<td>.............................................................................................171</td>
</tr>
<tr>
<td>LITERATURE CITED</td>
<td>..................................................................................176</td>
</tr>
</tbody>
</table>

| Chapter VI | Conclusion ......................................................................212 |
| CURRICULUM VITAE | ...........................................................................217 |
LIST OF TABLES

Table II – 1: Species, phenological groups and number of plots present in at each old
  growth and mature site.................................................................55
Table II – 2: Indicator species for mature and old growth forests .........................59
Table II – 3: Significance of the randomization process for partitioning diversity at each
  level for all, old growth and mature forest ages and each phenology.................60
Table III – 1: Highest scoring species along each axis of the partial canonical
  correspondence analysis in old growth forests ......................................104
Table III – 2: Highest scoring species along each axis of the partial canonical
  correspondence analysis in mature forests ..........................................105
Table IV – 1: Primary dispersal vectors reported for understory herb species..........140
Table IV – 2: Regressions between species spatial index and plot species richness in
  early spring and late spring...............................................................141
Table IV – 3: Regressions between species spatial index and plot abundance...........142
Table IV – 4: Regressions between species spatial index and percent canopy cover....143
Table V – 1: List and abbreviations of the 51 species that occurred in > 5% of the plots
  and were measured for functional traits..............................................188
Table V – 2: Functional traits for light, nutrient and water use..........................189
Table V – 3: Percent of plots with significant trait underdispersion and overdispersion
  for the nearest neighbor for all, mature and old growth plots....................190
Table V – 4: Percent of plots with significant trait under- and over-dispersion for nearest
  interspecific neighbor within 5 cm for all, mature and old growth plots.........191
LIST OF FIGURES

Figure II – 1: Diversity sampling design for each cove forest………………………………64
Figure II – 2: Nested sampling design with four hierarchical scales ……………………..65
Figure II – 3: Additive partitioning model…………………………………………………66
Figure II – 4: Boxplot of species richness for old growth and mature forests for all species and each phenology……………………………………………………….67
Figure II – 5: Boxplot of abundance for old growth and mature forests for all species and each phenology……………………………………………………….68
Figure II – 6: Rarefaction of mean species richness for old growth and mature forests...69
Figure II – 7: Percent of diversity partitioned into within and among components……70
Figure II – 8: Percent of diversity partitioned into within and among components within old growth and mature forests…………………………………………………71
Figure II – 9: Non-metric multidimensional plot for forest age and herb layer composition……………………………………………………………………………72
Figure III - 1: Partitioning of species composition variation into environmental, spatial, combined environmental and spatial, and unexplained components………………108
Figure III - 2: Histogram of ramet abundance for all species………………………….109
Figure III - 3: Boxplots showing the range and median of macronutrients in old growth and mature forests………………………………………………………….110
Figure III - 4: Boxplots of micronutrients in old growth and mature forests………….111
Figure III - 5: Boxplots of aboveground environmental parameters in old growth and mature forests…………………………………………………………….112
Figure III - 6: Boxplots of litter depth, ammonium, nitrate, organic matter, total exchangeable cations, pH and SMP buffer in old growth and mature forests.

Figure III - 7: Partitioning variation in species composition for all species and each phenology in old growth and mature forests.

Figure IV – 1: Boxplot of spatial pattern index for all species across all plots in early spring.

Figure IV – 2: Boxplot of spatial pattern index for all species across all plots in late spring.

Figure IV – 3: Boxplot of mean spatial index for old growth and mature forests in early spring.

Figure IV – 4: The number of plots each species is aggregated in early spring.

Figure IV – 5: The number of plots each species is aggregated in late spring.

Figure IV – 6: Boxplot of mean spatial index for old growth and mature forests in late spring.

Figure IV – 7: Principle component analysis of soil variables.

Figure IV – 8: Boxplot of spatial pattern index for species categorized according to dispersal mode.

Figure IV – 9: Boxplot of spatial pattern index for clonal versus non-clonal species.

Figure V – 1: Flow chart showing the analysis for trait under- and over-dispersion among nearest neighbors.

Figure V – 2: Histograms of individual trait distances for leaf area and total chlorophyll content.
Figure V – 3: Histograms of individuals trait distances for chlorophyll a:b ratio and leaf lobation................................................................. 197

Figure V – 4: Histograms of individuals trait distances for thickest root diameter and leaf shape................................................................. 198

Figure V – 5: Histograms of individuals trait distances for specific leaf area (SLA) and succulence................................................................. 199

Figure V – 6: Boxplots of total chlorophyll concentrations............................................. 200

Figure V – 7: Boxplots of chlorophyll a:b ratios......................................................... 201

Figure V – 8: Boxplots of leaf area measurements..................................................... 202

Figure V – 9: Boxplots of leaf shape ................................................................. 203

Figure V – 10: Boxplots of leaf lobation............................................................. 204

Figure V – 11: Boxplots of thickest root diameter................................................... 205

Figure V – 12: Boxplots of specific leaf area.......................................................... 206

Figure V – 13: Boxplots of leaf succulence............................................................ 207

Figure V – 14: Correlations between early spring canopy cover, sulfur, aluminum, ammonium with mean plot trait distances for leaf area, chlorophyll a:b and root diameter................................................................. 208

Figure V – 15: Correlations between sodium, litter depth, SMP buffer and tree species richness with mean plot trait distances for leaf shape and specific leaf area...... 209

Figure V – 16: Principal component analysis of mean trait plot values for old growth and mature forests................................................................. 210
ABSTRACT

Wyatt, Julie L.

RECOVERY AND RESILIENCE OF APPALACHIAN HERBS

Dissertation under the direction of Miles R. Silman, Ph.D.

The herbaceous layer of rich cove forests in the Southern Appalachians represent one of the highest biodiversity habitats in North America. These forests, however, have undergone large-scale logging disturbance that has altered 99% of the original forested landscape, leaving few old growth forests. With logging rotations of 100 – 150 years, understanding long-term recovery and resilience in the diverse herb community in terms of not just diversity, but also the processes structuring the community is necessary for understanding and conserving this species rich community. The studies presented here address long-term recovery of the herbaceous community while taking into account spatial and temporal variation in the community. Intersite heterogeneity was accounted for by comparing paired sites of old growth forest and mature forest that were logged 100 – 150 years ago. To address both patterns and processes, several components of the herb layer were addressed: species richness, abundance, composition, spatial patterns, environmental filtering and trait based species assembly. The results demonstrate that understory herb communities do not return to their pre-disturbance states even after over a century of recovery in nearly all important respects. Both species richness and abundance was greater in old growth forests than mature forests, and species composition differed significantly between the two. The mechanisms that assemble communities play out over long time scales and different processes operate in old growth forests compared to mature forests. Species composition in old growth forests is largely explained by
environmental variables while mature forests have not reached equilibrium with the environment. Environmental filtering happens slowly over time with less and different environmental coupling in logged forests. Additionally, mechanisms of competitive coexistence are not yet fully structured in mature forests. Succession in the understory herb layer of cove forests takes much longer than suspected, and recovery time exceeds the 100 – 150 years between harvest rotations. These findings show that mature forest stands should not be used as a baseline for herb layer recovery. Continued assessment over time will determine if and when the herb layer regains the species richness, abundance, composition and, more importantly, the ecological processes that interact to form communities in old growth forests.
CHAPTER I

INTRODUCTION

At this rural retirement were assembled a charming circle of mountain vegetable beauties;...Anemone thalictroides, Anemone hepatica, Erythronium maculatum, Leontice thalictroides, Trillium sessile, Trillium cern, Cypripedium, Arethusa, Ophrys, Sanguinaria...Some of these roving beauties stroll over the mossy, shelving, humid rocks...bending over the floods, salute their delusive shade, playing on the surface; some plunge their perfumed heads and bathe their flexible limbs in the silver stream; whilst others by the mountain breezes are tossed about, their blooming tufts bespangles with pearly and chrystaline dew-drops collected from the falling mists...

William Bartram, Travels, pg. 280

The diverse plant community described by Bartram occurs in the understory of eastern deciduous forests and puts on spectacular displays, attracting thousands of visitors to Southern Appalachian parks every spring (Meier et al 1995). Early explorers and naturalists to these forests commented on the widespread and abundant occurrence of wildflowers in the understory (Bartram 1792, Gray 1841). These forests of eastern North America underwent extensive clear cutting over the past century (Meier et al. 1996) with old growth forests now covering less than 1% of the original forested landscape (Davis 1993). The impact of logging on the understory herb community became a concern with Duffy and Meier (1992) first reporting reduced species richness 87 years after logging. With logging rotations rarely longer than 150 years, understanding long term recovery and resilience in the diverse herb community in terms of not just diversity, but also the processes structuring the community is necessary for understanding and conserving this species rich community.
The mosaic of forest communities across the landscape with varying ages makes up the larger community, or metacommunity, of eastern deciduous herbs. The metacommunity concept links spatial and temporal scales, providing insights not observed within a single, local community (Leibold et al. 2004). This community of communities approach provides an opportunity to address not only the recovery and resilience of the diverse herb layer, but also address larger ecological processes of community assembly and structure across spatial and temporal scales.

In this dissertation, I investigated whether an understory herb community of rich cove forests was resilient to large scale logging disturbance that occurred over a century ago. Several components of the herb layer: diversity, abundance, species composition, environmental filtering, fine-scale spatial patterns and species assembly based on traits are addressed. Each of these components was placed in a metacommunity framework by incorporating spatial scales and seasonal community variation. To establish a context for this research, I introduce the processes determining community assembly and how disturbance can impact these processes. I then provide background on the understory herb community of rich cove forests in the Southern Appalachians.

Species assembly

Understanding the assembly of species into communities is a core tenet of ecology (Gleason 1927, Clements 1938, Cody and Diamond 1975, Weiher and Keddy 1999, Ernest et al. 2008). Recent mechanistic models of community assembly have focused on niche based processes (Chase 2003, Tilman 2004) or processes involving dispersal and stochastic demographics (Hubbell 2001). These models differ in where the
emphasis is placed (Ernest et al. 2008). Hubbell (2001) emphasized dispersal and demographic stochasticity to the exclusion of niche based processes. Other models have combined both niche and neutral processes for explaining community structure (Tilman 2004). Regardless of the model used, community assembly is a filtering process (Belyea and Lancaster 1999). The objective in ecology is to determine the relative strength and importance of each filter for determining community structure.

Community Assembly

The species that make up any given local community come from a regional species pool. For a species to occur in a given community, they must go through multiple filters. First, species must be able to disperse into a habitat. Once species arrive there are environmental filters that determine whether a species can survive within a habitat (Keddy 1992). In addition, there are biotic filters such as competition and predation that can limit membership into a community. Dispersal combined with environmental and biotic filters determine which species comprise the local community. The relative role of each of these filters may vary among communities and across spatial and temporal scales.

Dispersal limitations

Spatial processes are essential for determining whether species make it from the regional species pool to the local metacommunities (Tilman and Kareiva 1997). This has been established since Gleason (1927) observed that different species colonize the same environments. The mode of dispersal combined with distance to the local community can affect a species probability of arriving. The location of the local community and any
landscape barriers can affect dispersal rates. High connectivity and high dispersal rates homogenize species composition among local communities (Chase 2003). Those species with long distance dispersal vectors are more likely to colonize communities. Arrival of a species is not only dependent on the dispersal vector, but also the fecundity. This gives a range of strategies, from ruderal species that are wind-dispersed and produce large quantities of seeds to those species that produce few seeds and have limited dispersal ability (Grime 1977). The disparity in dispersal vectors and seed quantity along with stochastic probabilities of arrival comprises the first filter for community assembly.

Environmental filters

Not all the species that disperse into a local community can survive and become part of the community due to the abiotic conditions present. Environmental filters act by removing species from the pool that lack the traits necessary to survive in the habitat (Booth and Swanton 2002). Environmental filters such as soil nutrients, light and moisture can limit the establishment and survival of species within a community (Facelli and Pickett 1991b, Adkison and Gleeson 2004, Bellemare et al. 2005). Environmental filters between vegetation and climate have been established at regional and global scales (Woodward and Williams 1987). In addition, Diaz et al. (1998) found that environmental conditions were associated with plant attributes along a steep regional gradient. At smaller scales, microsite selection can also filter species assembly (Beatty 2003, Elmarsdottir et al. 2003).
**Biotic filters**

If species can disperse into a local community and have the necessary traits for the environmental conditions, then they must pass through any biotic filters. Biotic filters include competition, predation or mutualism that can limit species from recruiting and surviving in a local community. Competition can occur directly between individuals and limit the ability of species to coexist (Lotka 1926, Volterra 1926, May 1973, Cody and Diamond 1975). Interactions with seed predators, herbivores or pathogens can also play a critical role in determining which species assemble into a local community (Bruehl 1987, Tofts and Silvertown 2002, Burt-Smith et al. 2003, Garcia and Houle 2005). Mutualistic interactions such as the presence of soil mycorrhizae also influence the structure and composition of plant communities (van der Heijden et al. 1998, Koide and Dickie 2002). Those species that pass through the dispersal, environmental and biotic filters comprise the local community.

**Disturbance**

Disturbance can be an additional filter in the process of community assembly by filtering out those species that are not capable of surviving or re-colonizing after a disturbance event. Natural disturbances (eg. fire and hurricanes) can maintain species diversity and often result in low species turnover because many of the species are resistant to the disturbance (Zavala and Zea 2004, Morrison and Spiller 2008, Pausas and Verdu 2008). Anthropogenic disturbance, however, introduces a novel filter to the local community that can alter species assembly. Anthropogenic disturbance can come in a variety of forms such as land conversion, invasive species, or the loss of herbivores,

**Community resilience**

An important question to address is whether alterations in community assembly filters due to disturbance result in changes in species composition. Addressing how resilient communities are to disturbance is essential for conservation and restoration of plant communities. Community composition has an important role in ecosystem functioning (Wedin and Tilman 1993, Hobbie 1996, Tilman 1999). Species differ in their traits and how they function in the environment in terms of water, nutrient and light use which impacts ecosystem processes (Hooper and Vitousek 1997). Nutrient dynamics, productivity and invisibility have all been tied to species composition (Tilman 1999). Changes in species composition due to anthropogenic disturbance can alter ecosystems processes, so it is critical to understand whether communities are resilient to disturbance.

**Ideal community**

Diverse plant communities provide the ideal setting to address the role of filters in community composition. Within the temperate zone, rich cove forests of the Southern Appalachians harbor some of the highest plant diversity (Cain 1943, Whittaker 1956). Coves are mesic forests that occur in sheltered concave stream drainages with north-facing slopes (Braun 1950, Whittaker 1956, Glenn-Lewin 1977, Whittaker and Levin
In the Southern Appalachians, cove forests are found primarily at low to mid-elevations (700 – 1200 m) and represent a small fraction of the area in the Southern Appalachians, but they contain some of the highest diversity (Ford et al. 2000).

**Abiotic environment**

The topography of coves gives unique abiotic conditions in the amount of incident light, temperature regimes, moisture availability and soil properties. The topography of a cove reduces both the duration and intensity of light providing a shady environment when the canopy is leafed out. During leafless periods (winter/spring) there is more radiation on the forest floor; however, the topography of the cove still reduces incident light. The shape of a cove brings in runoff moisture from all sides and is collected in the depression (Parker 1987). Cove hardwood forests receive 127-152 cm of rain annually (Olano and Palmer 2003). As a result, they are very moist habitats and have rich, deep soil due to acting as a catchment for the build up of organic matter. Coves are pockets of high nutrients in the highly eroded slopes of the Southern Appalachians where low cation availability is the norm (Ulrey 2002). Topography of coves also alters the temperature regime with cold air drainage from the upper slopes creating cold night time temperatures. Due to the low intensity and duration of light in coves (especially north-facing coves), the temperature remains relatively cool during the day as well (Bolstad et al. 1998).

**Vegetation**

The abiotic and topographic conditions of rich coves create an ideal habitat for a diverse array of species. Cove forests are characterized by high diversity of plant species
in both the overstory and understory due to the abundant moisture and nutrients. The overstory is dominated by mesic, shade-tolerant species. Characteristic tree species of cove forests include *Acer saccharum*, *Aesculus octandra*, *Betula lutea*, *Fagus grandifolia*, *Halesia carolina*, *Liriodendron tulipifera*, *Quercus rubra* and *Tilia heterophylla* (Schafale and Weakly 1990). However, most of the diversity is found in the understory herb layer. On average, for every tree species there are six herb species in the understory (Gilliam 2007). The understory herbaceous layer is characterized by *Actaea pachypoda*, *Asarum canadense*, *Caulophyllum thalictroides*, *Viola canadensis*, *Hepatica acutiloba*, *Laportea canadensis*, *Polygonatum biflorum*, and *Tiarella cordifolia* (Schafale and Weakly 1990).

Due to life history characteristics of understory herbs, they are susceptible to disturbance and act as indicators of forest site quality (Jolls 2003). Most woodland herbs are perennial (94%) and exhibit clonal growth (Neufeld and Young 2003, Whigham 2004). Life spans can range from 1 – 50 years (Bender et al. 2000, 2002, Whigham 2004). Many of these species are slow growing, taking years to reach reproductive maturity (Bierzychudek 1982). For example, *Trillium* species take at least 7 years to go from germination to producing first flower (Patrick 1973). Species within the understory have distinct temporal guilds based on leaf phenologies. In addition they have clumped distributions due to dispersal limitation and clonal growth (Bierzychudek 1982).

**Phenology**

Variability in light levels and temperature throughout the year is utilized by different temporal guilds in the understory. These temporal guilds include spring
ephemerals, summer greens, wintergreens and evergreens. Spring ephemerals are those species that leaf out in early spring and senesce prior to canopy closure. They are shade intolerant, but can tolerate low temperatures by staying close to the soil surface. To take advantage of this early growing season, they photosynthesize as soon as their leaves expand with high photosynthetic rates and low shade acclimation (Lapointe 2001). Low soil temperatures restrict water absorption, which is necessary for high photosynthetic rates. Optimal temperature for photosynthesis in spring ephemerals is ~ 20°C which has been attributed to high protein content in leaves to offset low enzymatic activity (Mamushina and Zubkova 1996).

Most of the understory species in temperate deciduous forests are summer greens (Uemura 1994). These species usually emerge prior to canopy closure, but after the temperatures have increased. However, unlike spring ephemerals, they retain their leaves throughout the summer. Summer greens generally senesce their leaves in late summer or fall (Neufeld and Young 2003). Carbon gain occurs primarily before canopy closure with more than half of the total annual carbon gained during this brief window (Rothstein and Zak 2001). Temperatures generally rise high enough for adequate carbon gain during the period before canopy closure (Graves 1990). Summer greens, unlike spring ephemerals, can tolerate the shade and assimilate some carbon in the low light conditions beneath a closed canopy. Due to light competition after canopy closure, summer greens are the tallest of the phenologies (Neufeld and Young 2003).

Two leaf phenologies, wintergreens and evergreens, have leaves present during the winter when both spring ephemerals and summer greens are dormant. Wintergreens have overwintering leaves that are produced in late summer or fall and are lost the
following late spring or summer (Uemura 1994). Evergreens are those species that retain their leaves for more than one year (Neufeld and Young 2003). Even though both evergreens and wintergreens have leaves present in early spring, their photosynthetic capacity is much lower than spring ephemerals (Gonzalez 1972, McCarron 1995). Evergreens gain limited amounts of carbon during the shaded summer months when wintergreens are dormant. Both phenologies gain most carbon during spring and fall when temperatures are moderate and light levels are highest (Neufeld and Young 2003).

