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Centuries-old logging legacy on spatial and temporal patterns in understory herb communities

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ABSTRACT

Understory herb communities in the Southern Appalachians are among the highest biodiversity plant communities in North America. In the mid-1990s, a debate began over whether understory herb communities recover to their pre-disturbance states following logging. Studies showing reduced herb-layer diversity in previously logged forests were criticized for not accounting for intersite environmental heterogeneity. More recent studies have addressed environmental heterogeneity, but have neglected long-term recovery by using "mature forests" as young as 80 years old as the benchmark for diversity comparison, even though old growth stands have disturbance return intervals exceeding 500 years. Here we address concerns clouding previous studies of high-diversity Appalachian herb communities and investigate their long-term recovery by comparing paired sites of old growth forest and forest logged 100–150 years ago. 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 among old growth and mature forests accounted for 11% of the total species richness and was significantly greater than expected. Species turnover at intermediate (5–50 m) and landscape-scales (>10 km) contributed the most towards total species richness. Herb communities in rich cove forests have successional trajectories that exceed 150 years, with important community changes still occurring long after the forest returns to what has been previously termed a "mature" state. To conserve the diverse herb layer, we conclude that mature forest stands are too young to serve as baselines for recovery, landscape-scale preservation of multiple forest stands is needed to maximize species richness, and maintaining 100–150-year logging rotations will likely lead to loss of biodiversity.

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1. Introduction

Temperate forests worldwide and their understory herb communities have undergone large-scale and long-term anthropogenic disturbance through land conversion and logging (Houghton, 1995; Goodale and Aber, 2001; Schulte et al., 2007; Miyamoto and Sano, 2008). Knowing the time course of recovery and long-term implications of disturbance on biodiversity and community structure is essential for conserving these plant communities (Duffy and Meier, 1992; Foster et al., 1996). 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, and today old growth forests have been reduced to small tracts of 10–100 acres totaling 750,000 acres (0.09% of the original area) due to harvesting and clear cutting (Davis, 1993).

While old growth forests have been reduced to relicts, they are the only means for assessing recovery of secondary forests. Old growth forests provide a baseline for evaluating the effects and effectiveness of conservation strategies (Foster et al., 1996), and remnant old growth forests provide a valuable point of reference for ecological patterns and processes occurring in the absence of direct anthropogenic disturbance (McCarthy, 2003). To manage the high-diversity herbaceous communities found in Southern Appalachian forests, stands logged at the turn of the 20th century, termed "mature forests" in the literature, are used as the benchmark for assessing recovery of recently logged forests (Ford et al., 2000). However, minimum times between stand initiating events in Appalachian forests are on the order of 400–500 years (Lorimer, 1980), meaning that recovery has been studied over 20% or less of their successional trajectory. Focusing on short-term implications of logging neglects the critical question of whether forests recover from logging. Studies conducted on forests less than 100 years old may provide an inadequate baseline for effective biodiversity conservation. In this study we ask how conclusions about biodiversity and ecosystem recovery and management decisions might change if we look at the remaining 80% of succession not accounted for by past studies.

The diverse understory herb community in old growth temperate forests provides a glimpse at patterns and processes widespread across forested landscapes in eastern North America prior to

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widespread anthropogenic disturbance. The understory herb community has high species diversity, 3×–5× that of shrubs and trees (Gilliam, 2007). The herb layer also provides habitats for many animal species, plays an important role in nutrient cycling, and is a sensitive indicator of forest site quality (Collins et al., 1985; Thomas et al., 1999; Gilliam, 2007).

The impact of logging on the understory herb layer in rich cove forests of the Southern Appalachians has been the focus of numerous studies. Conclusions, however, remain contentious because key studies suffer from different confounding factors that make results hard to reconcile. 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 are known to vary with elevation, aspect, soil and forest type (Gilliam and Turrill, 1993; Ohtsuka et al., 1993; McCarthy et al., 2001; Verheyen et al., 2006). 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 herb communities over the time course studied. 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.

Here we examine how diversity of the understory herb community differs between old growth forests and forests recovering from logging 100–150 years ago across four spatial scales. Importantly, we address the long-term recovery of the herb layer while taking into account intersite heterogeneity, the annual phenology of forest species (see Section 2), and spatial scale, providing a comprehensive baseline of the plant community in old growth forests that can be used to assess recovery in previously logged forests.