**Dispersal**

Seed production varies greatly among herbaceous species with some species failing to produce seeds for several years (Whigham 2004) and others producing copious quantities (Kawano 1975). Most understory herbaceous species invest more in asexual reproduction than sexual reproduction (Whigham 2004). Herbaceous species seeds range from 0.03 mg for *Desmodium glutinosum* to 34.4 mg from *Arisaema triphyllum* with a median weight of 1.8 mg (Bierzychudek 1982). Dispersal distances are known for few herbaceous species (Cain et al. 1998). For those species that have been studied, dispersal includes ant, bird, wind and ballistic vectors with dispersal distances often < 1 m and occasionally > 10 m (Bierzychudek 1982, Matlack 1994, Cain et al. 1998). Long distance dispersal by deer is possible, although little is known on this vector for forest herb species (Myers et al. 2004).
Clonal growth

Many woodland herbs have clonal growth with varying degrees of patch size and physiological integration (Jonsdottir and Watson 1997). Species range from having small to large patches with either short- or long-lived connections between ramets (Whigham 2004). *Podophyllum peltatum* is an example of an herb with large patches that are highly integrated with long-lived connections (Landa et al. 1992). Clonal growth provides a competitive edge in high density communities (Stoll and Prati 2001) and allows species to forage for resources (Hutchings and Dekroon 1994).

Logging disturbance

Small-scale disturbances are commonplace in temperate forests under natural conditions through canopy gaps which are quickly recolonized (Thompson 1980a, Beatty 1984). Anthropogenic activity has increased the size, frequency and intensity of disturbances through large-scale timber extraction (Brunet and von Oheimb 1998). In 1923, 822 million acres in eastern North America were covered with old growth forests (Leverett 1996). Over the past century, these forests have been extensively logged and clear cut (Meier et al. 1996). East of the Mississippi, forests in National and State parks and forests comprise approximately 12,960,000 acres. No large tracts of continuous old growth forest remain; however, there are numerous remnants that have been reduced to small tracts of 10 to 100 acres. Today old growth forests are estimated to cover 750,000 acres (0.09% of the original area) due to harvesting and clear cutting (Davis 1993).

Most of the logging took place at the turn of the century by private lumber companies. In the Southern Appalachians, 50% of the timberlands were owned by large
private companies in 1901 (Yarnell 1998). In the twenty years that followed, narrow logging railroads combined with overhead cables enabled harvesting from remote mountains (Lambert 1961). Harvesting methods caused extensive damage to the understory due to skidding massive logs out of the forests. This caused large disturbances to the soil including leaching and erosion along with increased fire frequency (Mastran and Lowerre 1983).

After the majority of the forests were logged, they underwent natural regeneration (United States Department of Agriculture 1994). Today these forests have been recovering for over a century and are referred to as mature forests. Studies often compare recently harvested areas to mature forests, despite that mature forests may still be recovering from previous disturbance (Ford et al. 2000). Recommendations for timber harvesting based on mature forests may not give an adequate representation of patterns and processes in the herbaceous layer in the absence of anthropogenic disturbance. While reduced to small relicts in eastern North America, old-growth forests serve as important controls for studying natural processes (McCarthy 2003).

Old Growth Forests

Old growth forests are those forests that have never been harvested for timber and show little evidence of anthropogenic disturbance (Meier et al. 1995). They contain massive living trees over 200 years old and an average basal area of 25 m²/ha. Canopy structure is uneven due to natural tree regeneration (Martin 1992). Old growth forests are also characterized by gap-phase dynamics that increase light availability in the understory (Martin 1992, Busing 1998, Bellemare et al. 2002). Natural tree mortality results in
standing snags and downed logs at varying stages of decay and creates microtopophy in the understory with the formation of pits and mounds (Beatty 1984, Hardt and Swank 1997, Miller et al. 2002, Christie and Armesto 2003). These characteristics distinguish old growth forests from mature forests and may have important implications for the patterns and processes occurring in the understory herb layer.

**Objectives**

The objective of this study was to determine whether the understory herb community of rich cove forests is resilient to large scale logging disturbance that occurred over a century ago. To address resilience I looked at several components of the herb layer to determine not only if community composition differs, but also how the processes driving communities differ between old growth forests and mature forests logged over a century ago. First I addressed how species diversity, abundance and composition changes in recovering forests in comparison to old growth forests across spatial scales and with phenology. Next, I determined whether the processes that govern species composition - dispersal limitation and environmental filtering - operate similarly in old growth and previously logged forests while taking into account temporal niches of leaf phenology. Then fine-scale patterns of aggregation were assessed in both aged forests to determine whether the spatial components of the herb community are consistent between old growth and hundred year forests. Finally, I addressed fine scale interactions between nearest neighbors to determine how species assemble in this diverse community. I used a trait based approach to determine how neighboring individuals and species coexist- whether by niche partitioning or environmental filtering. I addressed how
neighbors interact in old growth forests and whether the process of species assembly operates the same in hundred year old forests.

Addressing how resilient communities are to disturbance is essential for conservation and restoration of plant communities. However, to address resilience it is necessary to understand the patterns and processes that occur in old growth forests to establish a baseline. Knowing the underlying patterns and process sets the stage for assessing recovery and resilience of Appalachian herbs after large-scale logging disturbance over a century ago. This study provides a mechanistic understanding of understory herb communities and the implications of current forest management on this community. The goal of this study is to be able to accurately understand Appalachian herb community structure and diversity under large-scale forest disturbance regimes. It is crucial to know how communities respond to disturbance for conservation efforts to be most effective.
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CHAPTER II

CENTURY-OLD LOGGING LEGACY ON SPATIAL AND TEMPORAL PATTERNS AMONG HERBACEOUS SPECIES WITHIN SOUTHERN APPALACHIAN COVE FORESTS

Abstract

Over a decade ago, a debate began over whether understory plant communities recover to their pre-disturbance states following logging. Evidence showing reduced diversity in previously logged forests was criticized for not accounting for intersite environmental heterogeneity. Recent studies have addressed environmental heterogeneity, but have neglected long-term recovery by using mature forests as the benchmark for diversity comparison. Here we address both of these concerns and investigate long-term recovery of an understory herbaceous community by comparing paired sites of old growth forest and forest logged over a hundred years ago. A hierarchical nested sampling design was used to additively partition total species diversity and diversity within phenological groups across four scales. We found that species richness and individual abundance is greater in old growth forests than mature forests and that species composition differed significantly between the two. Turnover in species with logging history accounted for 11% of the total species richness and was greater than expected. Species turnover at intermediate and landscape-scales contributed the most towards total species richness. These results indicate that even after 100 – 150 years of recovery, rich cove forests demonstrate a shift in the diversity baseline. These findings have important implications for land use management- using mature forest stands as a baseline for herb layer recovery will lead to loss of biodiversity.
Introduction

The diverse herb community in undisturbed forests provides a glimpse at patterns and processes occurring in once widespread communities prior to anthropogenic disturbance. In 1923, old growth forests covered 822 million acres in eastern North America (Leverett 1996). Over the past century, these forests have been intensively logged. Today old growth forests have been reduced to small tracts of 10 to 100 acres totaling 750,000 acres (0.09% of the original area) due to harvesting and clear cutting (Davis 1993). Assessing herb layer recovery from large-scale anthropogenic disturbance requires having baseline data on the abundance and distribution of species in unaltered habitats.

Remnant old growth forests provide a valuable point of reference for ecological patterns and processes occurring in the absence of anthropogenic disturbance (McCarthy 2003). While old growth forests have been reduced to relicts, they are the only means for assessing recovery of secondary forests. However, the long-term implications of logging on species diversity have been neglected in favor of immediate consequences (Pykala 2004, Gotmark et al. 2005). Often mature forests, logged at the turn of the century, are used as the benchmark for assessing recovery in recently logged forests (Ford et al. 2000). With stand initiating events on the order of 400-500 years (Lorimer 1980), focusing on short-term implications of logging neglects the critical question of whether forests recover from logging.

The impact of logging on the understory herb layer in rich cove forests of the Southern Appalachians has been a focus of studies, but conclusions remain contentious because key studies suffer from different confounding factors that make results hard to
reconcile. The understory herb community contributes largely to species diversity, provides habitats for many species, plays an important role in nutrient cycling and has been used as an indicator of forest site quality (Collins et al. 1985, Thomas et al. 1999, Gilliam 2007). Duffy and Meier (1992) found that herb diversity was greater in old growth forests compared to forests logged at the turn of century. However, herb communities vary in composition, and individual species abundances vary with elevation, aspect, soil and forest type (Gilliam and Turrill 1993, Ohtsuka et al. 1993, McCarthy et al. 2001, De Keersmaeker et al. 2004). Failure to account for these potentially confounding intersite factors was a major criticism of Duffy and Meier (1992). Ford et al (2000) took into account intersite heterogeneity, but neglected long-term recovery by comparing recently logged sites to “mature” forests that were as young as 85 years old, finding little differentiation between the herb communities. Since stand initiating events require hundreds of years, herb communities in forests termed “mature” may be early in their successional trajectory (Lorimer 1980). Strategies for conserving the high biodiversity in these communities require understanding the full trajectory of herb layer recovery, and developing logging rotations and landscape management plans that take the potential long term successional cycles into account. With present logging cycles of 40 to 150 years in the southern Appalachians, recovery of the herbaceous community to predisturbance levels of diversity is unlikely (Meier et al. 1996).

To establish a thorough baseline understanding of the herb community, we combined diversity, abundance, and species composition across spatial scales while taking into account phenological groups. This multifaceted approach better addresses persistence the herb community (e.g. Symstad et al. 1998, Loreau et al. 2001). Spatial
dependency of diversity can occur at a range of scales (Whittaker 1960, Levin 1992). Large-scale spatial processes include landscape-level land use history and heterogeneity between forest sites (Gering et al. 2003). High turnover in diversity at landscape scales is generally a signature of dispersal limitation (Freestone and Inouye 2006, Vellend et al. 2007). At smaller spatial scales, intraspecific aggregation through clonal growth or environmental processes such as patchy distribution of light and nutrients in the understory and forest floor microtopography can affect diversity (Miller et al. 2002, Barbier et al. 2008). Diversity surveys often provide a snapshot of diversity at the plot scale, which is only one component of total diversity (Clough et al. 2007). Using multiple spatial scales to address diversity provides a more comprehensive view of the community and can indicate underlying processes based on the scales at which diversity accumulates (Miller et al. 2002, Gering et al. 2003, Barbier et al. 2008).

Plant communities are dynamic on an annual cycle with species having temporal niches based on leaf phenology. This is an often overlooked, but important component of diversity. Three primary phenologies in the understory (spring ephemerals, summer greens and evergreens) differentiate in the timing and duration of their carbon gain (Neufeld and Young 2003). These phenologies utilize resources and habitats at different times, which contributes to greater diversity by allowing more species to coexist over an annual cycle (Chesson 2000). Combining phenology with spatial scales in old growth forests provides a comprehensive baseline of the plant community that can be used to assess recovery in previously logged forests.

Here we examine how diversity of the understory herb community differs between old growth forests and forests recovering from logging a century ago. This
study is novel in that it addresses long-term recovery of the herb layer while taking into account intersite heterogeneity. We used a hierarchical nested sampling design to additively partition total species diversity and diversity within phenological groups across four scales. We predict that diversity and abundance of the herb layer will be greater in old growth forests in comparison of recovering forests. This hierarchical analysis allows a more detailed understanding of how diversity differs, whether among phenological groups or spatial scales or both. We expect that phenological groups should show different responses to spatial scales due to life history differences. By comparing mature forests to old growth forests, we extend our understanding of herb layer recovery across a longer trajectory of succession to provide better data for landscape management plans.

Materials and Methods

Study Sites

Within the Southern Appalachians, cove forests comprise 25% of wooded area. These forests are highly susceptible to anthropogenic disturbance because they contain quality sawtimber for harvesting and fertile soils for agriculture sites (Beck 1988, Turner et al. 2003). Cove forests harbor the highest diversity in the Southern Appalachians with the understory herb layer diversity averaging 80% of the species richness (Gilliam 2007). We selected sites of similar slope, aspect (0° – 90°), elevation (700 to 1200 m), and rich cove hardwood forest type in the southern Appalachians of North Carolina in the Nantahala National Forest (NNF) based on US Forest Service Continuous Inventory and Stand Condition (CISC) data and USGS digital elevation models (ArcGIS 8.0, USGS
digital elevations models and USFS CISC). The underlying geology in this area is composed of metamorphosed rocks with mostly Dsytrochrepts and Hapludults soils (Pittillo et al. 1998). Annual temperatures range from -13.2°C to 33.2°C with an average temperature of 13.6°C. Rainfall averages 82.6 cm annually (www.weatherunderground.com).

Six sites were chosen with paired old growth and mature forest sites using CISC data. Old growth describes forests that have never been logged and have little or no evidence of anthropogenic disturbance (Meier et al. 1995). High tree diversity, massive living trees, uneven canopy structure, standing snags, tree fall gaps and log accumulation distinguish old growth forests from secondary forests (McCarthy 1995, Hardt and Swank 1997). Logging rotation times are 100 to 150 years in the Southern Appalachians (USFS), therefore these mature forests represent the amount of recovery that is likely to occur before a subsequent logging rotation. Data from the CISC layers indicate that these forests were logged between 1864 – 1906. This time period coincided with intensive clearcut logging of the Southern Appalachians prior to Forest Service ownership (Western North Carolina Alliance 1995). Forests clearcut by private lumber companies at the turn of the century used methods that caused extensive damaged to the understory. Harvesting techniques did not minimize damage caused by falling trees and massive logs were skidded out of the forest, causing large disturbances to soils and widespread erosion (Mastran and Lowerre 1983). Since harvesting a century ago, these forests have undergone natural regeneration (United States Department of Agriculture 1994).
Diversity and Partitioning Sampling

At each site, twelve transects consisting of five 0.25 m\(^2\) plots spaced 5 m apart and running perpendicular to the cove drainage were established following Ford et al. (2000, Figure II – 1). Presence/absence of understory herbaceous species was surveyed for each of these 360 - 0.25m\(^2\) plots to assess overall diversity. Surveys took place beginning in early March 2005 and once monthly until August. All stands were surveyed within seven days to minimize temporal variation in floral phenology.

For diversity partitioning, a subset of the diversity plots were used for abundance sampling. Ten randomly chosen 0.25 m\(^2\) plots at each site were expanded to 1 m\(^2\) quadrats (Figure II – 2). The four 0.25 m\(^2\) subplots within each quadrat comprise the lowest hierarchical scale with 40 subplots per site for a total of 240 – 0.25 m\(^2\) subplots across all forest sites. Abundance of individual ramets was surveyed within each subplot during the same time intervals as the diversity sampling. The 1 m\(^2\) quadrats make up the second hierarchy with a total of 60 – 1 m\(^2\) quadrats followed by site scale (6 six forest sites) and the highest hierarchy (age) with two forest ages (Figure II – 2).

Phenology

Species were categorized according to their phenological guilds: spring ephemerals, summer greens, wintergreens and evergreens. Spring ephemerals are those species that leaf out in early spring and senesce prior to canopy closure. Summer greens can leaf out before, during or after canopy closure, but retain their leaves throughout the summer. Summer greens generally senesce their leaves in late summer or fall (Neufeld and Young 2003). Wintergreens have overwintering leaves that are produced in late
summer or fall and are lost the following late spring or summer (Uemura 1994). 

Evergreens retain leaves for more than one year (Neufeld and Young 2003). Due to the small number of wintergreen species, they were categorized with the evergreen species as those species that have overwintering leaves. A single parasitic species, *Conopholis americana*, did not fall into these phenological strategies and was included in analyzes for all species but was not grouped into a phenological guild.

**Diversity Analysis**

Species richness per plot was tallied for all species and separately for spring ephemeral, summer green and evergreen groups. Ramet abundance per subplot was calculated for all species and each phenological group. Randomization tests were used to determine whether mean species richness or abundance differed between old growth and mature forests for all species and for each group separately by randomly assigning the species richness of the 360 – 0.25 m² plots to each forest age and taking the difference between species richness means. The null probability distribution was based on 10,000 random permutations, and the p-value was calculated as the proportion of sampled permutations where the absolute difference between means was greater than or equal to the absolute value of the difference between the observed means using R 2.6.2 (http://www.R-project.org/). The same randomization process was used to assess differences in abundance by randomly assigning the 240 – 0.25 m² abundance subplots to each forest age and calculating the difference between abundance means.

Rarefaction was used to determine whether differences in the number of species were independent of abundance. This method randomly samples the same number of
individuals from each forest age (old growth and mature forests) 10,000 times for a range of sample sizes. Sample sizes ranged from 200 individuals to 9000 individuals using increments of 200 individuals. Mean and 95% confidence intervals for species richness at each sample size for old growth and mature forests were compared to determine whether diversity differs between forest ages given the same abundance (Gotelli and Entsminger 2000).

Similarity of species composition between sites and with forest age was assessed using non-metric multidimensional scaling (NMS) with Sorensen’s distance measure for all species that were present in more than one plot based on diversity sampling (PC-ORD 4.41). Significant groups in species composition with forest age was based on multi-response permutation procedure (MRPP) using Sorensen distance measure with \( n_i / \Sigma (n_i) \) as a weighting option where \( n_i \) is the number of species in group i (Biondini et al. 1985). An indicator species analysis for old growth and mature forests was used to determine how species separate based on occurrence within each forest age. Values greater than 25% determine which species are good indicators (Dufrene and Legendre 1997). A Monte Carlo test of significance based on observed maximum indicator value for species was based on 1000 permutations (PC-ORD 4.41).

Additive Partitioning

Species richness was partitioned within and between the four hierarchical scales (subplots, quadrats, sites and forest age) to determine the contribution of various spatial scales to total diversity (Gering et al. 2003, Figure 2). Randomization was used to determine if diversity partitioned at any given spatial scale differs from a random
distribution of individuals among samples at all scales using PARTITION v2 (Veech et al. 2002, Crist et al. 2003, Gering et al. 2003). Three measurements of diversity were used: species richness ($N_o$), Shannon’s index ($H'$) and Simpson’s index ($\lambda$). Species richness is the number of species per sample. Shannon’s index is calculated as $H' = \sum p_i \ln(p_i)$ and Simpson’s index is $\lambda = [1 - \sum p_i^2]$ where $p_i$ is the proportional abundance of species $i$ for $i = 1$ to the total number of species in the sample.

Level 1 refers to the lowest hierarchy (subplot) and level 4 to the highest (forest age) (Figure II – 3). Within 1 is the mean diversity in plots and among 1 is the diversity that accumulates among plots. Within diversity at a given scale is the sum of the within and among diversity components at the next lowest scale, thus within 2 (mean diversity within quadrats) is the sum of within 1 and among 1. Total diversity is partitioned into: within 1 + among 1 + among 2 + among 3 + among 4 (Figure II – 3). Additive partitioning was conducted for all species and for each phenological group. Within each forest age type, diversity was partitioned into three hierarchies (subplot, quadrat, and site) for all species and for each phenological group.

Significance of scale-specific within and among values was determined by complete randomization in which the total number of individuals within a subplot is kept the same, but individuals are randomly assigned to samples, generating a new number of species per subplot. The randomized data are partitioned and diversity metrics calculated 10,000 times to obtain a null distribution of each within and among estimate of diversity at each of the four hierarchical scales. To test the null hypothesis that the observed within and among diversity values are due to a random distribution of species among samples at all scales, the null distribution was compared to the scale-specific values.
Statistical significance was determined by the proportion of null values greater (or less) than the estimate (Crist et al. 2003, Gering et al. 2003).

Results

Old growth (Og) forests exhibited greater species richness than mature (Ma) forests for all species, spring ephemerals, summer greens, but not evergreens (Figure II – 4). A total of 83 species were surveyed in the 360 - 0.25 m$^2$ presence-absence plots distributed across six rich cove forests (8% spring ephemerals, 79.5% summer greens and 10.8% evergreens; Table I – 1). Old growth forests have significantly greater abundance than mature forests for all species, spring ephemerals, summer greens and evergreens (Figure II – 5). A total of 23,164 individual ramets were recorded in the 240 – 0.25 m$^2$ abundance plots (35.1% spring ephemerals, 51.6% summer greens and 8.8% evergreens). Species richness was greater in old growth compared to mature forests for all species when abundance was taken into account with rarefaction (Figure II – 6).