2. Materials and methods

2.1. Study sites

Within the Southern Appalachians, coves are mesic forests that occur in sheltered concave stream drainages and comprise 25% of wooded area (Whittaker, 1956; Hicks, 1980). Cove forests are highly susceptible to anthropogenic disturbance because they contain quality sawtimber for harvesting and fertile soils for agriculture sites (Turner et al., 2003; Rock et al., 2004). 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 (700–1200 m), and "rich cove hardwood" forest type in the Southern Appalachians of North Carolina in the Nantahala National Forest (NNF) with 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).

We chose six sites with paired old growth and mature forest sites based on CISC data. Old growth describes forests that have never been logged and have little or no evidence of anthropogenic disturbance (Duffy and Meier, 1992). High tree diversity, massive living trees, uneven canopy structure, standing snags, tree fall gaps and log accumulation distinguish old growth forests from mature forests (McCarthy, 1995; Hardt and Swank, 1997). Mature forests are those sites that have been logged in the past and have had over
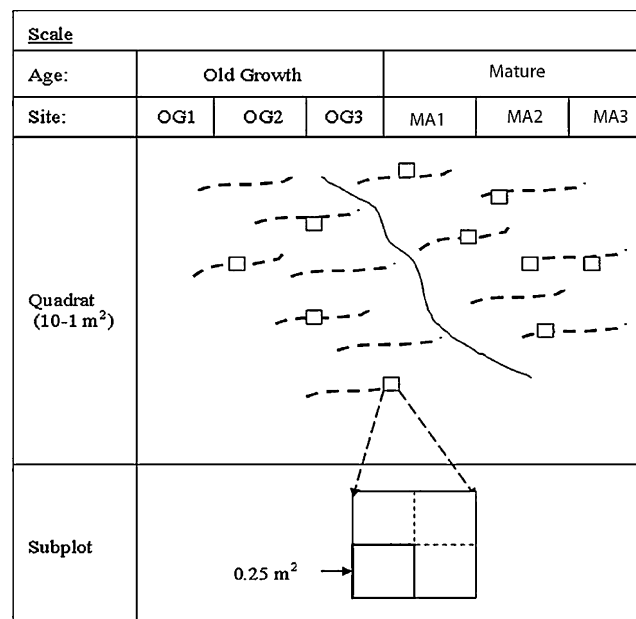

Fig. 1. Overview of study design. Nested sampling design with four hierarchical scales (age, forest site, quadrat and subplot) was established in six rich cove forests. Each of the three old growth sites and three mature sites has ten 1 m² quadrats randomly selected from the diversity sampling plots.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

100 years of recovery time. Logging rotation times are 100–150 years in the Southern Appalachians (USFS), therefore forests of this age represent the amount of recovery that occurs before a subsequent logging rotation. The forest stands used in this study were logged between 1864 and 1906 (CISC). This time period coincided with intensive clearcutting of the Southern Appalachians prior to Forest Service ownership (Western North Carolina Alliance, 1995). Clearcutting techniques used by private lumber companies at this time did not minimize damage caused by falling trees and massive logs were skidded out of the forest, causing extensive damage to the understory through soil disturbance and erosion (Mastran and Lowerre, 1983). Since harvesting more than a century ago, the mature forest stands used in this study have undergone natural regeneration (United States Department of Agriculture, 1994).

2.2. Diversity and partitioning sampling

At each site, we established twelve transects consisting of five 0.25 m² plots spaced 5 m apart and running perpendicular to the cove drainage following Ford et al. (2000, Fig. 1). We surveyed presence/absence of understory herbaceous species for each of the 360–0.25 m² plots to assess overall diversity. We used a subset of the diversity plots for abundance sampling, counting individual ramets. Ten randomly chosen 0.25 m² plots at each site were expanded to 1 m² quadrats (Fig. 1). Surveys took place beginning in early March 2005 and once monthly until August, with all stands surveyed within seven days to minimize variation in floral phenology.

2.3. Phenology

We categorized species according to their phenological guilds: spring ephemerals, summer greens, wintergreens and evergreens (Appendix A). 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 1 year (Neufeld and Young, 2003). Due to the small number of winter-green 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.

2.4. Diversity analysis

We tallied species richness per plot 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. We used randomization tests to determine whether mean species richness or abundance differed between old growth and mature forests for all species and for each phenological group separately by randomly assigning the species richness of the $360–0.25\,m^2$ plots to each forest age and taking the difference between species richness means. The null probability distribution used 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 (R 2.6.2, http://www.R-project.org/, Appendix B). We used the same randomization process to assess differences in abundance by randomly assigning the $240–0.25\,m^2$ abundance subplots to each forest age and calculating the difference between abundance means.