NMS ordination of all species yielded a three dimensional solution that explained 64.4% of the variation in plot species composition. Species composition forms significant groups according to forest age ($A = 0.08$ (chance-corrected within group agreement), $p < 0.001$) with forest age explaining 18.6% of variation in species composition along axis 1 (Figure II – 7). One species, *Anemone quinquefolia*, is a significant indicator species of mature sites. Old growth forests have several significant indicator species including spring ephemerals (*Claytonia caroliniana, Dicentra spp.*), summer greens (*Cardamine diphylla, Stellaria pubera*) and an evergreen (*Tiarella cordifolia*) (Table I – 2).
Partitioning

Diversity among the highest scales (forest age and forest sites) was greater than expected by chance for the entire community and each phenology based on all diversity metrics, except Simpson’s index for spring ephemerals (Table I – 3). The highest species richness for all herb species occurs between 1 m² quadrats across sites (34%) closely followed by between sites (33.3%). Species richness between forest ages accounted for 11% of the total species richness (Figure II – 8). Within plot diversity contributes the greatest to overall diversity based on Shannon and Simpson indices, but does not differ from random (H’ = 50.4%; λ = 81.6%).

Diversity was partitioned across space similarly in both mature and old growth forests. Species richness was partitioned equally between the highest scales (among sites and among quadrats) for both old growth and mature forests (Figure II – 9). Significantly greater species richness than expected occurred between sites for both ages (Table I – 3). For Simpson’s and Shannon’s indices, within plot diversity contributed the greatest to total diversity in old growth and mature forests (Figure II – 8). However, the amount of diversity within plots did not differ from what was expected in either aged forest (Table I – 3).

Phenology

For all phenologies, diversity among quadrats across a forest site contributes the most to overall species richness (Figure II – 8). The two highest scales (between sites and between ages) have significantly more species richness than expected for all phenologies. Based on Simpson’s index, within plot diversity contributes the most to
diversity for all phenologies (Figure II – 8), but only spring ephemerals had more diversity than expected within plots (Table I – 3). Using Shannon’s index, among quadrats contributed the greatest proportion to spring ephemeral (40.5%) and evergreen (32.4%) diversity. About half of the summer green diversity (47.2%) comes from within plots and is not predictable based on landscape variables at any spatial scale. All phenologies had greater than expected diversity based on Shannon’s index for the highest scales (among site and among forest age; Table I – 3).

Of the phenologies, only evergreens demonstrate differences in how diversity is partitioned within old growth and mature forests. Summer greens exhibit similar patterns to all species with minimal differences between old growth and mature forests (Figure II – 9). Most of the spring ephemeral diversity was accounted for among quadrats in both old growth and mature forests based on species richness (Ma = 42%, Og = 33.3%) and Shannon’s index (Ma = 46.6%, Og: $\beta_2 = 52.6\%$). Simpson’s index showed the greatest contribution to spring ephemeral diversity at the within plot scale (Ma = 96.1%, Og = 96.6%; Figure II – 9). Evergreen diversity is partitioned differently in old growth and mature forests. Old growth forests have most evergreen diversity partitioned among sites based on species richness (42.9%) and Shannon’s index (40.2%). In mature forests, diversity is partitioned among quadrats based on species richness (53.3%) and Shannon’s index (52.6%; Figure II – 9). Simpson’s index was partitioned mostly within plots for both forest ages (Ma = 95.9%, Og = 61.4%; Figure II – 9).
Discussion

Previously logged forests are not equivalent to remnant old growth stands after a century of recovery in terms of species richness, abundance and composition when intersite heterogeneity is taken into account. Old growth forests have greater species richness and abundance than previously logged forests along with a distinct species composition (Figure II – 4, 5, 7). These results support previous arguments that timber harvesting alters the herb layer (Brewer 1980, Meier et al. 1995, Vellend et al. 2007) and refutes conclusions that timber extraction retains species richness and composition (Ford et al. 2000, Gilliam 2002, Scheller and Mladenoff 2002, Kraft et al. 2004, Aubin et al. 2007). Recovery of the understory may take centuries and may never reach the same baseline found in undisturbed forest (Brewer 1980, Vellend et al. 2007). Previous studies in the southern Appalachians show a lack of recovery after 45-87 years (Meier et al. 1995) and similar conclusions have been made in systems with much shorter harvesting intervals (Decocq et al. 2004). This study demonstrates that timber harvesting intervals of 100 – 150 years are still more frequent than herb layer recovery time in rich cove forests. After a century of undisturbed recovery, logged stands are not equivalent to remnant old growth stands.

Spatial Partitioning

In the debate over whether herb layer diversity recovers from timber harvesting, spatial scale has not been taken into account despite the importance of scale for determining conservation practices (Meier et al. 1995, Ford et al. 2000, Whittaker et al. 2005). We demonstrate that there is greater species turnover than expected at large
spatial scales (between sites and between forest ages). Most of the herb layer diversity accumulates at the forest site scale (34%) and among forest sites scale (33.3%). Diversity between forest ages accounted for 11% of the total species richness and there was greater diversity than expected in the old growth forests. Despite that diversity differs between old growth and mature forests, the partitioning of diversity across spatial scales is similar within mature and old growth forests. Diversity among forest sites and among plots at the forest site scale contributed the most towards total species richness for both forest ages. High diversity among forest sites demonstrates the importance of landscape scale variation in preserving diversity and requires conserving multiple forest stands to maximize species richness.

Dispersal limitation, habitat heterogeneity and intraspecific aggregation drive patterns of how diversity is partitioned across space (Jacquemyn et al. 2001, Small and McCarthy 2002, Freestone and Inouye 2006). Species turnover at large-scales (between sites and ages) was greater than expected, which could be due to dispersal limitation or environmental differences from logging disturbance. Previous studies give evidence for dispersal limitation in forests recovering from disturbance (Verheyen et al. 2006, Tessier 2007) with species recovery constrained by characteristics of the disturbed forest such as isolation and size (Honnay et al. 2002). In addition, the majority of understory herbs have limited dispersal abilities (Bierzychudek 1982, Whigham 2004). A similar pattern was shown for butterflies in which species turnover was higher than expected at scales at which dispersal did not readily occur (Crist and Veech 2006). Most of the total herb diversity occurs at the site scale (Figure II – 8), which indicates finer-scale intraspecific
aggregation due to clonal growth and species sorting along fine-scale environmental gradients (Condit et al. 2002, Legendre et al. 2005).

Previous studies have addressed partitioning of diversity for several taxa across landscape and ecoregion scales (Wagner et al. 2000, Gering et al. 2003, Roschewitz et al. 2005, Chandy et al. 2006, Clough et al. 2007). However, we are the first to apply this technique to a single forest type and compare differences in diversity partitioning with land use history and phenology. Only one other study compared how diversity was partitioned in differently managed habitats (organic versus conventional wheat fields; Clough et al. 2007). Previous studies support our results of plant species accumulating mostly at the landscape scale (Wagner et al. 2000), however, other studies found that larger scales contribute more to diversity (Roschewitz et al. 2005). One study in a forested landscape found that intermediate scales similar to the within site scale of our study contributed the most to diversity (Chandy et al. 2006). This study focused on trees and woody understory species, excluding the herbaceous layer. We found that herbaceous layer diversity was partitioned primarily at the intermediate-scale (within forest site) and landscape-scale (among forest sites).

**Diversity Indices**

Using multiple diversity indices that take into account proportional abundance of species allows for understanding how abundant and rare species are distributed across spatial scales. Shannon’s index is more sensitive to rare species than species richness or Simpson’s index (Chandy et al. 2006). Simpson’s index is more sensitive to changes in common species and is the probability of drawing two individuals of the same species at
random from a sample (Gering et al. 2003). Contrasting partitions between species richness and Shannon’s index for all species and summer green species indicates that abundant species are widespread and rare species occur in a single plot (Figure II – 8). Similar contrasting partitioning patterns have been observed for both beetles (Gering et al. 2003) and plants (Wagner et al. 2000). Contrasting partition between species richness and Shannon’s index was not seen for spring ephemerals or evergreens (Figure II – 5). These phenologies do not have a strong distinction between dominant and rare species. Spring ephemerals and evergreens are more evenly distributed across the landscape at all spatial scales.

Phenology

All phenologies are affected by past timber harvesting based on species richness or abundance. Mature forests have lower spring ephemeral and summer green species richness along with decreased ramet abundance for all phenologies. Differences in species richness and abundances between old growth and mature forest are not random, but rather can be traced to life histories. In mature forests, spring ephemerals and summer greens occur in fewer plots, fewer species occur in a single plot and total site abundance is lower. These differences result from slow growth rates and limited dispersal that make them more susceptible to logging (Meier et al. 1995). For example, *Erythronium americanum* and *Allium tricoccum* take 7 - 8 years to go from seed to reproducing with high mortality at the young life history stages (Holland 1981, Nault and Gagnon 1993). Reproduction occurs via clonal growth or by sexual reproduction with
dispersal distances generally less than a meter (Bierzychudek 1982, Nault and Gagnon 1993, Whigham 2004).

Only evergreens differed in their partitioning of diversity across space with land use history. Species turnover in evergreens occurs at larger scales in old growth forests than mature forests (Figure II – 9). Small-scale processes of clonal growth and unassisted dispersal could be limiting the spread of evergreens across a site even after over a hundred years of recovery (Handel et al. 1981, Bierzychudek 1982, Whigham 2004). Patterns in old growth sites demonstrate that landscape-scale processes rather than the spread of species within a site are more important for evergreens. Large-scale environmental heterogeneity between old growth forest sites and limited dispersal among sites plays a more defining role in old growth forests.

Conservation Implications

Logging impacts forests worldwide and understanding the successional trajectory of recovering forests is critical for conservation. We demonstrate that century old forests should not be used as the benchmark for understanding understory diversity. Rather, remnant old growth forests need to be the standard by which recovery is assessed. A century is not enough time for the herb layer to recover from timber harvesting in a diverse community. Species richness, abundance and composition in mature forests have not recovered to old growth levels. Spring ephemeral and evergreen phenologies are the hardest hit by harvesting, but respond in different ways due to life history characteristics with evergreens having altered spatial patterns and spring ephemerals differing in species richness and composition.
Turnover in species across a site and between forest sites contributes the greatest amount to diversity and should be the focus for conservation. Multiple forest stands need to be preserved to maximize herb layer diversity in rich cove forests of the Southern Appalachians. Species turnover across a forest site needs to be further addressed to determine whether differences in environmental heterogeneity or intraspecific aggregation through dispersal limitation or clonal growth drive these patterns.
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Table II – 1. Species, phenological groups and number of plots present in at each old growth (OG) and mature (MA) site.

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<th>OG2</th>
<th>OG3</th>
<th>MA1</th>
<th>MA2</th>
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Table II – 2: Indicator species for mature and old growth forests for the top five species with indicator values >25%.

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<th>Indicator Value (%)</th>
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Table II – 3: Results of randomization process to determine whether the diversity partitioned at each level is more or less than what would be expected by chance. The observed species richness ($N_o$), Shannon’s index ($H'$) and Simpson’s index ($\lambda$) from additive partitioning were compared to null estimates for all forest ages, old growth forests alone and mature forests alone. The randomization process was conducted for all species and each phenological group. Significance was determined at the 0.05 level; + indicates significantly greater than expected and ns is not significant.

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<th>Summer</th>
<th>Evergreens</th>
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<td>$H'$</td>
<td>$\lambda$</td>
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<td>among 3</td>
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<tr>
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<td>$H'$</td>
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</tr>
<tr>
<td><strong>Old Growth</strong></td>
<td>$N_o$</td>
<td>$H'$</td>
<td>$\lambda$</td>
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**Figure legends**

Figure II – 1: Diversity sampling design for each cove forest following Ford et al. (2000). Twelve transects, consisting of 5 – 0.25 m² plots placed 5 m apart, are placed perpendicular to the cove drainage. Presence/absence of understory herbaceous species was surveyed for each plots beginning in early March and once monthly until August.

Figure II – 2: Nested sampling design with four hierarchical scales (age, forest site, quadrat and subplot) was established in six rich cove forests. Each of the three old growth sites and three mature sites has ten 1 m² quadrats randomly selected from the diversity sampling plots. Each quadrat is divided into four subplots (lowest hierarchy) in which herb layer ramet abundance were surveyed.

Figure II – 3: Additive partitioning model based on Gering et al. (2003) showing the relationships among hierarchical levels from the lowest (subplot) to the highest (age). Each scale has a within and among diversity component. Within is the mean number of species that occurs within a unit at each scale. Among is the mean number of species among units at each scale. Based on additive partitioning, the within value at any scale is the sum of the within and among components of the next lowest scale. Using this additive approach, total diversity (within 5) is calculated as within 1 + among 1 + among 2 + among 3 + among 4 as shown by the arrows.
Figure II – 4: Boxplot of species richness for old growth (OG) and mature forests (MA) for all species, spring ephemerals, summer greens and evergreens. Old growth forests have significantly more species richness for all species (OG = 9.8 ± 2.8 spp/plot; MA = 7.4 ± 3.1 spp/plot; p < 0.001), spring ephemerals (OG = 2.0 ± 1.2 species/plot; MA = 1.0 ± 1.1 species/plot; p < 0.001) and summer greens (Og = 6.9 ± 2.3 spp/plot; MA = 5.6 ± 2.4 spp/plot; p < 0.001). Evergreen richness does not differ with forest age (Og = 0.9 ± 0.8 spp/plot; MA = 0.8 ± 0.9 spp/plot; p = 0.11).

Figure II – 5: Boxplot of abundance for old growth (OG) and mature forests (MA) for all species, spring ephemerals, summer greens and evergreens. Old growth forests have significantly greater abundance for all species (OG = 117.8 ± 66.8 ind./plot; MA = 75.3 ± 60.0 ind./plot; p < 0.001), spring ephemerals (OG = 40.6 ± 48.4 ind./plot; MA = 27.2 ± 41.3 ind./plot; p = 0.005) summer greens (Og = 56.7 ± 35.0 ind./plot; MA = 42.9 ± 27.2 ind./plot; p < 0.001), and evergreens (Og = 11.9 ± 12.5 ind./plot; MA = 5.2 ± 6.9 ind./plot; p < 0.001).

Figure II – 6: Rarefaction showing greater mean species richness for old growth (OG; open circles) than mature forests (MA; closed circles). Samples ranged from 200 – 9,000 individuals with 200 individual increments. Each sample size was randomly sampled 10,000 from each forest community with 95% confidence intervals shown by the envelopes.
Figure II – 7: Non-metric multidimensional scaling biplot axes 1 and 2 for forest age x herb layer community composition sampled in 360 plots across six rich cove forests for all species.

Figure II – 8: Percent of diversity partitioned into within and among components using species richness ($N_o$), Shannon’s diversity index ($H'$) and Simpson’s index ($\lambda$) for all species and for each phenological group.

Figure II – 9: Percent of diversity partitioned into within and among components within old growth (Og) and mature (Ma) forests based on species richness ($N_o$), Shannon’s index ($H'$) and Simpson’s index ($\lambda$) for all species and each phenological group.
### Scale

<table>
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<th>Old Growth</th>
<th>Mature</th>
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<td>Site:</td>
<td>OG1 OG2 OG3</td>
<td>MA1 MA2 MA3</td>
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**Quadrat (10-1 m²):**

![Quadrat Diagram](image)

**Subplot:**

![Subplot Diagram](image)

0.25 m²

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Figure II – 2
<table>
<thead>
<tr>
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Figure II – 3
Figure II – 4
Figure II – 5

- **All**
  - **Spring Ephemeral**
  - **Summer Green**
  - **Evergreen**

**Number of Individuals per 1 m²**

OG | MA
---|---

0 | 50 | 100 | 150 | 200

0 | 50 | 100 | 150 | 200

0 | 50 | 100 | 150 | 200

0 | 50 | 100 | 150 | 200
Figure II – 6
Figure II - 8
Figure II – 9
CHAPTER III

DECOUPLING OF HERBACEOUS LAYER COMPOSITION FROM THE ABIOTIC ENVIRONMENT AFTER LONG TERM RECOVERY FROM LARGE-SCALE DISTURBANCE

Abstract

A central debate in community ecology has been the degree to which communities bear the mark of history in their composition. Community composition includes two processes: arrival of species followed by environmental filtering. Anthropogenic disturbance has altered these processes by changing environmental conditions and imposing additional dispersal limitations. Large-scale logging disturbance has been shown to alter species composition, but whether environmental or spatial processes drive these changes is not known. This study examined long-term recovery from logging disturbance of the diverse understory herb layer community in rich cove forests of the Southern Appalachians. We asked, do the processes of dispersal and environmental filtering operate similarly in old growth and previously logged forests? The percent of species composition explained by environmental parameters alone, space alone and the interaction of space and environment was partitioned out. The percent of species composition explained by environmental variables and spatial variables was determined in old growth and previously logged forests separately using partial canonical
correspondence analysis (CCA). The results show that species composition in understory herbs in old growth forests is predominately explained by the environment. In previously logged forests, this relationship between species composition and the environment is decoupled. Environmental variables related to soil fertility (Mn, Mg, total exchangeable cations) explained 37% of the variation in species composition across old growth forest landscapes, and none in mature forests. The only significant environmental factor in mature forests was Zn, which explained 5.1% of the variation. These distinctions were found even when controlling for species differences. Logging disturbance a century ago decouples species composition from environmental conditions demonstrating that a hundred years of recovery is inadequate for species to reach equilibrium with the environment.
Introduction

The suite of species observed in a given area arises from a two part process, with species first arriving at sites, and then establishing and surviving given the biotic and abiotic environmental filters they encounter (Tilman 1994, Chase and Leibold 2003, Ricklefs 2004). Dispersal into sites creates spatial patterns independent of the local environment and plays a critical role in determining plant community composition (Tilman 1994, Hubbell 2001, Bolker et al. 2003, Clark et al. 2004). The spatial pattern is modified as species abundances change given their responses to the environment and biotic interactions (Tilman 1994, Harrelson and Matlack 2006). Species responding to the environment creates a coupling between species composition and environmental variables, causing sorting along environmental gradients in relation to their traits (Ford et al. 2000, Huebner et al. 2007). Anthropogenic disturbance can alter both dispersal and subsequently environment, changing the successional trajectory of communities (Bellemare et al. 2002, Fraterrigo et al. 2006a, Wiegmann and Waller 2006, Vellend et al. 2007).

A central debate in community ecology has been the degree to which communities bear the mark of history in their composition and structure. Foster et al. (1998) found that historical records of tree species distributions showed strong correlations with environmental variables. Post- European tree distributions, however, have broken the correlation between species distributions and environmental variables effectively increasing the niche breadth of Eastern tree species. This has resulted in modern forests with distinct species compositions that are largely decoupled from gradients in temperature, precipitation, and soil types. Similar patterns of a weakened
species-environment relationship have been found for former agricultural fields in North America and Europe (Vellend et al. 2007). Dispersal plays a more prominent role in structuring these previously disturbed communities (Bellemare et al. 2002). While composition has been shown to reflect historical events, we do not know how long it will take or if the relationship between species composition and the environment will return.

Human disturbance differs from natural disturbance in both scale and intensity. Logging is a large-scale and widespread human disturbance that has been demonstrated to alter species composition for many organisms in forest communities (Nowacki and Abrams 1994, Hardt and Swank 1997, Miller et al. 2002, Thompson et al. 2002, Hamer et al. 2003, Selmants and Knight 2003, Kavanagh and Stanton 2005, Kreyling et al. 2008). However, knowing that composition changes with logging disturbance does not shed light on how the processes that determine communities have changed, as logging can alter both dispersal and environment and biotic interactions. Logging changes environmental conditions of soil nutrients, light availability and moisture (Covington 1981, Brown and Parker 1994, Small and McCarthy 2005, Fraterrigo et al. 2006a). Dispersal of species at both the local and landscape scales can also be altered by logging. Recovery of species composition in logged forests has been linked to dispersal limitation based on the distance from old growth species pools and connectivity between forest patches (Donohue et al. 2000, Ford et al. 2000, Graae et al. 2003, Verheyen et al. 2003b).