We used rarefaction to determine whether differences in the number of species were independent of abundance using rarefy command in Vegan library for R (Vegan; http://r-forge.r-project.org/projects/vegan/). This method randomly samples the same number of individuals from each forest age 10,000 times for a range of sample sizes. Sample sizes ranged from 200 individuals to 9000 individuals with 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) on Sorensen's distance in PC-ORD (Version 4.41, McCune and Mefford, 1999). Presence absence data from the $360–0.25\,m^2$ plots was used in the NMS analysis. We determined significant groups in species composition with forest age by applying multi-response permutation procedure (MRPP) with Sorensen distance measure and $n_i/\Sigma(n_i)$ as a weighting option where n_i is the number of species in group *i* (Biondini et al., 1985).

2.5. Additive partitioning

We partitioned species richness 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, Fig. 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. 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, corresponding to the two forest age categories (old growth and mature forests; Fig. 1).

We used randomization tests to determine if diversity partitioned at any given spatial scale differs from a random distribution of individuals among samples at all scales (Partition v2, Veech et al.,
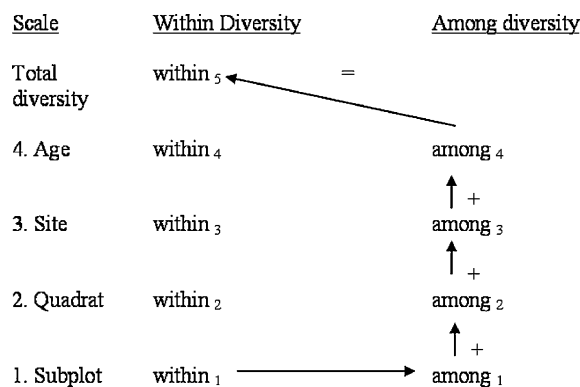

Fig. 2. Additive partitioning model based on Gering et al. (2003) showing the relationships among hierarchical levels from the lowest (subplot) to the highest (age). Each scale has a within and among diversity component. Within is the mean number of species that occurs within a unit at each scale. Among is the mean number of species occurring among units at each scale. In additive partitioning, the within value at any scale is the sum of the within and among components of the next lowest scale. With 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.

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 (λ). Species richness is the number of species per sample. Shannon's index is calculated as $H' = [-\Sigma p_i \ln(p_i)]$ and Simpson's index is $\lambda = [1 - \Sigma p_i^2]$ where p_i is the proportional abundance of species *i* for *i* = 1 to the total number of species in the sample (Appendix C).

In our partitioning, level 1 refers to the lowest hierarchy (subplot) and level 4 to the highest (forest age) (Fig. 2). 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. For example, the mean diversity within quadrats (within_2) is the sum of the mean diversity in a plot (within_1) plus the diversity that accumulates among plots (among_1). Total diversity is partitioned into: within_1 + among_1 + among_2 + among_3 + among_4 (Fig. 2). We conducted additive partitioning for all species and for each phenological group. Within each forest age type, we partitioned diversity into three hierarchies (subplot, quadrat, and site) for all species and for each phenological group.

We determined significance of scale-specific within and among values by complete randomization in which the total number of individuals within a subplot is kept the same, but with individuals randomly assigned to samples, thereby generating a new number of species per subplot. We partitioned the randomized data and calculated diversity metrics 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, we compared the null distribution to the scale-specific values. We determined statistical significance by the proportion of null values greater (or less) than the estimate (Crist et al., 2003; Gering et al., 2003). All values reported are parameter ± standard error unless otherwise noted.