The diverse herb community of rich cove forests provides the ideal setting to address the role of logging on community structuring processes of dispersal and environmental filtering. The herb layer contains more than 80% of the species in a forest (Gilliam 2007). They are susceptible to disturbance and act as indicators of forest site
quality due to life history characteristics of slow growth, limited dispersal and clonal growth (Jolls 2003). Although this community only makes up 1% of the forest biomass, it has a significantly role in ecosystem functions of energy and nutrient flow by contributing 12% of the total litter fall that is easily decomposed (Gilliam 2007).

The intensity of disturbance may affect the time it takes for environmental coupling to return. On former agricultural land intense soil disturbance caused by tilling homogenizes the soil and has been demonstrated to weaken environmental filtering (Vellend et al. 2007). Logging disturbance may have a lesser impact on the environment than agriculture. Average soil nutrients remain unchanged after logging; however, the variance and spatial structure of the soil changes (Frattirigo et al. 2006a). Forests of Eastern North America were extensively logged and clearcut at the turn of the 20th century, with more of the landscape altered by logging than agriculture (Davis 1996). Forests ranging from 100 – 150 years old now dominate forested landscapes and are referred to as “mature” in terms of forest management (United States Department of Agriculture 1994). These “mature” forests have been used as the standard for assessing recovery of younger forests (Ford et al. 2000, Gilliam 2002, Selmants and Knight 2003, Small and McCarthy 2005). However, even though logging is a lower intensity disturbance, and that these communities have had 100-150 years recovery time, it remains unknown whether environmental coupling and dispersal limitation play an equal role in the herb community of old growth and previously logged forests, even though designing effective conservation and management strategies relies crucially on the relative strengths of these factors (Keddy and Drummond 1996, McLachlan and Bazely 2001, 2003). With large-scale logging, most of the species are kept, but the connections
between species composition and ecosystem processes may take much longer to recover.
Understanding community composition, for management and responses to climate
growth and 100 – 150 year old stands in the Southern Appalachians to assess the effects of logging disturbance by clearcutting over a century ago. We ask, (1) what is the relative role of dispersal and environmental coupling in determining composition in a diverse, old growth community? (2) Do previously logged forests that have been recovering for over a century exhibit the same processes?

Methods

Study species and sites

The study was conducted on the understory herbaceous community of rich cove hardwood forests in the Nantahala National Forest (for definitions see Schafale and Weakly 1990). Six sites were chosen, three old growth sites and three ~100 year sites of similar slope, aspect ($0^\circ – 90^\circ$), elevation (700 to 1200 m), using GIS in the southern Appalachians of NC and TN based on US Forest Service Continuous Inventory and Stand Condition (CISC) data and USGS digital elevation models (ArcGIS 8.0, USGS digital elevations models and USFS CISC). Definition of old growth forest follows Meier (1995) and are characterized by having never been logged and have little or no evidence of anthropogenic disturbance, and are characterized by downed timber in varying states of decay, standing dead trees and live trees of different ages. We compared old growth to secondary forest stands logged between 1864 and 1906 (based on CISC data) because
they represent the standard logging rotation time of 100 to 150 years in the Southern Appalachians (Brown, E., pers. com.) and give the recovery likely to occur before subsequent logging. Forests 100 – 150 years old are also the end points of many recovery studies (Ford et al. 2000, Gilliam 2002, Small and McCarthy 2002). The time period between 1864 – 1906 coincided with intensive clearcut logging of the Southern Appalachians prior to Forest Service ownership (Western North Carolina Alliance 1995). These forests were logged by private lumber companies before Forest Service management and have undergone natural regeneration (United States Department of Agriculture 1994).

**Sampling**

Each forest site was 1 ha in size with the cove drainage dissecting the center of the site. As a part of a larger study, twelve transects consisting of five 0.25 m² plots spaced 5 m apart and running perpendicular to the cove drainage were established following Ford et al. (2000) at each site. A subset of these plots was used for this study. Ten randomly chosen 0.25 m² plots at each site were expanded to 1 m² plots for a total of 60 – 1 m² plots. In each plot, all ramets were mapped, identified and counted once monthly between March and August. Surveys among all sites were conducted in the same week to minimize any variations in phenology among sites.

**Environmental Monitoring**

We analyzed 24 environmental factors at each site that have been shown in previous studies to be predictors of herb composition and diversity (Ford et al. 2000,
Adkison and Gleeson 2004, Burrascano et al. 2008). Canopy cover was measured in the center of the 10, 1-m$^2$ plots at each site in both early spring and summer when the canopy was fully leafed out using hemispherical photographs analyzed in Image J (Rasband 2008). Litter depth was measured from litter layer top to soil surface in the center of each plot. In five randomly selected plots total tree basal area and tree species richness were surveyed for a ten meter radius surrounding each site. Soil samples were collected (8 cm diameter, 4 cm depth) from the center of the five, 1-m$^2$ plots. Samples were analyzed for total exchangeable cations (TEC), pH, lime requirement, organic matter, macronutrients, micronutrients, ammonium and nitrate by Brookside Laboratories, New Knoxville, Ohio.

**Analysis**

Randomization tests

Ramet abundance per plot was calculated and randomization tests based on 10,000 random permutations were used to determine whether abundance differed between old growth and mature forests using R 2.6.2 (http://www.R-project.org/). Randomization tests were also used to determine whether environmental parameters differed between old growth and mature forests based.

Partial Canonical Correspondence Analysis

To address the hypothesis that logging leaves a long-term impact on the processes determining species composition, we used a partial canonical correspondence analysis (CCA) to partition variation in community composition among measured environmental
parameters, spatial parameters, and the interaction of both environmental and spatial parameters. CCA requires species abundance data, environmental data and spatial data. Environmental parameters included 24 variables. Soil data was natural logarithm transformed for CCA due to the higher probability of plants reacting to nutrient changes at low concentration than when a nutrient is readily available (Jones et al. 2008).

To include space as a predictor in community composition, a continuous spatial variable set was generated from the plot x and y coordinates using principal coordinates of neighbor matrices (PCNM) method (pcnm.all.R; http://r-forge.r-project.org/R/?group_id=195). PCMN allows for all spatial scales in the data to be included as predictors for community composition, while other methods lose much spatial information (Borcard et al. 2004). PCNM performs a principle coordinate analysis on the geographical distance matrix resulting in a set of eigenvectors that model all possible spatial scales in the data, and are used as the spatial variables (Dray and Legendre 2008). These eigenvectors model spatial processes continuously at the plot (< 0.1 km), site (2 – 10 km), or regional (15 – 35 km) spatial scales. Spatial variables were generated for the mature forests and old growth forests separately.

Partial CCA Model

The partial CCA model includes the measured environmental parameters, spatial parameters and plot abundance data to partition variation in community composition. Abundance data was Hellinger transformed to reduce the weight of the most abundant species (BiodiversityR; http://cran.r-project.org/web/packages/BiodiversityR/index.html). Forward selection was used to reduce the number of terms included in the model (packfor;
https://r-forge.r-project.org/plugins/scmsvn/viewcvs.php/pkg/ packfor/? rev=54& root=sedar). As we had no a priori predictions on the importance of different environmental variables, the environmental data and spatial variables were individually run through forward selection for each forest age and only those terms that were significant (p = 0.05) after 999 permutations were selected for subsequent analyzes.

CCA was used to determine the contribution of environmental and spatial variables in explaining variation in community composition within mature and old growth forests (vegan; http://r-forge.r-project.org/projects/vegan/). The total variation in species composition is partitioned into four components (Figure III - 1). The first component is the amount of variation explained by the environment independent of spatial structure. The second component is the amount of variation in species composition that is shared by both the environmental and spatial components. The third component is the proportion explained by spatial data alone. The remaining variation in species composition makes up the unexplained proportion (Figure III - 1). The environmental component, spatial component and shared spatial and environmental component was determined for species composition in the old growth and mature forests separately (Borcard et al. 1992).

An analysis was conducted to explain how individual species respond to the significant environmental and spatial parameters that determine community composition. The resulting constrained axes from the partial CCA for the environmental and spatial components alone were used to determine which species sort along each axis based on ramet abundance. The top ten high scoring species along each environmental and spatial
axis were selected to determine which species sort along significant environmental and spatial gradients.

Different species have varying environmental requirements and spatial patterns. To determine whether differences in the relative contribution of space and environment in old growth and mature forests is due to differences in species composition, we repeated the analysis including only species present in both forest ages.

**Phenology**

To further investigate how environmental and spatial variables contribute to explaining variation in community composition, species were categorized according to leaf phenologies: spring ephemerals, summer greens, wintergreens and evergreens. Spring ephemerals are those species that leaf out in early spring and senesce prior to canopy closure. Summer greens leaf out in spring, but retain their leaves throughout the summer (Neufeld and Young 2003). Wintergreens have overwintering leaves that are produced in late summer or fall and are lost the following late spring or summer (Uemura 1994). Evergreens retain leaves for more than one year (Neufeld and Young 2003). Due to the small number of wintergreen species, they were categorized with the evergreen species as those species that have overwintering leaves. Ramet abundance per plot was calculated for each phenological group and randomization tests were used to determine whether mean plot abundance differed between old growth and mature forests. Partitioning variation between environment and space by CCA was analyzed for each phenology separately within old growth and mature forests. This was done for all species in a phenology and then for only those species that are shared between forest ages.
Results

Environmental and Vegetation Summary

A total of 23,164 individual ramets representing 85 understory herbaceous taxa were surveyed in the 60 – 1 m$^2$ plots across both old growth and mature forests (Figure III - 2). The number of ramets per plot varied from 31 to 1,130 (mean ± SE = 399.5 ± 252.1; median = 365.5). *Stellaria pubera* had the greatest abundance with 3,571 ramets. Old growth forests had higher numbers of ramets per plot (471.0 ± 258.53) compared to mature forests (322.8 ± 224.9; randomization test, p< 0.001). Nine of the 24 environmental variables differed significantly between old growth and mature forests (Figure III - 3 – 6), with old growth forests having greater macronutrients (P and estimated N released; Figure III - 3), micronutrients (Fe, Na and Zn; Figure III - 4), tree basal area (Figure III - 5), total exchangeable cations (TEC), organic matter (OM) and NO$_3$ (Figure III - 6).

Partitioning Species Composition

Environment

All environmental models are significant. In old growth forests, three environmental variables (Mn, Mg and TEC) are significant predictors of variation in community composition. The environmental model resulted in three constrained axes that explained 37.2% of the variation in species composition. The first axis explains 18.1% of the variation in species composition with Mn concentrations correlating with this axis. Several species have positive scores along this axis including four species of *Trillium sp.* (Table III – 1) indicating that there is a positive correlation between the species abundances and Mn concentrations. Axis 2 correlates negatively with TEC and
Mg and explains 10.0% while the third constrained axis is negatively correlated with TEC and explains 9.2% of the variation.

In mature forests, forward selection included only one significant predictor (Zn) that explained 11.1% of community variation. Several species were positively correlated with this constrained axis (V. blanda, Eupatorium rugosum and Potentilla sp) by having higher abundances at the high end of the Zn gradient. Other species were negatively associated with Zn (Geranium maculatum, Goodyera pubescens, V. palmate; Table III – 2) and decreased abundance with high Zn concentrations.

Space

Out of the continuous spatial data variables (PCNMs), three were significant predictors of species composition in old growth and mature forests. In old growth forests, the first significant spatial variable describes broad spatial patterns across the landscape (29 – 32 km). The second significant spatial variable models patterns between forest sites (5 – 10 km) while the third significant spatial variable describes between plot patterns (< 0.1 km) at two of the sites. In mature forests, two of the significant variables model broad scale patterns (14 – 19 km) while the third spatial variable describes spatial patterns between plots (< 0.1 km). A CCA using these spatial variables resulted in significant models that explained 35% of the variation in mature understory community composition and 44.1% in old growth forests.
Partial CCA

Partitioning variation in old growth species composition with both the environmental and spatial model explained 62.4% of community composition variation (Figure III - 7). The environment alone accounts for 18.3% of the variation in community composition. Space alone explains 25.2% of the variation while the interaction between the spatial and environmental components explains 18.9% of the variation in species composition. 37.6% of the variation is unexplained in old growth forests.

In mature forests, less of the variation in community composition was explained by the model combining space and environmental terms (40.2%; Figure III - 7). Environment alone explains little of the variation in species composition (5.1%). Space alone explains the largest portion of the variation (29.1%) with the interaction of space and environment accounting for 6.0%. The majority of the variation in mature forest composition is unexplained (59.8%).

Shared Species

Using only those species that are present in both forest ages, forward selection selected the same environmental parameters. In old growth forests, an additional spatial variable was significant modeling between plot scales (< 0.1km). In mature forests, the shared species data resulted in only one significant broad scale spatial variable (14 – 19 km) along with a between plot (< 0.1 km) spatial variable.

More of the variation was explained in old growth forests compared to mature forests (Figure III - 7). Little of the overall variation in shared species was explained by the environment alone in mature forests (6.2%) compared to old growth forests (16.8%).
Most of the explained variation in both forest ages arose from space alone (old growth: 33.1%; mature: 18.2%). The interaction of space and environment accounted for more of the variation in species composition in old growth forests (16.3%) compared to mature forests (5.7%).

Phenology

Spring ephemerals comprised 35.1% of the total ramets, summer greens 51.6% and evergreens 8.8%. Spring ephemerals were common and variable (old growth = 162.4 ± 188.8 ramets per plot; mature = 116.5 ± 160.9 ramets per plot; randomization p = 0.23). Summer greens make up the majority of species with *S. pubera* having the most ramets (3,571). Old growth forests have greater summer green ramets per plot (232.7 ± 128.8) than mature forests (184.1 ± 92.6; randomization p = 0.04). Evergreens also have greater ramet density in old growth forests (47.5 ± 40.8) compared to mature forests (22.3 ± 22.6; randomization p = 0.004).

Spring ephemeral composition in mature forests was not explained by any of the environmental variables. In old growth forests, Mn was a significant predictor of variation in species composition with both the entire community (4.3%) and using only shared species (4.7%). Space alone explained 12.0% for the entire community and 13.8% for shared species in old growth forests with site scale spatial patterns significant predictors (Figure III - 7). In mature forests, space alone explained 18.2% for the entire community and 33.2% for shared species with plot scale spatial patterns significant predictors. The majority of variation in spring ephemeral composition in old growth
forests is explained by the interaction of space and environment (whole community: 28.2%, shared: 31.4%; Figure III - 7).

Partitioning summer green variation within mature and old growth sites showed similar patterns. Most of the variation was explained by space alone (OG: 23.2%; MA=24.1%) or environment alone (OG: 18.3%; MA=19.1%; Figure III - 7). Several environmental parameters were significant predictors (Old growth: Mg, Mn and TEC; Mature: Mg, Zn and Ca). Using only shared species, partitioning of summer green composition in mature had little variation explained by environment alone (5.7%) with Zn the only significant variable. Old growth partitioning patterns using shared summer green species were similar to patterns observed for the entire community (Figure III – 7).

Evergreens in mature forests had no significant spatial variables (Figure III - 7). Summer canopy cover and estimated nitrogen released (ENR) were significant environmental variables for explaining composition in mature forests (39%). In old growth forests, Mn and Ca were significant environmental variables for explaining evergreen composition, however, within site spatial scales (2 – 10 km) contributed the most to explaining variation (31.4%; Figure III - 7). When only shared species between ages are considered, 92% of the variation in old growth evergreen composition was explained by the partial CCA model with greatest contributions coming from environment alone (40.2%) and the interaction of space and environment (42.7%; Figure III - 7). Several environmental variables were significant (Mn, Ca, K, ENR and P). In mature forests, shared evergreen species had no variation explained by spatial variables and 14.8% by the environment with only ENR a significant contributor.
Discussion

Results from this study show that logging a century ago results in decoupling of species composition from the environment. Environmental filtering is an important component for determining species composition in old growth forests and this process takes longer than a century to occur. Our results support previous conclusions that human land use disrupts existing biotic-environmental relationships (Foster et al. 1998, Vellend et al. 2007), while demonstrating that less intense logging disturbance also disrupts this relationship.

An alternative hypothesis may be that logging causes changes in species composition and that different composition, rather than disturbance per se is responsible for the difference in importance of environment in community structure. However, differences in environmental filtering were not due to intrinsic differences in the species that inhabit each aged forests. When including only those species that occur in both aged forests, species composition in old growth forests was coupled to the environment in ways not evident in logged sites even though the logging occurred 100 – 150 years ago.

The Role of the Environment

The environment plays a larger role in determining species composition in old growth forests than in mature forests. In mature forests, only zinc explains any significant portion of the variation in species composition and only a small percentage (5.1%). This is a site-specific phenomenon with one site having higher Zn concentrations than the other two sites. Excessive zinc concentrations from mining can cause distinct species composition (Brown 1994, Szarek-Lukaszewska et al. 2007); however,
concentrations found at this site does not indicate excessive amounts and is likely due to differences in parent rock material (Figure III - 4).

In old growth forests, species sort along a fertility gradient based on total exchangeable cations (TEC; Figure III - 6) and Mg (Figure III - 3). Species presence does not sort along a fertility gradient in previously logged forests. The fertility gradient differs between old growth and mature forests with a larger gradient present in old growth forests compared to mature forests (Figure III – 6, 3). The fertility gradient may be due to input of nutrients from plants, and the plants themselves may alter the environment (Facelli and Pickett 1991a, Xiong and Nilsson 1999). Input material from plants differs depending on species composition of both the herb and canopy layer (Muller 2003b). Decomposition is driven by moisture, temperature, carbon availability and manganese concentrations which can vary with forest age (Berg 2000, Knoepp et al. 2005). In old growth forests, plants have input nutrients into the soil over a longer time period than formerly logged forests, allowing adequate time for the plants to alter soil fertility. Old growth forests also have strong species spatial patterning due to interspecific interactions over time, creating patchy species distributions (Chapter IV). This patchy distribution of species leads to patchy input of nutrients into the environment. This has resulted in a coupling between species composition and the environment. In previously logged forest, a hundred years is not enough time for this coupling to occur which may be due to changes in the decomposition process, differences in the input plant material due to species composition or less species spatial patterning. Within mature forests, species have not had enough time for species interactions to play out and establish spatial patterns with pronounced environmental gradients.
Manganese concentration (Figure III - 4) is also a significant predictor of species composition in old growth forests. Although the concentrations do not differ between old growth and mature forests, the Mn gradient is greater in old growth forests compared to mature forests (Figure III – 4). Newell and Peet (1998) found a positive correlation between Mn concentration and herb layer diversity and abundance in the southern Appalachians. The enzyme manganese peroxidase (MnP) is produced by the majority of wood-degrading fungi and has an important role in lignin breakdown. Wood-inhabiting fungi have been shown to have greater species richness in old growth forests compared to forest logged 60 – 80 years ago (Lindblad 1998). This suggests that species composition in old growth forests may be coupled with a decomposition gradient due to wood-degrading fungi as indicated by Mn concentrations, but confirmation would require direct measurements of MnP or other indicators of fungal action.

Logging disturbance can alter the environmental gradient by changing the availability and distribution of soil nutrients and light availability. Soil nutrients vary in concert with changes in biogeochemical cycling due to mechanical disturbance during harvesting, as well as nutrient export through log removal and runoff (Likens et al. 1970, Martin et al. 2000). Logging reduces the amount of carbon and nitrogen available (Covington 1981, Small and McCarthy 2005). Our data demonstrate more nitrogen and organic matter in old growth forests and a larger environmental gradient compared to previously logged forests (Figure III - 3, 6). Logging disturbance also alters the light environment with maximum light transmittance in 50 year old forests and decreasing with age due to the increase of shade-tolerant canopy species that intersect more light (Brown and Parker 1994). Although the light environment did not differ between mature
forests and old growth forests (Figure III - 5), gap-phase dynamics in old growth forests create a patchy and heterogeneous understory light environment that may not be captured when measuring canopy cover (Martin 1992, Busing 1998, Miller et al. 2002).

**The Role of Space**

Spatial processes contribute the most to explaining species composition in mature forests (35%) with between forest site scales (2 – 10 km) the main significant contributor (Figure III - 7). We interpret this as indicating landscape-level dispersal limitation. In old growth forests, each site has high diversity and the species composition is explained by within site gradients. In mature forests, within site gradients do not explain species composition and species vary due to vagaries of dispersal (Figure III – 7). Noted dispersal distances are known for few herbaceous species (Cain et al. 1998). For those species that have been studied, dispersal includes ant, bird, wind and ballistic vectors with dispersal distances often < 1 m and occasionally > 10 m (Bierzychudek 1982, Matlack 1994, Cain et al. 1998). Potential long distance dispersal by deer has recently been emphasized with little known on this vector for forest herb species (Myers et al. 2004). Dispersal limitation at the scales of 2 – 10 km is shown in this study to be the primary predictor of species composition in mature forests.

**Phenology**

In mature forests, the environment does not explain any of the spring ephemeral species composition while in old growth forests the interaction between space and environment explains most of the composition. All of the known variation in spring ephemerals in previously logged forests is due to dispersal limitation. Spring ephemerals
disperse either by ants or lack dispersal vectors (Beattie and Culver 1981, Handel et al. 1981, Singleton et al. 2001), which can make these species slow to reoccupy sites (Meier et al. 1995). Composition and abundance of seed dispersing ants may also be altered by logging disturbance. Evidence for this has only been determined in highly and continually disturbed habitats (Heithaus and Humes 2003). However, comparisons between old growth forests and century old forests have not been conducted for ant communities.

Evergreen composition is only explained by the environment in mature forests with no contribution from spatial processes while in old growth forests both environment and space contribute to explaining species composition. Evergreen composition is explained by a summer light gradient along with available nitrogen in mature forests. Evergreen carbon gain occurs primarily in spring and fall, but additional carbon may be gained during the summer (Neufeld and Young 2003). In addition, nitrogen is an important component for many photosynthetic compounds (Lambers et al. 2000). A photosynthetic gradient appears to explain the largest proportion of evergreen composition in mature forests. In old growth forests, Mn and Ca were the important predictors for evergreen species composition in old growth forests. Soil calcium and species richness and composition in North Carolina piedmont forests have previously been found to be correlated with foliar calcium concentrations (Peet and Christensen 1980, Palmer 1991, Falkengren-Grerup et al. 2006).
Despite the reduced intensity of logging disturbance in comparison to agricultural land use, logging leaves a legacy on the understory community. Large-scale logging disturbance decouples species composition from the environment even after a century of recovery. Dispersal limitation between sites (2 – 10 km) explains most of the variation in species composition in mature sites while environmental gradients within sites explain old growth species composition. To conserve and manage these diverse communities, arrival of species into recovering forests needs to be addressed. In addition, more recovery time is needed to determine how long and if the environmental gradients that species sort along in old growth forests will take to return in logged forests.
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Rasband, W. S. 2008. ImageJ. in. US National Institutes of Health, Bethesda, Maryland, USA.


Table III - 1: Top ten highest scoring species along each axis of the partial canonical correspondence analysis in old growth forests based on the environment model with significant parameters of Mn, Mg and TEC along with three significant spatial parameters.

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Table III - 2: Top ten highest scoring species along each axis of the partial canonical correspondence analysis in mature forests based on the environment model with Zn the only significant parameter and three significant spatial parameters.

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Figure legends

Figure III - 1: Adapted from Borcard et al. (1992) showing how the variation is species composition is partitioned through CCA. Variation is partitioned into the environmental component alone (a), the spatial component alone (c), the intersection of the environmental and spatial components (b), and the unexplained variance in species composition (d).

Figure III - 2: Distribution of ramet abundance for all species surveyed in the 60 – 1 m² plots.

Figure III - 3: Boxplots showing the range and median of macronutrients (calcium, magnesium, phosphorous, potassium, sulfur and nitrogen) in old growth and mature forests. Significant differences (p < 0.05) between forest ages based on randomization tests using 10,000 permutations is indicated by *.

Figure III - 4: Boxplots showing the range and median of micronutrients (aluminum, iron, manganese, sodium, zinc, boron and copper) in old growth and mature forests. Significant differences (p < 0.05) between forest ages based on randomization tests using 10,000 permutations is indicated by *.

Figure III - 5: Boxplots showing the range and median of aboveground environmental parameters (spring and summer canopy cover, tree diversity and tree basal area) in old
growth and mature forests. Significant differences (p < 0.05) between forest ages based on randomization tests using 10,000 permutations is indicated by *.

Figure III - 6: Boxplots showing the range and median of other environmental parameters (litter depth, ammonium, nitrate, organic matter, total exchangeable cations, pH and lime requirements based on SMP buffer) in old growth and mature forests. Significant differences (p < 0.05) between forest ages based on randomization tests using 10,000 permutations is indicated by *.

Figure III - 7: Partitioning species composition into space, environment, combined environmental and spatial components along with unexplained components for all species (ALL), spring ephemerals (SP), summer greens (SU) and evergreens (EV) in old growth and mature forests. The first row shows the percent variation explained for the entire community and the second row includes only shared species that are found in both old growth and mature forests.
Figure III - 1
Figure III - 3
Figure III - 4
Figure III - 5
Figure III - 6
Figure III - 7
CHAPTER IV

FINE – SCALE SPATIAL PATTERNS IN AN UNDERSTORY APPALACHIAN
HERB COMMUNITY

Abstract

Fine-scale spatial patterns within plant communities determine which individuals
and species interact, having important implications for population dynamics and
community structure. The spatial segregation hypothesis states that intraspecific
aggregations can minimize competitive interactions between species allowing more
species to coexist. We explored fine-scale spatial patterns in the diverse understory
herbaceous layer of rich cove forests during two seasonal time periods and with and
without a history of logging. Dispersal limitation, clonal growth and environmental
factors were analyzed as potential explanatory variables for intraspecific aggregation.
Individuals were mapped across six forest sites (three old growth and three mature
forests). Intraspecific aggregation dominates spatial patterns regardless of logging
history and during both early and late spring. Spatial segregation hypothesis was
supported only in early spring with greater clumping occurring in old growth forests
compared to mature forests. Segregating species interactions in early spring may be a
mechanism by which old growth forests have greater species richness. Over a century
following disturbance, these slow growing spring herbs have not had enough time to form
aggregations found in undisturbed forests.
Introduction

Spatial segregation hypothesis predicts that intraspecific spatial aggregation promotes stable coexistence by decreasing interspecific competition, which would lead to competitive exclusion (Silander and Pacala 1985, Tilman 1994, Levin and Pacala 1997, Neuhauser and Pacala 1999, Eppstein et al. 2006). Empirical evidence for this hypothesis is less abundant than theoretical evidence (Plotkin and Muller-Landau 2002, Bolker et al. 2003). Clumping correlates with greater species richness in field studies of both wetland and sand dune communities (Rees et al. 1996, Weiher et al. 1998). De Boeck (2006) found that spatial aggregation reduced niche segregation and decreased community resource uptake, allowing greater plant density. An alternative expectation is that greater intraspecific aggregation will decrease alpha diversity by having fewer species than expected due to space taken up by clumping. Veech (2005) found this to be the case for arthropod species in which richness was not correlated with the amount of intraspecific aggregation except at the beta diversity level.

Diverse plant communities provide the biggest challenge for untangling processes of species coexistence. Tropical rainforests have been the focus of much research whereas experimental evidence stems primarily from grassland and sand dune communities (Tilman 1994, Stoll and Prati 2001, Condit et al. 2002). A unique and diverse community for addressing the roles of spatial aggregation for species coexistence is the understory herbaceous layer of rich cove hardwood forests. This community has more non-tree vascular plant species than any other region of North America (Wofford 1989, Ricketts et al. 1999). The herb species are predominantly long-lived perennials,
many of which have clonal growth and short dispersal distances (Bierzychudek 1982, Jolls 2003). There are also distinct temporal niches in this community with some species utilizing early spring to grow and reproduce before canopy leaf out, spending the remainder of the year belowground (true spring ephemerals). Other species may emerge in spring, but remain throughout the summer (summer greens) (Bierzychudek 1982).

**Spatial drivers**

Potential drivers of spatial patterns within the understory herbaceous layer include dispersal ability, clonal growth, and environmental conditions (Silvertown et al. 1993, Coomes et al. 1999, Jacquemyn et al. 2001). Dependence of spatial patterns on environmental heterogeneity can either be driven directly by abiotic conditions for a species or indirectly through resource use mediated by competition (Miller et al. 2002). If clumping is due to the distribution of abiotic conditions then environmental variables will correlate with aggregation (e.g. Svenning and Skov 2002, Hardy and Sonke 2004, Fraterrigo et al. 2006). Clonal growth and spatially restricted dispersal can drive patterns of aggregation, both of which are common among the understory herbaceous species (Hurtt and Pacala 1995, Hardy and Sonke 2004, Whigham 2004). Within the understory, dispersal limitation has a strong role in structuring communities at the 100 m scale with most species dispersing less than 1 m (Bierzychudek 1982, Matlack 1994, Cain et al. 1998, Svenning and Skov 2002).
Temporal drivers

Drivers of spatial patterns vary across time. Distinct temporal patterns in the understory result in species utilizing different temporal niches. Spring ephemerals emerge and flower prior to canopy closure whereas the majority of species are summer greens and may emerge before canopy closure, but persist throughout the summer (Jolls 2003). Distinct temporal patterns in the understory are subjected to different environmental conditions may alter spatial patterns. In particular, light and nutrients are more available in early spring than later in summer (Lapointe 2001).

Disturbance

Understanding whether there are long-term effects of disturbance on spatial patterns is important for understanding community recovery and ecosystem dynamics. Duncan and Stewart (1991) suggest that spatial patterns can offer indirect evidence for the importance of disturbance on shaping community structure.

Large scale disturbance for the understory herbaceous layer occurs through timber harvesting. Most studies have focused on herbaceous layer diversity and abundance with logging disturbance (Duffy and Meier 1992, Ford et al. 2000). Of the studies that addressed spatial patterns with disturbance, Honnay et al. (1999) found that spatial patterns in the understory are influenced by past land use. *Maianthemum canadense* aggregates in later successional forests but exhibits a regular distribution in early successional forests (Collins 1988). Studies suggest that old growth and late successional forests have more aggregation than disturbed forests, which may be an important legacy of disturbance that affects species coexistence (Scheller and Mladenoff 2002). However,
Fraterrigo et al. (2006b) found random spatial patterns in understory abundance for both disturbed and undisturbed cove hardwood forests.

Scale

Plant neighborhoods can be small with spatial patterns occurring within a few centimeters affecting population dynamics more than large scale spatial patterns (Molofsky 1999, Purves and Law 2002). Crawley and Harral (2001) suggested that ecological interactions are most important at small spatial scales. The size of the plant's neighborhood scales with the size of the individual or smaller (Okland and Bakkestuen 2004). For tropical tree saplings, spatial autocorrelation for growth was strongest within 5 m (Uriarte et al. 2004). Among grassland species, plants within a 3 cm distance of the target individual had the greatest influence on biomass (Milbau et al. 2007). These studies suggest that it is the neighboring plants at small spatial scales that have the greatest effect on plant performance and coexistence. However, most studies address mesoscale (1 m – 100 m) patterns in species aggregations (Svenning and Skov 2002, Fraterrigo et al. 2006b) with little understanding of the small scale patterns between individuals. In a plant community comprised of long-lived perennials many of which are clonal with short dispersal distances, the interactions among species at fine spatial scales are essential for understanding the role of spatial aggregation for species coexistence.

Within the understory herb layer we addressed whether aggregation occurs at small spatial scales (< 1 m²). If aggregation is allowing species to coexist at small spatial scales, then it is expected that those plots with greater aggregation will exhibit greater species richness. Factors such as environmental variables, total plant abundance,
dispersal mode and clonal growth form were evaluated as potential drivers for aggregation. We also addressed how community spatial pattern changes through the growing season in the understory herb community to determine if there are temporal patterns for aggregation.

Large-scale logging disturbance in the Southern Appalachians has impacted most of the forested landscape. Understanding how spatial patterns mediate coexistence in old growth and recovering forests is necessary for conserving this diverse community. Are there persistent effects of logging disturbance on patterns of aggregation? Do the drivers of aggregation (environmental parameters, abundance, dispersal modes or clonal growth) vary with logging history? Can aggregation account for differences in species richness between old growth and logged forests in the understory?

Methods

Study sites

Cove hardwood forests comprise a quarter of the forested area in the Southern Appalachians, but they harbor the highest diversity of understory herbaceous species and are highly vulnerable to land-use changes (Ford et al. 2000, Turner et al. 2003). Six forest sites were selected in the Nantahala National Forest, North Carolina located in the Blue Ridge Mountain Physiographic Province. All forest sites had similar slope, aspect (north, northeast, or east), elevation (700 to 1200 m), and hardwood rich cove forest type (Ford et al. 2000) as determined using GIS based on US Forest Service Continuous Inventory and Stand Condition (CISC) data, USGS digital elevation models, and old growth surveys conducted by the Western North Carolina Alliance (Western North
Carolina Alliance 1995; ArcGIS 8.0). Three forests were old growth and three forests were mature forests, logged 100 – 150 years ago.

Old growth describes forests that have never been clear cut and have little or no evidence of anthropogenic disturbance (Duffy and Meier 1992). The old growth forests are not managed by the Forest Service (United States Department of Agriculture 1994). Logging rotation times are 100 to 150 years in the Southern Appalachians (Brown, E., pers. com.), therefore, mature forests represent the amount of recovery that is likely to occur before a subsequent logging rotation. These forests were logged by private lumber companies prior to the Forest Service management, and have undergone natural regeneration (United States Department of Agriculture 1994).

Spatial Mapping

Each forest site was 1 ha with the cove drainage dissecting the center of the site. As a part of a larger study, twelve transects consisting of five 0.25 m$^2$ plots spaced 5 m apart and running perpendicular to the cove drainage were established following Ford et al. (Ford et al. 2000) at each site. A subset of the plots was used for this study. Ten randomly chosen 0.25 m$^2$ plots at each site were expanded to 1 m$^2$ plots for a total of 60 – 1 m$^2$ plots. In each plot, all ramets were mapped and identified once monthly between March and August. Surveys among all sites were conducted in the same week to minimize any variations in phenology among sites.
Drivers of aggregation

The light environment was assessed by percent canopy cover. Canopy cover was measured in the center of the 10, 1-m$^2$ plots at each site in both early spring and summer when the canopy was fully leafed out using hemispherical photographs analyzed in Image J (Rasband 2008). Five of the 10-1 m$^2$ plots at each site were randomly selected. Soil samples were collected (8 cm diameter, 4 cm depth) from the center of the five, 1-m$^2$ plots. Samples were analyzed for total exchangeable cations (TEC), pH, lime requirement, organic matter, macronutrients, micronutrients, ammonium and nitrate by Brookside Laboratories, New Knoxville, Ohio. Soils data were analyzed using principal components analysis on Box-Cox transformed data to reduce the number of variables for subsequent analysis. Disperal vector and clonal growth of each species was categorized based on published data (Table IV – 1).

Aggregation Analysis

For each herb species with an abundance > 5 individuals in a plot, aggregation was determined with a nearest neighbor distance spatial index (R splancs; http://cran.r-project.org/web/packages/splancs/index.html). This index calculates the mean nearest neighbor distance (NND) for each species in each plot. The species within the plot is then randomized 1000 times without replacement and the nearest neighbor distance is calculated during each permutation. The spatial index for each species within each plot is calculated by:

\[
\text{Spatial Index (SI)} = \frac{\text{observed mean NND} - \text{median randomized NND}}{\text{standard deviation of randomized NND}}
\]
If the SI value is less than -2 then the species is significantly clumped. Between -2 and 2 indicates a random distribution while SI values greater than 2 demonstrate a regular distribution. Plot level SI values were calculated as the mean of the SI values for the species within the plot. Wilcox tests were used to determine whether the clumping index differed significantly between mature and old growth forests for early and late spring (R 2.6.2; http://www.R-project.org/).

Results

Aggregation

A total of 24,169 individual ramets were mapped during the surveys across all six forest sites. Aggregation predominated for all species in both early and late spring at small spatial scales (Figure IV – 1, 2). In early spring there were 41 species that were abundant enough to calculate aggregation (> 5 individuals per plot; Figure IV – 1). The randomly distributed species are likely aggregated at larger spatial scales (i.e. *Podophyllum peltatum*). Eight species were significantly aggregated in all plots they were present in (*Prenanthes sp, Iris cristata, Viola canadensis, Galearis spectabilis, Viola pubescens, Dryopteris intermedia, Caulophyllum thalictroides, Uvularia grandifolia*; Figure IV – 3). One species (*Viola hastata*) in a one mature forest plot was regularly spaced. This single outlier was removed from subsequent analyses.

In late spring, 63 species were analyzed for spatial patterns with most individuals showing clumped distributions within plots (Figure IV – 2). 21% of the species were aggregated in all the plots they occurred with *Stellaria pubera, Tiarella cordifolia* and *Anemone quinquefolia* having the greatest number of plots with aggregation (Figure IV –
Most of the species ranged from having either a clumped or random distribution in all plots (Figure IV – 2).

**Plot spatial index**

Plot spatial index was calculated as the mean of the species spatial indices that occurred in each plot. In early spring, plots in old growth forests were significantly more clumped than in mature forests (Wilcox test; W = 510, p = 0.01; Figure IV – 5). All the mature forest plots exhibited random spatial distributions. In late spring there was no difference between old growth and mature forests in their spatial index (W = 346, p-value = 0.26; Figure IV – 6). The amount of clumping did not differ between early and late spring for all sites (W = 1565, p = 1.0), old growth forests (W = 386, p = 0.47) or mature forests (W = 400, p = 0.38).

**Richness and aggregation**

In early spring, there is a significant correlation between plot species richness and mean clumping index. Plots with more species tend to be more clumped, although little of the variation in clumping is explained by species richness ($r^2 = 0.07$, $F_{(1,52)} = 4.02$, $p = 0.05$). Within old growth and mature forests separately there is not a correlation between plot mean clumping index and richness (Og: $r^2 = 0.05$, $F_{(1,27)} = 1.35$, $p = 0.26$, Hu: $r^2 = 0.05$, $F_{(1,23)} = 1.20$, $p = 0.28$). Fourteen species were abundant enough to calculate SI for a minimum of ten plots. One species, *Claytonia caroliniana*, was clumped significantly more in plots with greater species richness (Table IV – 2). Clumping of all other species was not related to species richness of the plot.
In late spring there was not an overall relationship between plot species richness and spatial patterns \( (r^2 = 0.01, F_{(1, 56)} = 0.62, p = 0.43) \) along with no correlations within old growth \( (r^2 = 0.00, F_{(1, 28)} = 0.02, p = 0.90) \) or mature forests \( (r^2 = 0.01, F_{(1, 26)} = 0.03, p = 0.59) \) separately. Eighteen species had > 5 individuals in a minimum of ten plots and of these none showed a significant correlation between spatial patterns and plot species richness (Table IV – 2).

**Density**

Clumping was also not explained by the number of individuals within a plot in early spring \( (r^2 = 0.04, F_{(1, 52)} = 2.03, p = 0.16) \) or within only old growth \( (r^2 = 0.05, F_{(1, 27)} = 1.36, p = 0.25) \) or mature forests \( (r^2 = 0.08, F_{(1, 23)} = 2.08, p = 0.16) \). In early spring, only *C. caroliniana* had greater clumping in plots with more individuals (Table IV – 3). Similarly, there were no significant correlations between clumping and abundance (square root transformed) in late spring \( (r^2 = 0.04, F_{(1, 56)} = 2.12, p = 0.15) \). Within old growth forests there was no pattern \( (r^2 = 0.00, F_{(1, 28)} = 0.00, p = 0.95) \), however mature forests tended to have more clumping when more individuals were present in a plot \( (r^2 = 0.13, F_{(1, 26)} = 3.93, p = 0.06) \). *Cardamine diphylla* and *Ranunculus sp* exhibited significantly greater clumping in plots with more individuals whereas *Dicentra sp*. showed the opposite pattern (Table IV – 3).

**Environmental parameters**

A PCA of 19 soil variables after Box-Cox transformations yielded five components with eigenvalues greater than 1, together explaining 80.5% of the total
variation. The first axis reflected a gradient of low to high Ca and Mg and high to low Al levels. The second axis is largely a gradient ranging from high to low organic matter, estimated nitrogen release, and Zn (Figure IV – 7). The second axis is predominately a gradient from old growth forests to mature forests. The first two components explain 61.2% of the total variation. Neither PC axes were correlated with mean plot clumping in early spring (PCA1: \( r^2 = 0.08, p = 0.09 \); PCA2: \( r^2 = 0.01, p = 0.30 \)) or late spring (PCA1: \( r^2 = -0.01, p = 0.44 \); PCA2: \( r^2 = 0.02, p = 0.21 \)). Early spring spatial index was negatively correlated with Ca (\( r^2 = 0.12, p = 0.05 \)), NO\(_3\) (\( r^2 = 0.18, p = 0.02 \)) and total exchangeable cations (\( r^2 = 0.17, p = 0.02 \)). Only leaf litter depth was significantly positively correlated with late spring spatial index (\( r^2 = 0.18, p = 0.01 \)).

Percent canopy cover (square root transformed) in early spring was not correlated with mean plot clumping at all sites (\( r^2 = 0.03, p = 0.17 \)) nor within old growth (\( r^2 = 0.05, p = 0.27 \)) or mature forests (\( r^2 = 0.001, p = 0.86 \)). For individual species, only *E. americanum* exhibited a significantly pattern with more clumping in plots with low percent canopy cover (Table IV – 4). In late spring, no patterns were found between clumping and percent canopy cover at all sites (\( r^2 = 0.02, p = 0.31 \)), old growth (\( r^2 = 0.03, p = 0.39 \)), or mature forests (\( r^2 = 0.02, p = 0.43 \)).

**Dispersal and clonal growth**

Dispersal vectors do not show a clear pattern with aggregation (Figure IV – 8). As expected ant, gravity and those species lacking dispersal vectors showed a mean spatial index with significant clumping. However, wind dispersal species also have significant clumping (Figure IV – 8). Clonal growth did not explain species patterns of
aggregation (Figure IV – 9). All species except for four (*Galium aparine*, *Geranium maculatum*, *Impatiens sp.* and *Poa sp.*) exhibit some form of clonal growth.

**Discussion**

Aggregation dominates at fine spatial scales in the understory herbaceous layer of rich cove forests in both old growth and mature forests, resulting in most neighborhood interactions occurring among conspecifics. In early spring, plots with more aggregations contain more species, consistent with the spatial segregation hypothesis (Levin and Pacala 1997, Neuhauser and Pacala 1999, Eppstein et al. 2006). The more aggregated plots occur in old growth forests, which coincide with greater spring ephemeral richness in old growth forests compared to mature forests (Wyatt 2009, Chapter II). Studies in other communities have found a similar relationship between species richness and aggregation (Rees et al. 1996, Weiher et al. 1998, De Boeck et al. 2006, Weigelt et al. 2007).

The late spring community, however, did not support the spatial segregation hypothesis. This community had no relationship between species richness and aggregation along with no differences in the amount of aggregation occurring among plots in old growth and mature forests. It could be that aggregation alters mean plant size but not establishment or survival of neighbors (Lortie et al. 2005). To address this it would be necessary to measure biomass in addition to aggregation.

The alternative hypothesis that greater intraspecific aggregation will decrease diversity by having fewer species due to clumps taking up space (Veech 2005) was not supported by either early or late herb communities. Aggregation within the diverse
understory herb community is either associated with an increase in species richness or no relationship to richness.

**Density**

Aggregation is not a method to pack more individuals into a given space as there is no relationship between clumping and plot ramet density. The only exception to this occurred in late spring in mature forests where plots with higher densities tended to have greater aggregation. In old growth forests, clumping is independent of density. (Stoll and Prati 2001) provided experimental evidence of intraspecific aggregation suppressing the dominant species while increasing performance in the weaker competitors with the strongest patterns observed in high density communities. The same processes took place at low density, but density played an important role in the strength of the relationship. If this was the case for understory herb communities then it would be expected that plots with high density would have greater species richness and more aggregation, which was not the case. There is a large gradient in ramet abundance across plots (5 – 303 individuals/plot), so the absence of a relationship between aggregation and density is not due to a lack of a density gradient. Plots with a few ramets are just as likely to be clumped as those plots with hundreds of ramets.

**Drivers of aggregation**

Some of the fine scale aggregation is explained by dispersal vectors with ant dispersal and gravity dispersal having clumped distributions. These dispersal mechanisms are known to create a distinct clumped spatial pattern (Howe and Smallwood
1982, Kalisz et al. 1999). Inconsistent with expectations was wind dispersed species showing significant clumping, which is opposite from the expected pattern (Clark et al. 1998). This pattern is driven by Monarda sp., which is wind dispersed but forms dense clumps with short underground stolons.

Clonal growth predominates among understory herbs with vegetative reproduction far more common than sexual reproduction (Bierzychudek 1982, Eriksson 1989). Clonal growth likely has a much stronger role in aggregation than our results show. Different species exhibit various forms of vegetative growth with some species having short stolons or rhizomes while other species have large distances between ramets (Antos 1988, Whigham 2004). Coexistence among different types of clonal growth has been demonstrated in which shorter rhizomatous perennials grow in clumps to survive among guerilla-growth strategy perennials that have large spacing between ramets (Rebele 2000). Qualifying the type of clonal growth rather than the presence or absence of clonal growth would likely explain more of the differences in clumpiness among species.

Environment and aggregation

The greater aggregated distribution of species in old growth forests in early spring leads to patchy input of nutrients into the environment through leaf litter input. In early spring, plots with greater clumping have higher concentrations of Ca, total exchangeable cations (TEC) and NO$_3$. Both TEC and NO$_3$ have higher concentrations in old growth forests compared to mature forests and TEC is a predictor of species composition in old growth forests (Wyatt 2009, Chapter III). The species that are clumped in these plots
likely cause the observed higher concentrations through leaf litter input rather than the environment dictating aggregation patterns.

**Disturbance**

Spatial patterns with disturbance can be altered by changes in species composition (Duffy and Meier 1992), dispersal limitation (Jules and Rathcke 1999) and changes in nutrient heterogeneity (Fraterrigo et al. 2006b). Reduced dispersal would predict greater aggregation in disturbed forests, which was not observed. Old growth forests have greater clumping than mature forests, but only in early spring. Species composition does differ between old growth and mature forests (Wyatt 2009, Chapter II) so differences in clonal growth or dispersal vectors could account for the clumpiness. Another possibility is that vegetative growth is slow and that aggregations form over many years. Over a century following disturbance, these slow growing spring herbs have not had enough time to form aggregations like those found in undisturbed forests. Segregating species interactions due to clumping in early spring may be a mechanism by which old growth forests have greater species richness.
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Georgia Press, Athens, GA.

Trillium (spp.) seeds in eastern North America. American Midland Naturalist
146:444-446.

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Table IV – 2: Results of regressions between species spatial index (SI) with plot species richness in early spring and late spring. Regressions were conducted on those species with > 5 individuals in a minimum of ten plots, which included 14 species in early spring and 18 species in late spring. Significant correlations indicated by *.

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Table IV – 3: Results of regressions between species spatial index and square root transformed plot abundance. Regressions were conducted on those species with > 5 individuals in a minimum of ten plots, which included 14 species in early spring and 18 species in late spring. Significant correlations indicated by *.

| Early Spring | | | | |
| Species | r^2 | p-value | |
| Cardamine clematitis | 0.05 | 0.54 | |
| Cardamine diphylla | 0.18 | 0.08 | |
| Claytonia caroliniana | 0.21 | 0.004 | |
| Dicentra sp | 0.07 | 0.33 | |
| Erythronium americanum | 0.10 | 0.13 | |
| Impatiens sp | 0.00 | 0.76 | |
| Monarda sp | 0.00 | 0.99 | |
| Polystichum acrostichoides | 0.14 | 0.23 | |
| Ranunculus sp | 0.00 | 0.96 | |
| Solidago sp | 0.00 | 0.95 | |
| Stellaria pubera | 0.00 | 0.60 | |
| Tiarella cordifolia | 0.11 | 0.35 | |
| Viola sp | 0.12 | 0.06 | |

| Late Spring | | | | |
| Species | r^2 | p-value | |
| Anemone quinquefolia | 0.01 | 0.73 | |
| Cardamine clematitis | 0.05 | 0.39 | |
| Cardamine diphylla | 0.41 | 0.01 | |
| Claytonia caroliniana | 0.12 | 0.27 | |
| Dicentra sp | 0.36 | 0.02 | |
| Erythronium americanum | 0.00 | 0.81 | |
| Eurybia divaricata | 0.10 | 0.31 | |
| Impatiens sp | 0.00 | 0.82 | |
| Laportea canadensis | 0.01 | 0.70 | |
| Osmorhiza longistyris | 0.05 | 0.53 | |
| Polystichum acrostichoides | 0.15 | 0.24 | |
| Ranunculus sp | 0.64 | 0.003 | |
| Solidago sp | 0.03 | 0.50 | |
| Stellaria pubera | 0.00 | 0.93 | |
| Tiarella cordifolia | 0.02 | 0.52 | |
| Trillium sp | 0.15 | 0.17 | |
| Viola hastate | 0.02 | 0.70 | |
| Viola sp | 0.05 | 0.19 | |
Table IV – 4: Results of regressions for species spatial index with percent canopy cover (square root transformed in early spring). Regressions were conducted on those species with > 5 individuals in a minimum of ten plots, which included 14 species in early spring and 18 species in late spring. Significant correlations indicated by *.

<table>
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<th>Early Spring</th>
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Figure legends

Figure IV – 1: Boxplot of spatial pattern index for all species across all plots in early spring. Only those species that have > 10 individuals in at least one 1 m$^2$ plot are included. A spatial index (SI) $\leq$ -2 (dotted line) signifies aggregation, $2 > SI > -2$ (between dotted and dashed lines) indicates random distribution within the plot and SI $>$ 2 (above the dashed line) shows a regular distribution.

Figure IV – 2: Boxplot of spatial pattern index for all species across all plots in late spring. Only those species that have > 10 individuals in at least one 1 m$^2$ plot are included. A spatial index (SI) $\leq$ -2 (dotted line) signifies aggregation, $2 > SI > -2$ (between dotted and dashed lines) indicates random distribution within the plot and SI $>$ 2 (above the dashed line) shows a regular distribution.

Figure IV – 3: Boxplot of mean spatial index for old growth and mature forests in early spring. A spatial index (SI) $\leq$ -2 (dotted line) signifies aggregation, $2 > SI > -2$ (between dotted and dashed lines) indicates random distribution within the plot and SI $>$ 2 (above the dashed line) shows a regular distribution.

Figure IV – 4: The number of plots each species is aggregated in early spring. Species are ranked in descending order of the number of plots aggregated.
Figure IV – 5: The number of plots each species is aggregated in late spring. Species are ranked in descending order of the number of plots aggregated.

Figure IV – 6: Boxplot of mean spatial index for old growth and mature forests in late spring. A spatial index (SI) ≤ -2 (dotted line) signifies aggregation, 2 > SI > -2 (between dotted and dashed lines) indicates random distribution within the plot and SI > 2 (above the dashed line) shows a regular distribution.

Figure IV – 7: Principle component analysis of all soil variables at all sites showing the first two axes, which explain 61.2% of the total variation. A biplot of age shows that the second axis is predominately a gradient from old growth forests (closed triangles) to mature forests (open triangles). The first component mostly reflected a gradient of low to high Ca and Mg and high to low Al levels. The second component is largely a gradient ranging from high to low organic matter, estimate nitrogen release, and Zn.

Figure IV – 8: Boxplot summarizing the spatial pattern index for species categorized according to their primary dispersal mode (see Table IV – 1). A spatial index (SI) ≤ -2 (dotted line) signifies aggregation and 2 > SI > -2 (above dotted line) indicates a random spatial distribution.

Figure IV – 9: Boxplot summarizing the spatial pattern index for species categorized according to whether they exhibit clonal growth or not (non-clonal). All species except four (Galium aparine, Geranium maculatum, Impatiens sp. and Poa sp.) exhibit clonal
growth. A spatial index (SI) $\leq -2$ (dotted line) signifies aggregation and $2 > SI > -2$
(above dotted line) indicates a random spatial distribution.
Number aggregated plots

Figure IV – 3
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**Figure IV – 4**
Figure IV – 5
Figure IV – 6
Figure IV – 7
Figure IV – 8
Figure IV – 9
CHAPTER V

A TRAIT BASED ANALYSIS OF COEXISTENCE MECHANISMS IN THE UNDERSTORY HERB LAYER OF RICH COVE FORESTS

Abstract

Neighborhood plant interactions cause differential survival among species and over time communities are assembled through species sorting. The alpha niches within these local neighborhoods are those traits that allow species to utilize necessary resources. Alpha niche traits can either be different between co-occurring species (trait overdispersion), similar among co-occurring species (trait underdispersion) or represent a random sample of traits from the species pool. Trait overdispersion allows differentiation in resource use through niche partitioning while trait underdispersion demonstrates environmental filtering. Large-scale logging can impact community structure and environment gradients, potentially altering the process by which species assemble into communities. We used a trait based approach to determine whether neighboring individuals in the understory herbaceous community of Southern Appalachian cove forests exhibit traits that are more or less similar than expected in old growth forests and forests logged over a century ago. Eight functional traits were used as proxies for a plant’s ability to use light, water, and nutrient resources for 51 species. Trait similarity between nearest neighbors was analyzed based on a model in which species were randomly sampled and their trait distance determined. Environmental filtering predominates at fine spatial scales in the diverse understory herb community.
Conspecific clumping accounted for some of the trait similarity at fine spatial scales. However, nearest heterospecific neighbors also showed significant trait similarity due to environmental gradients. More environmental filtering for light capture traits occurs in old growth forests than forests that were previously logged while the opposite pattern is found for nutrient uptake. After long term recovery from logging disturbance, fine-scale species assembly operates according to different processes than those found in old growth forests.
Introduction

Plant community composition depends on a complex set of factors that occur on many spatial and temporal scales (Leibold et al. 2004, Cottenie 2005, Ernest et al. 2008, Hillebrand et al. 2008). However, at the basic level, sessile organisms must avoid being directly displaced by neighbors through competitive interactions (Peet and Christensen 1980, Silander and Antonovics 1982). These neighborhood interactions cause differential survival among species, and over time the communities are assembled through species sorting (Silander and Pacala 1985).

Though the possible interactions among species are myriad, these interactions are all mediated by traits that have fitness consequences (Belyea and Lancaster 1999, McGill et al. 2006). Functional traits are those traits with specific relationships between the environment and the species (Diaz et al. 1998). Functional traits can affect community assembly by affecting the outcome of neighborhood competition which can differ with spatial and temporal scales (Diaz et al. 1998, Weiher et al. 1998, Thompson et al. 2001, Rodriguez et al. 2003, Mouillot et al. 2007). Along environmental gradients, differential survival due to niche partitioning sorts species with similar traits into coexisting communities (Silvertown et al. 2006, Schamp and Aarssen 2009). This species-sorting can occur along environmental gradients from large to small spatial scales, and is a fundamental process in creating beta (among habitat) diversity. Traits sorting species along environmental gradients are known as a species’ “beta niche”, the range of environmental conditions under which the species is maintained (Ackerly et al. 2006, Silvertown et al. 2006).
At any position along an environmental gradient, however, species face competitive exclusion by other species competing for the same resources (Racz and Karsai 2006). The result of this competition determines the alpha- or within-habitat diversity of a site, and traits differentiating among species within locales are termed the “alpha niche.” These traits allow the species to use the resources within a local community. Examples include traits that finely partition resources such as light, water, nutrients or pollinators (Mann and Shugart 1983, Beatty 1984, Sydes 1984, Shaukat 1994, Nordbakken 1996, Ackerly et al. 2006).

Theories predict that species sorting based on traits is important for coexistence (Ackerly et al. 2006, McGill et al. 2006, Schamp et al. 2008). A trait-based approach can provide evidence for how species assemble into communities based on trait dispersion among co-occurring species. Trait overdispersion predicts that traits among co-occurring species are less similar than expected. Trait overdispersion allows species to minimize competitive interactions and differentiation in resource use through niche partitioning (MacArthur and Levins 1967, Abrams 1983). In contrast, Keddy (1992) viewed community assembly as the process by which the environment removed species that lacked the traits necessary to persist in a specific location. This environmental filtering is evident in a community by trait underdispersion, in which co-occurring species are more similar in their traits than expected (Schamp et al. 2008).

Empirical investigations on trait dispersion between coexisting species have lagged behind theoretical predictions. Overdispersion of traits among species has been found in rooting patterns and leaf water control within a sand dune community (Stubbs and Wilson 2004), in height and shoot biomass in wetland communities (Weiher et al. 159).
1998), in desert plant rooting patterns (Schenk and Jackson 2002) and in tropical forest communities (Kraft et al. 2004). Trait underdispersion has been demonstrated for seed size and seed number in a grassland community (Franzen 2004), among species inhabiting similar microtopographies (Beatty 1984), along a water-table gradient (Nordbakken 1996) and with soil pH and leaf litter (Mann and Shugart 1983). Soil fertility within a community requires similarity in traits such as growth rate, leaf longevity, defense and leaf litter decomposition (Sydes 1984, Reich et al. 1992, Grime et al. 1996). Other studies, however, have shown no significant trait over- or underdispersion between coexisting species (Schamp et al. 2008).

The challenge of understanding species coexistence is increased in diverse plant communities (Kraft et al. 2004). The understory herb community of rich cove forests in the Southern Appalachians provides high diversity and fine-scale environmental heterogeneity in which to address the dispersion of traits among co-occurring species (Lorimer 1980, Runkle 1982, Canham et al. 1994, Meier et al. 1995). Potential competitive resources in the understory community are light, water and nutrients (Motten et al. 1981, Pearcy et al. 1987, Eickmeier and Schussler 1993, Anderson and Eickmeier 1998, Lapointe 2001). Light in the understory is patchy due to the overstory with little known about how light is partitioned among co-occurring herb species (Pearcy et al. 1987). Due to the abundance of available water in cove hardwood forests (127-152 cm annually; Olano and Palmer 2003), research on water relations among herbaceous species is limited. However, herbaceous roots are usually limited to surface soils and can not tap into deeper water sources, which may restrict the amount of water available (Muller
Nutrient availability in forests also varies across temporal and spatial scales (Small and McCarthy 2005, Fraterrigo et al. 2006b, Barbier et al. 2008).

**Spatial Scale**

The spatial scale at which trait dispersion occurs has important implications for how communities are structured (Levin 1992). The most important scale for competitive interactions occurs at fine-scales where individuals directly interact for light, nutrients and water (Peet and Christensen 1987, Crawley and Harral 2001). These direct interactions are more consequential than the indirect interactions such as competition for seed dispersers and pollinators or herbivore avoidance (Callaway and Walker 1997). Neighboring plants at small spatial scales have the greatest effect on plant performance and coexistence (Uriarte et al. 2004, Milbau et al. 2007). Environmental heterogeneity also occurs at fine-scales through soil resource gradients, overstory characteristics and microtopography (Hicks 1980, Beatty 1984). In a plant community comprised of long-lived perennials, many of which are clonal with short dispersal distances (Whigham 2004), the interactions among species at the local scale are essential for understanding community assembly.

**Disturbance**

Species sorting requires time, and the temporal aspect of species sorting is little understood (Verheyen et al. 2003a). Disturbances of different sizes and intensity can disrupt the sorting process by changing the spatial and temporal availability of resources, and also by limiting both the time that species are in competition, and the time species have to effectively track their environment (Paine 1976, Thompson et al. 2001, Small and
McCarthy 2002, Vellend et al. 2007, Schamp and Aarssen 2009). Disturbances can range from small-scales such as tree-falls and the action of large mammals, to large-scale disturbances such as ice storms and hurricanes (Lorimer 1980, Duncan and Stewart 1991, Gerhardt and Foster 2002, Morrison and Spiller 2008). Anthropogenic disturbance may present an extreme case of this by having large effects on community structure and environmental gradients (Laurance et al. 1998, Flinn and Marks 2007, Vellend et al. 2007). Understanding how traits are distributed in disturbed forests provides a window on how these communities are structured and any differences they exhibit from undisturbed communities.

Here we address the dispersion of eight functional traits among coexisting species in the diverse understory herb layer of rich cove forests. We predict that if niche partitioning is occurring, then significant trait overdispersion will be found among co-occurring species. If the environment is assembling the community, then trait underdispersion will be the dominant pattern among coexisting species. We also investigate the impact of large-scale anthropogenic disturbance on coexistence mechanisms. Trait dispersion patterns among coexisting species in old growth communities are compared to communities that have undergone 100 – 150 years of recovery from logging disturbance.

**Methods**

*Vegetation Survey*

The study was conducted in rich cove forests in the Nantahala National Forest in North Carolina, USA, which is located in the southern portion of the Appalachian
Mountains. Cove forests comprise 25% of forested land, but are the highest diversity habitat in the Southern Appalachians. Within these forests, the highest diversity by far is found in the understory herb layer, with herb communities having ~6x the diversity of the surrounding overstory (Gilliam 2007). We selected six rich cove hardwood forests with similar slope, aspect (0° – 90°) and elevation (700 to 1200 m) using US Forest Service Continuous Inventory and Stand Condition (CISC) data and USGS digital elevation models (ArcGIS 8.0, USGS digital elevations models and USFS CISC). The understory vegetation includes a diverse and well-developed herbaceous layer comprised predominately of perennial species that are long-lived, slow growing with short dispersal distances and clonal growth (Whigham 2004).

The Nantahala National Forest harbors old growth forests that have never been logged. Three of the forest sites were old growth forests that are characterized by large living trees, uneven aged trees, tree fall gaps and snags (Martin 1992, Hardt and Swank 1997). Paired with the old growth forests were rich cove sites that were clear-cut between 1864 – 1906 and are designated as mature forest (USFS CISC). These 100-150 yr old mature forests have undergone natural regeneration (Western North Carolina Alliance 1995; US Department of Ag 1994). Landscape logging rotation times are managed to be 100 to 150 years in the Southern Appalachians (USFS), so the mature forests in this study represent the maximum amount of recovery possible before subsequent logging.

Each forest site was 1 ha with the cove drainage dissecting the center of the site. As a part of a larger study, twelve transects consisting of five 0.25 m² plots spaced 5 m apart and running perpendicular to the cove drainage were established following Ford et
al. (2000) at each site. A subset of the plots was used for this study. Ten randomly chosen 0.25 m$^2$ plots at each site were expanded to 1 m$^2$ plots for a total of 60 – 1 m$^2$ plots. In each plot, all ramets were mapped, identified and counted once monthly between March and August. Surveys among all sites were conducted in the same week to minimize any variations in phenology among sites.

_Traits_

Eight functional traits indicative of light, nutrient and water acquisition were measured for each species by sampling ten individuals at random of all species that occurred in > 5% of the plots (51 species; Table V – 1). A range of traits demonstrated in other systems to be functional and easily measured were selected (Cornelissen et al. 2003, Bernhardt-Romermann et al. 2008). This design allows plants to “report” what traits are important in structuring this particular community (Table V – 2). Potential competitive resources in the understory community are light, water and nutrients (Motten et al. 1981, Pearcy et al. 1987, Eickmeier and Schussler 1993, Anderson and Eickmeier 1998, Lapointe 2001). Standard methods were used for measuring each of the functional traits (see references in Table V – 2).

_Analysis_

_Trait Dispersion_

Using the x, y coordinates of each individual within a plot, the nearest neighbor for each individual was determined. Trait similarity between nearest neighbors was assessed by taking the observed mean species trait values and calculating the Euclidean
distance in trait space between species (Figure V – 1). This was repeated for each individual within the plot and the mean nearest neighbor trait distance within a plot was calculated. Monte-carlo simulation was used to determine whether traits are more or less similar than expected by chance (Gotelli 2000). The simulation was conducted as follows: All 51 species were included in the regional species pool. From this pool, two species were chosen at random with replacement, and their distance in trait space determined. This was repeated 5000 times to obtain a random distribution of trait distances. To determine the probability of trait underdispersion, the number of times the observed trait distances was less than the expected random trait distances was summed and divided by the number of randomizations (5,000). The probability of trait overdispersion is the sum of the number of times the observed trait distances was greater than expected divided by the number of randomizations. This was repeated for each plot and each trait (Figure V – 1). For each plot, the probability determined whether overall the species within the plot were more similar (trait underdispersion) or less similar (trait overdispersion) than expected by a random sampling of species. All analyzes were programmed and run in R (R 2.6.2; http://www.R-project.org/) (code for the analyses is in appendix 1).

Clonal growth and intraspecific aggregation is common among understory herb species (Whigham 2004), therefore it is likely that the nearest neighbor is a conspecific. Intraspecific clumping would tend to reduce the mean distance in trait space between neighbors. To determine whether patterns of trait dispersion are due to intraspecific clumping, the analysis was repeated in which the nearest heterospecific neighbor was selected. To ensure that neighbors were within distance to interact, the interaction
neighborhood was limited to within 5 cm of the focal individual. The same random model and probability of trait similarity was assessed for the nearest interspecific neighbor within 5 cm (Figure V – 1).

Interactions in Relation to Forest History

To determine whether trait dispersion differed between old growth and hundred year old forests, the number of plots with significant trait underdispersion and overdispersion were counted and a Chi-squared test was used to determine whether there was a significant difference in the proportion of plots. This was repeated for each of the eight traits under both the nearest neighbor and the nearest interspecific neighbor model.

Trait ordination

A principal component analysis (PCA) was used to explore patterns of multiple covariation among traits by ordinating the mean trait values for each plot. To assess differences in mean trait values between old growth and mature forests plots, forest age centroids were mapped onto ordination space. Significance was determined following Oksanen and Minchin (2002) using a simulation that compares the observed $r^2$ value with 1000 permutations of the data (vegan; http://r-forge.r-project.org/projects/vegan/).

Environmental Analysis

To determine whether environmental parameters explain trait underdispersion, environmental data was correlated with trait dispersion for those traits that had significant underdispersion in > 15% of the plots in the interspecific analysis. Trait dispersion
results from interspecific analysis were used because any effects due to intraspecific clumping were removed. We analyzed 24 environmental factors (Wyatt 2009, Chapter III; Figure 3 – 6). Canopy cover was measured in the center of the 10, 1-m² plots at each site using hemispherical photographs analyzed in Image J (Rasband 2008). Litter depth was measured from litter layer top to soil surface in the center of each plot. Five of the 10-1 m² plots were randomly selected. In these plots, tree basal area and tree species richness was surveyed within a ten meter radius. Soil samples were collected (8 cm diameter, 4 cm depth) from the center of the plots and analyzed for total exchangeable cations (TEC), pH, lime requirement (SMP buffer), organic matter, macronutrients, micronutrients, ammonium, nitrite and nitrate by Brookside Laboratories, New Knoxville, Ohio.

Results

For the 23,169 individual ramets mapped in the 60 – 1 m² plots across six forest sites, trait underdispersion prevailed. More trait underdispersion occurred among nearest neighbors when conspecifics were included (Table V – 3). However, trait underdispersion still occurred when only interspecific neighbors were included in the analysis (Table V – 4). Old growth forests showed greater trait underdispersion than mature forests for traits associated with light capture while traits for nutrient uptake were more likely to be underdispersed in mature forests among co-occurring species.
Nearest neighbor individuals

Nearest trait distance between species for each of the 23,169 individuals shows frequency distributions skewed towards small trait distances (underdispersion). Randomized sampling from the species pool exhibits a similar skewed distribution indicating that few species combinations from the species pool have large differences in trait values (Figure V – 2 – 5). Most species have overlapping trait values for total chlorophyll (Figure V – 6), chlorophyll a:b ratio (Figure V – 7) and SLA (Figure V – 12). The most divergent traits among species are leaf area (Figure V – 8), leaf shape (Figure V – 9) and root diameter (Figure V – 11).

All traits demonstrate individuals having significantly smaller trait distances than expected by the random community (Figure V – 2 – 5). Differences among individual trait distances between old growth and mature forests support plot mean results for chlorophyll a:b (Figure V – 3) and leaf lobation (Figure V – 3) having greater underdispersion in old growth forests while leaf succulence (Figure V – 5) and leaf shape (Figure V – 4) are more similar among species occupying the same plot in mature forests.

Nearest neighbor plot means

Of the 60 – 1 m² plots, 57 had traits more similar than expected for at least one trait when the nearest neighbor included conspecifics. Only two plots had significant trait overdispersion with leaf succulence. In these plots, thick- and thin- leaved species co-occurred more often than expected. Total chlorophyll, leaf area, leaf shape, leaf lobation,
thickest root diameter, chlorophyll a:b and SLA have significant trait underdispersion in more than half of the plots (Table V – 3).

When interspecific neighborhoods were restricted to only plants in direct proximity (within 5 cm), 46 of 60 – 1 m² plots had significant trait underdispersion for at least one trait. The proportion of plots with significant trait underdispersion among heterospecifics was reduced in comparison to when conspecific neighbors were included. Leaf area, thickest root diameter and SLA were the most common traits to be more similar than expected (Table V – 4). More plots had significant trait overdispersion between heterospecifics than when intraspecific neighbors are included. The most overdispersion (15% of the plots) occurred for chlorophyll a:b and leaf succulence (Table V – 4).

*Forest age plot comparison*

When nearest neighbors included conspecifics, significantly more plots have underdispersion in old growth forests for total chlorophyll, chlorophyll a:b, leaf area and leaf succulence than mature forest plots. Traits associated with gas exchange, water retention and nutrients were more similar in mature forests compared to old growth forests (Table V – 3).

With the removal of intraspecific clumping, nearest heterospecific neighbors show significantly more trait underdispersion in old growth forests for leaf area, leaf lobation, SLA, and chlorophyll a:b (Table V – 4). Overdispersion of leaf succulence occurred more in old growth forests than mature forests while the opposite pattern was found for chlorophyll a:b and total chlorophyll. Leaf shape, succulence and thickest root
diameter had significant more underdispersion among nearest neighbors in mature forests compared to old growth forests (Table V – 4).

**Environmental correlations**

After removal of within-species spatial clumping as a cause of trait similarity, environmental gradients partially explain the patterns of trait similarity. Leaf area was significantly positively correlated with early spring canopy cover with similar leaf areas occurring in plots with little canopy cover (Figure V – 14A). Plots with similar chlorophyll a:b ratios are significantly correlated with low soil sulfur concentrations (Figure V – 14B). No environmental factors significantly explained underdispersion of leaf lobation. Both high concentrations of Al and NH$_4$ are correlated with underdispersion of thickest root diameter (Figure V – 14C, D). Plots with more similar leaf shapes than expected occur in plots with high Na concentrations and deep leaf litter (Figure V – 15A, B). SLA underdispersion occurred in plots with low SMP buffer and high tree species richness (Figure V – 15C, D).

**Trait ordination**

When functional traits were ordinated to look for patterns of covariation, the first two PCA axes explained together 22.9% of the among-plot mean trait variation (14.5% and 4.3%, respectively). Three traits were most strongly negatively associated with axis 1, thickest root diameter (trait score along PCA1: $r = -1.09$) and leaf area ($r = -1.84$). The second axis was negatively correlated with chlorophyll a:b ($r = -1.08$). Using forest age as a centroid class, a simulation comparing the observed $r^2$ value with 1000 permutations
of the data determined that the fit of the forest age centroids to the plots was significant ($r^2 = 0.06, p < 0.001$; Figure 16).

**Discussion**

Trait underdispersion predominates among co-occurring species in the understory herbaceous layer of rich cove forests indicating that environmental filtering regulates community assembly. Though part of the trait similarity among co-occurring individuals is accounted for by intraspecific clumping, significant environmental filtering occurs among co-occurring heterospecifics. Traits indicative of light capture are more similar among co-occurring species in old growth forests while traits for nutrient uptake are more similar among co-occurring species in mature forests (Table V – 4). The environmental filters that determine species membership in herb communities differ with land use history.

*Disturbance*

Land use history due to logging alters the processes that determine species assembly at small spatial scales. Fundamental changes in how species assemble within communities have changed even after over a century of recovery. The light environment filters species in old growth forests with coexisting species having more similar chlorophyll a:b ratios and SLAs than expected. In mature forests traits for light capture tend toward the opposite pattern with species differentiating in their chlorophyll a:b ratios (Table V – 4). This could indicate a more competitive light environment in mature forests where species must utilize the available light in different ways to survive.
Species assembled within mature forests do not represent a random sample of traits. The predicted pattern under niche assembly is that a community would start as a random sample of traits and then gradually whittle down to similar traits due to environment filtering (Decocq et al. 2004, Garnier et al. 2004, Schamp et al. 2008, Schamp and Aarssen 2009). Since forests that have been recovering for 100 – 150 years were used in this study, earlier successional stages would have to be assessed to determine whether the community starts as a random sample of traits.

In mature forests the species partition the light resource within plots, and then gradually move towards compositions where species with similar traits are found together. As the canopy matures, species have long periods of time to interact with surrounding species and sort according to their optimal environment. The successional trajectory of light availability in the understory includes maximum light transmittance in 50 year old forests followed by decreasing availability due to the increase of shade-tolerant canopy species that intersect more light (Brown and Parker 1994). The light environment did not differ between mature forests and old growth forests (Wyatt 2009, Chapter III), however, gap-phase dynamics in old growth forests create a patchy and heterogeneous understory light environment that may not be captured when measuring canopy cover (Martin 1992, Busing 1998, Miller et al. 2002). A more uniform low light environment in mature forests likely drives the need to partition light among co-occurring species and imposes greater competition for light and less similar light capture traits. The patchy light environment in old growth forests allows species to sort according to their light requirement needs.
Intraspecific vs. Interspecific Neighbors

Given clonal growth and limited dispersal of herbaceous species (Whigham 2004), there is a high probability that the nearest neighbor will be a conspecific. As expected, traits are more similar than expected under this condition since conspecifics have the same traits. Conspecific clumping can have important implications for species assembly. By competing with intraspecific neighbors, it reduces the interactions that occur among species and can minimize competitive exclusion (Levin and Pacala 1997, Neuhauser and Pacala 1999, Eppstein et al. 2006).

By removing conspecifics from the model, we could determine whether intraspecific clumping accounted for the significant environmental filtering. Less trait underdispersion did occur when addressing only heterospecifics, however, there was still significant underdispersion. The environment is structuring the plant community such that only those species that share similar traits co-occur at small spatial scales. The exception to this is with chlorophyll a:b in mature forests and leaf succulence in old growth forests. Both of these traits demonstrate niche partitioning with co-occurring species less similar than expected.

Spatial scale

Weiher and Keddy (1995) proposed that trait overdispersion should occur at small spatial scales and trait underdispersion at larger spatial scales. However, the results of these analyses show that at fine spatial scales, species are more similar in their traits than expected. Silva and Batalha (2009) found the same pattern of environmental filters predominating at fine spatial scales among tree species in a woodland cerrado. This
demonstrates that at the scale where individuals interact, species sort according to the environment rather than partitioning resources. Species in the fine-scale neighborhood have similar alpha niches and must possess traits necessary for the environment at that location.

**Beta niche**

Although this study did not address changes in traits across habitats, the environmental gradients across sites were addressed. More extreme environmental conditions resulted in traits that were more similar than expected. This was the case for root diameter and plots with high concentrations of Al and NH$_4$ (Figure V – 14C, D). In plots with high light availability, species assemblages tended to be more similar in their leaf area (Figure V – 14A). Since most of the understory species are shade adapted (Neufeld and Young 2003), these higher light plots provide an environment filter for more light demanding, gap specialist species that have similar adaptations for utilizing increased light (Collins et al. 1985, Collins and Pickett 1988, Goldblum 1997).

Chlorophyll a:b ratios sorted along a sulfur concentration gradient (Figure V – 14B). Sulfur is an important component of ferredoxin, an iron-sulfur protein, that operates in electron transport within chloroplasts (Fromme et al. 2001). Those plots with lower sulfur concentrations have species assemblages with more similar than expected chlorophyll a:b ratios. Lack of sulfur can decrease chlorophyll concentration and represents a stronger environmental filter (Imsande 1998).
Conservation implications

Distinct differences exist in how species assemble within old growth forest communities compared to mature forests that have been recovering from logging disturbance for a 100 – 150 years. Different environmental filters drive assembly in each forest. In old growth forests, traits indicative of light capture are more similar among co-occurring species while traits for nutrient uptake are more similar among co-occurring species in mature forests. Logging disrupts the sorting process by limiting the time species have to effectively track their environment and by altering resource availability. Over a century of recovery is not enough time for the sorting process to return to that found in old growth forests and only continued assessment of these forests over time will determine whether species assembly processes ever become equivalent.
Literature Cited


Table V – 1: List and abbreviations of the 51 species that occurred in > 5% of the plots
that were measured for the eight functional traits.

<table>
<thead>
<tr>
<th>Species</th>
<th>Abbrev.</th>
<th>Species</th>
<th>Abbrev.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adiantum pedatum</td>
<td>ADPE</td>
<td>Podophyllum peltatum</td>
<td>POPE</td>
</tr>
<tr>
<td>Allium tricoccum</td>
<td>ALTR</td>
<td>Polystichum acrostichoides</td>
<td>POAC</td>
</tr>
<tr>
<td>Anemone quinquefolia</td>
<td>ANQU</td>
<td>Polygonatum biflorum</td>
<td>POBI</td>
</tr>
<tr>
<td>Arisaema triphyllum</td>
<td>ARTR</td>
<td>Prenanthes sp</td>
<td>PR</td>
</tr>
<tr>
<td>Asarum canadense</td>
<td>ASCA</td>
<td>Ranunculus sp</td>
<td>RA</td>
</tr>
<tr>
<td>Aster divaricatus</td>
<td>ASDI</td>
<td>Ranunculus hispidus</td>
<td>RAHI</td>
</tr>
<tr>
<td>Cardamine clematitii</td>
<td>CACL</td>
<td>Sanguinarian canadensis</td>
<td>SACA</td>
</tr>
<tr>
<td>Cardamine diphylla</td>
<td>CADI</td>
<td>Solidago caesia</td>
<td>SOCA</td>
</tr>
<tr>
<td>Caulophyllum thalicroides</td>
<td>CATH</td>
<td>Stellaria pubera</td>
<td>STPU</td>
</tr>
<tr>
<td>Claytonia caroliniana</td>
<td>CLCA</td>
<td>Thalictrum dioicum</td>
<td>THDI</td>
</tr>
<tr>
<td>Cryptotaenia canadensis</td>
<td>CRCA</td>
<td>Thalictrum thalicroides</td>
<td>TTHH</td>
</tr>
<tr>
<td>Dicentra sp</td>
<td>DI</td>
<td>Tiarella cordifolia</td>
<td>TICO</td>
</tr>
<tr>
<td>Disporum lanuginosum</td>
<td>DILA</td>
<td>Trillium erectum</td>
<td>TRER</td>
</tr>
<tr>
<td>Dryopteris intermedia</td>
<td>DRIN</td>
<td>Trillium grandiflorum</td>
<td>TRGR</td>
</tr>
<tr>
<td>Erythronium americanum</td>
<td>ERAM</td>
<td>Trillium luteum</td>
<td>TRLU</td>
</tr>
<tr>
<td>Eupatorium rugosum</td>
<td>EURO</td>
<td>Trillium vaseyi</td>
<td>TRVA</td>
</tr>
<tr>
<td>Galium aparine</td>
<td>GAAP</td>
<td>Uvularia grandiflora</td>
<td>UVGR</td>
</tr>
<tr>
<td>Galium latifolium</td>
<td>GALA</td>
<td>Veratrum parviflorum</td>
<td>VEPA</td>
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<tr>
<td>Geranium maculata</td>
<td>GEMA</td>
<td>Viola blanda</td>
<td>VIBL</td>
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<td>Hepatica acutiloba</td>
<td>HEAC</td>
<td>Viola canadensis</td>
<td>VICA</td>
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<td>Hydrophyllum virginianum</td>
<td>HYVI</td>
<td>Viola hastate</td>
<td>VIHA</td>
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<td>Impatiens sp</td>
<td>IM</td>
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<td>Iris cristata</td>
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<td>VIPA</td>
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<td>LACA</td>
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<td>VIPU</td>
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<td>Maianthemum racemosum</td>
<td>MARA</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Monarda sp</td>
<td>MO</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Osmorhiza longistyliis</td>
<td>OSLO</td>
<td></td>
<td></td>
</tr>
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</table>
Table V – 2: Functional characters for light, nutrient and water use obtained from (Stubbs and Wilson 2004) along with characters for herbivory resistance and life history characteristics relevant to competition and colonization.

<table>
<thead>
<tr>
<th>Character</th>
<th>Importance</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chlorophyll a:b ratio</td>
<td>Growth strategy</td>
<td>(Porra et al. 1989, Neufeld and Young 2003)</td>
</tr>
<tr>
<td>Total chlorophyll content of the leaves</td>
<td>Light capture</td>
<td>(Porra et al. 1989, Madakadze et al. 1999, Wang et al. 2004)</td>
</tr>
<tr>
<td>Specific leaf area (SLA)</td>
<td>Photosynthetic capacity</td>
<td>(Reich et al. 1998, Meziane and Shipley 1999)</td>
</tr>
<tr>
<td>Leaf area</td>
<td>Water retention, gas exchange</td>
<td>(Meziane and Shipley 1999, Fernandez et al. 2004)</td>
</tr>
<tr>
<td>Leaf lobation</td>
<td>Gas exchange, water retention, convection</td>
<td>(Smith et al. 1997)</td>
</tr>
<tr>
<td>Leaf shape</td>
<td>Gas exchange</td>
<td>(Smith et al. 1997)</td>
</tr>
<tr>
<td>Leaf succulence</td>
<td>Water retention</td>
<td>(Kramer 1995)</td>
</tr>
<tr>
<td>Root diameter of the thickest root</td>
<td>Nutrient storage</td>
<td>(Berendse et al. 1999)</td>
</tr>
</tbody>
</table>
Table V – 3: Percent of plots with significant trait underdispersion and overdispersion for the nearest neighbor (NN) which includes intraspecific neighbors for all plots (All), plots in mature forests (Ma) and old growth plots (Og). Significant differences (*) in the percent of plots with trait dispersion between hundred year and old growth forests were determined by Chi-squared tests.

<table>
<thead>
<tr>
<th>Trait Underdispersion</th>
<th>All NN</th>
<th>Ma NN</th>
<th>Og NN</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chlorophyll a:b *</td>
<td>71.67</td>
<td>53.33</td>
<td>90.00</td>
</tr>
<tr>
<td>Total chlorophyll *</td>
<td>55.00</td>
<td>46.67</td>
<td>63.33</td>
</tr>
<tr>
<td>SLA *</td>
<td>81.67</td>
<td>76.67</td>
<td>86.67</td>
</tr>
<tr>
<td>Leaf area *</td>
<td>71.67</td>
<td>60.00</td>
<td>83.33</td>
</tr>
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<td>Leaf lobation *</td>
<td>73.33</td>
<td>76.67</td>
<td>70.00</td>
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<tr>
<td>Leaf shape *</td>
<td>53.33</td>
<td>70.00</td>
<td>36.67</td>
</tr>
<tr>
<td>Leaf succulence *</td>
<td>45.00</td>
<td>56.67</td>
<td>33.33</td>
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<tr>
<td>Thickest root diameter *</td>
<td>85.00</td>
<td>86.67</td>
<td>83.33</td>
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</table>

<table>
<thead>
<tr>
<th>Trait Overdispersion</th>
<th>All NN</th>
<th>Ma NN</th>
<th>Og NN</th>
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<tr>
<td>Chlorophyll a:b</td>
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<td>0.00</td>
<td>0.00</td>
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<tr>
<td>Total chlorophyll</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>SLA</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Leaf area</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Leaf lobation</td>
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<td>0.00</td>
<td>0.00</td>
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<tr>
<td>Leaf shape</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Leaf succulence</td>
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<td>3.33</td>
</tr>
<tr>
<td>Thickest root diameter</td>
<td>0.00</td>
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Table V – 4: Percent of plots with significant trait underdispersion and overdispersion for the nearest interspecific neighbor (NN) within 5 cm all plots (All), plots in mature forests (Ma) and old growth plots (Og). Significant differences (*) in the percent of plots with trait dispersion between hundred year and old growth forests were determined by Chi-squared tests.

<table>
<thead>
<tr>
<th>Trait Underdispersion</th>
<th>All NN interspecific</th>
<th>Ma NN interspecific</th>
<th>Og NN interspecific</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total chlorophyll</td>
<td>10.00</td>
<td>10.00</td>
<td>10.00</td>
</tr>
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<td>SLA *</td>
<td>46.67</td>
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<td>53.33</td>
</tr>
<tr>
<td>Leaf area *</td>
<td>45.00</td>
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<td>56.67</td>
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<tr>
<td>Leaf lobation *</td>
<td>18.33</td>
<td>13.33</td>
<td>23.33</td>
</tr>
<tr>
<td>Leaf shape *</td>
<td>18.33</td>
<td>23.33</td>
<td>13.33</td>
</tr>
<tr>
<td>Leaf succulence *</td>
<td>10.00</td>
<td>13.33</td>
<td>6.67</td>
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<tr>
<td>Thickest root diameter *</td>
<td>43.33</td>
<td>46.67</td>
<td>40.00</td>
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<table>
<thead>
<tr>
<th>Trait Overdispersion</th>
<th>All NN interspecific</th>
<th>Ma NN interspecific</th>
<th>Og NN interspecific</th>
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<tbody>
<tr>
<td>Chlorophyll a:b *</td>
<td>15.00</td>
<td>26.67</td>
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</tr>
<tr>
<td>Total chlorophyll *</td>
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<td>6.67</td>
<td>0.00</td>
</tr>
<tr>
<td>SLA</td>
<td>1.67</td>
<td>3.33</td>
<td>0.00</td>
</tr>
<tr>
<td>Leaf area</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Leaf lobation</td>
<td>6.67</td>
<td>6.67</td>
<td>6.67</td>
</tr>
<tr>
<td>Leaf shape</td>
<td>1.67</td>
<td>0.00</td>
<td>3.33</td>
</tr>
<tr>
<td>Leaf succulence *</td>
<td>15.00</td>
<td>6.67</td>
<td>23.33</td>
</tr>
<tr>
<td>Thickest root diameter</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>
**Figure legends**

Figure V – 1: Flow chart showing the analysis for trait under- and over-dispersion among nearest neighbors. Trait dispersion was assessed by taking the observed mean species trait values and calculating the Euclidean distance in trait space between species for each individual within the plot. The mean nearest neighbor trait distance within a plot was calculated based on the nearest neighbor trait distance for each individual within the plot. This analysis was repeated for each plot and each trait.

Figure V – 2: Histograms show the frequency distribution of trait distances among interspecific individuals for leaf area and total chlorophyll content. Grey bars represent individuals in old growth forests and white bars are mature forests. The horizontal bar shows the trait distances from the randomized community with the thin line representing the 95th confidence interval and the thick bars the interquartiles.

Figure V – 3: Histograms show the frequency distribution of trait distances among interspecific individuals for chlorophyll a:b ratio and leaf lobation. Grey bars represent individuals in old growth forests and white bars are mature forests. The horizontal bar shows the trait distances from the randomized community with the thin line representing the 95th confidence interval and the thick bars the interquartiles.

Figure V – 4: Histograms show the frequency distribution of trait distances among interspecific individuals for thickest root diameter and leaf shape. Grey bars represent
individuals in old growth forests and white bars are mature forests. The horizontal bar shows the trait distances from the randomized community with the thin line representing the 95\textsuperscript{th} confidence interval and the thick bars the interquartiles.

Figure V – 5: Histograms show the frequency distribution of trait distances among interspecific individuals for specific leaf area (SLA) and succulence. Grey bars represent individuals in old growth forests and white bars are mature forests. The horizontal bar shows the trait distances from the randomized community with the thin line representing the 95\textsuperscript{th} confidence interval and the thick bars the interquartiles.

Figure V – 6 -13: Boxplots showing the median and range of the eight functional traits (total chlorophyll, chlorophyll a:b ratio, leaf area, leaf shape, leaf lobation, thickest root diameter, specific leaf area and leaf succulence) based on measurements on ten individuals for each of the 51 species. Species abbreviations are shown in Table V – 1.

Figure V – 14: Plots of the significant correlations between environmental variables and mean plot trait distances for A. early spring canopy cover and leaf area trait distance ($r^2 = 0.10$, df = 27, $p = 0.05$), B. sulfur concentration and chlorophyll a:b trait distance ($r^2 = 0.11$, df = 27, $p = 0.04$), C. aluminum concentrations and thickest root diameter ($r^2 = 0.17$, df = 27, $p = 0.02$) and D. ammonium concentrations and thickest root diameter ($r^2 = 0.11$, df = 27, $p = 0.04$).
Figure V – 15: Plots of the significant correlations between environmental variables and mean plot trait distances for A. sodium concentrations and leaf shape trait distance ($r^2 = 0.12$, df = 27, $p = 0.03$), B. litter depth and leaf shape trait distance ($r^2 = 0.25$, df = 27, $p < 0.01$), C. SMP buffer and SLA trait distance ($r^2 = 0.13$, df = 27, $p = 0.03$) and D. tree species richness and SLA trait distance ($r^2 = 0.30$, df = 27, $p < 0.01$).

Figure V – 16: Principal component analysis based on mean trait values for each old growth (circles) and mature (triangles) forest plots. The first two axes are shown, which explain 22.9% of the among-plot mean trait variation. A biplot shows the direction and strength of each of the eight traits along the first two axes of the ordination. Ellipses show the standard deviation of the age class centroids.
Vegetation Survey

X, Y coordinates of individuals

Find nearest neighbor

Trait distance matrix

Determine distance in trait space between nearest neighbors

Repeat for each individual in the plot and calculate the mean nearest neighbor trait distance (rnd.real)

P-values:
\[
\frac{\text{sum(rnd.real} \leq \text{rnd.rand})}{5000} \\
\frac{\text{sum(rnd.real} \geq \text{rnd.rand})}{5000} \\
\text{Two-tailed p} < 0.025
\]

Repeat 5000 times to obtain a random distribution of trait distances (rnd.rand)

Trait Measurements

Observed Species Traits

Species

<table>
<thead>
<tr>
<th>Traits</th>
<th>A</th>
<th>B</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>SLA</td>
<td>2</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Chl</td>
<td>5</td>
<td>6</td>
<td>7</td>
</tr>
<tr>
<td>Area</td>
<td>8</td>
<td>9</td>
<td>0</td>
</tr>
</tbody>
</table>

Random model:
Use trait distance matrix for regional species pool.
Randomly sample species (with replacement) and determine trait distance.

Figure V – 1
Figure V – 2
Figure V – 3

Chlorophyll a:b

Leaf lobation
Figure V – 4

Thickest Root Diameter

Leaf Shape

Figure V – 4
Specific Leaf Area

Leaf Succulence

Figure V – 5
Figure V – 6
Figure V – 7
Figure V – 9
Thickest root diameter (cm)

ADPE
ALTR
ANQU
ARTR
ASCN
ASDI
CACL
CADT
CATH
CLCA
COCA
DI
DILA
DRIN
ERAM
EURO
GAAP
GALA
GEMA
HEAC
HYVI
IM
IRCR
LACA
MAMA
MO
OSLO
POAC
POBI
POPE
PR
RA
RAHI
SACA
SOCA
STPU
THDI
THTH
TICO
TRER
TRGR
TRLU
TVRA
UVGR
VEPA
VIBL
VICA
VIHA
VIPA
VIPAL
VIPU

Figure V – 11
Figure V – 13
Figure V – 14
Figure V – 15
Figure V – 16
Appendix I

Code for analyzing trait similarity between nearest neighbors in R 2.6.2 (http://www.Rproject.org/) developed by K. Feeley.

```r
traits<-read.csv("traits.csv",header=T) # mean trait data for each species
plot<-read.csv("Ch1ls.csv") # x,y coordinate data
require(vegan)
geo.dist=vegdist(plot[,1])
m=match(plot[,1], colnames(traits))
plot.traits=t(traits[,m]) # choose your trait
t.dist=vegdist(plot.traits[,1], "euclidean") # trait distance
geo.dist=as.matrix(geo.dist) # nearest neighbor distance
m=matrix(0, nrow=dim(geo.dist)[1], ncol=dim(geo.dist)[1])
for(i in 1:dim(geo.dist)[1]){for(j in 1:dim(geo.dist)[1]){if(i==j)m[i,j]=1}
}
w=which(m==1)
geo.dist[w]=NA
nn=apply(geo.dist, 1, which.min)
t.dist=as.matrix(t.dist)
t.dist[w]=NA
nnd.real=c() # observed nearest neighbor trait distance
for(i in 1:dim(geo.dist)[1]){nnd.real[i]=t.dist[i,nn[i]]}
mnnd.real=mean(nnd.real) # mean observed nearest neighbor trait distance
allsp.dist=vegdist(t(traits[,1:-1]), "euclidean") # choose trait
allsp.dist=as.matrix(allsp.dist) # regional species pool
nn=apply(allsp.dist, 1, which.min)
mnnd.rand=c()
for(z in 1:5000){
s=sample(dim(allsp.dist)[1],dim(geo.dist)[1], replace=T)
rand.dist=allsp.dist[s,s]
nn.rand=c()
for(i in 1:dim(geo.dist)[1]){nn.rand=rand.dist[nn,i]}
mnnd.rand[z]=mean(nn.rand) # mean random nearest neighbor trait distance
chu<-sum(mnnd.rand<=mean(nnd.real))/length(mnnd.rand) # proportion underdispersed
cho<-sum(mnnd.rand>=(mnnd.real))/length(mnnd.rand) # proportion overdispersed
```
CHAPTER VI

CONCLUSION

Do Appalachian herbaceous understories ever recover from clearcutting?

Duffy and Meier 1992

This dissertation addresses a central question in community ecology, which is assessing the degree to which communities bear the mark of history. Over a decade ago, a debate began over whether understory herb layer within Southern Appalachian cove forests, among the highest biodiversity habitats in North America, recover to their pre-disturbance states following logging. Evidence showing reduced diversity in previously logged forests was criticized for not accounting for intersite environmental heterogeneity (Duffy and Meier 1992). Ford et al. (2000) addressed environmental heterogeneity, but neglected long-term recovery by using mature forests as the benchmark for diversity comparison. The studies presented here addressed both long-term recovery of an understory herbaceous community and accounted for intersite heterogeneity by comparing paired sites of old growth forest and forest logged over a century ago. The current studies also included seasonal variation within the community, which has been absent from most previous studies. In agreement with Duffy and Meier (1992), this dissertation shows that understory herb communities do not return to their pre-disturbance states even after 100 – 150 years of recovery in nearly all important respects; species richness, abundance, composition, spatial patterns, and ecological processes that assemble plant communities.
The lack of recovery and resilience in the herb community after over a century since logging was evident in the patterns of species richness, individual abundance, and species composition (Chapter II). Both species richness and abundance was greater in old growth forests than mature forests and species composition differed significantly between the two. Importantly, this study showed that diversity in the herb layer varies with spatial scales. Most of the understory herb species accumulate when going across a single forest cove and between forest coves.

The finding that old growth forests had greater species richness begs the question, “why?” One major factor contributing to coexistence in plant communities are mechanisms that minimize competitive interactions. Intraspecific aggregation is a mechanism that can minimize competitive interactions between species allowing more species to coexist, and this spatial segregation hypothesis was tested in Chapter IV. By mapping the spatial configurations of individuals it was determined that intraspecific aggregation dominates spatial patterns regardless of logging history in plant communities present during both early and late spring. The aggregation likely arises due to clonal growth and short dispersal, though the result of long-term competitive interactions is also spatial aggregation. The spatial segregation hypothesis was supported only in old growth forests in early spring where greater clumping correlated with species richness. Decreasing interspecific competitive interactions in early spring may be a mechanism by which old growth forests have greater species richness, however, experimental evidence is needed. The proximate drivers of aggregation also need further exploration. Aggregations in old growth forests have had many years of undisturbed growth, while in
mature forests these slow growing spring herbs have not had enough time to form extensive aggregations.

Differences in community composition are due to differences in the process of community assembly. Chapter III tested alternative hypotheses about the relationship of environmental factors to species composition in old growth and mature forests, respectively. The study focused on differences between the two ages. Results show that species composition in old growth forests is largely explained by environmental variables. In mature forests, even those up to 150 years old, the pattern of species composition was decoupled from the environment. Environmental variables related to soil fertility and decomposition largely explain species composition across old growth forest landscapes, while dispersal limitation between sites (2 – 10 km) explains most of the variation in species composition in mature sites. These results demonstrate that 100 – 150 years of recovery is inadequate for species to reach equilibrium with the environment.

The last chapter in this dissertation (Chapter V) moved from looking at broad-scale filtering of species by the environment to looking at the effects of neighborhood plant interactions based on the competing individuals’ functional traits. This analysis also supported the importance of environmental filtering for structuring communities and shows that this environmental filtering arises due to interactions that occur at fine spatial scales. Conspecific aggregation accounted for some of the trait similarity at fine spatial scales, and is consistent with the spatial aggregation hypothesis for diversity. However, nearest heterospecific neighbors also showed significant functional trait similarity, demonstrating the important role of even fine-grained environmental gradients in structuring understory herb communities. In mature forests, species were found to
partition light within plots whereas in old growth communities species sort along light
gradients. A likely explanation lies in the time it takes for the environmental gradients to
develop in these communities, and the even longer time it takes for dispersal and
competitive interactions to result in species sorting according to their optimal
environment. Fine-scale species assembly operates according to different processes in
mature forests compared to those found in old growth forests. Differences in colonization
ability were not addressed in the traits used in this study, but likely have an important
role in how species assemble. Adding traits such as seed size and seed number to the
analysis would provide an understanding of how colonization ability differs among co-
occurring species in mature versus old growth forests.

The conclusion of this research is that the herb community is not resilient and has
not recovered from logging occurring 100 – 150 years ago. These findings have
important implications for land use management. Mature forest stands should not be
used as a baseline for herb layer recovery as has been done up to the present. Mature
forests, even though 100-150 yrs old, represents a “baseline” for recovery that is still
early on the successional pathway to community patterns and function found in old
growth forest. The recovery period of 100 – 150 years corresponds to the amount of time
given to forests before subsequent logging. This research clearly demonstrates that
logging rotation times of 100 – 150 years are not long enough for the understory herb
layer to recover. Continued assessment over time is the only way to determine if and
when the herb layer regains the species richness, abundance, composition and, more
importantly, the same ecological processes that assemble communities found in old
growth forests.
CURRICULUM VITAE

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