3. Results

Old growth (Og) forests have $32.4 \pm 3.4\%$ greater species richness than mature (Ma) forests for all species (Og = 9.8 ± 0.2 spp/$0.25\,m^2$ plot; Ma = 7.4 ± 0.2 spp/plot; $p < 0.001$; Fig. 3a) along with significantly greater species richness for each phenology except evergreens (Fig. 3b–d). The number of individuals at the plot level is $56.4 \pm 9.0\%$ greater in old growth forests
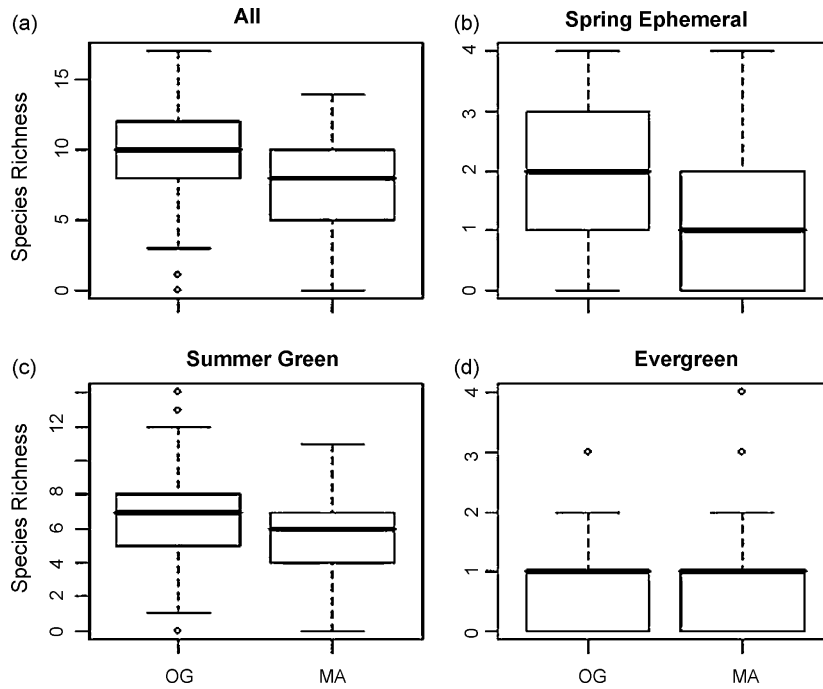
Fig. 3. Boxplot of species richness for old growth (OG) and mature forests (MA) for all species (a), spring ephemerals (b), summer greens (c) and evergreens (d). The horizontal line that forms the top of the box is the 75th percentile and the bottom of the box is the 25th percentile. The thick line that intersects the box is the median. Horizontal lines above and below the box represent maximum and minimum values that are no more than 1.5 times the span of the interquartile range. An open circle represents an outlier. Old growth forests have significantly more species richness for all species (OG = 9.8 ± 0.2 spp/plot; MA = 7.4 ± 0.2 spp/plot; $p < 0.001$), spring ephemerals (OG = 2.0 ± 0.1 species/plot; MA = 1.0 ± 0.2 species/plot; $p < 0.001$) and summer greens (Og = 6.9 ± 0.2 spp/plot; MA = 5.6 ± 0.2 spp/plot; $p < 0.001$). Evergreen richness does not differ with forest age (Og = 0.9 ± 0.1 spp/plot; MA = 0.8 ± 0.1 spp/plot; $p = 0.11$).
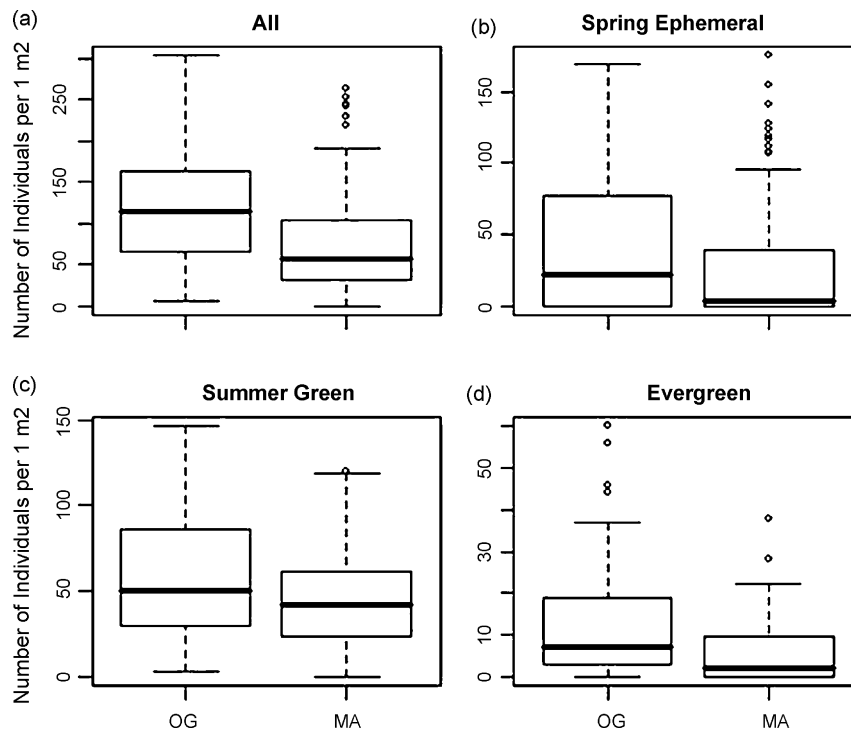

Fig. 4. Boxplot of abundance for old growth (OG) and mature forests (MA) for all species (a), spring ephemerals (b), summer greens (c) and evergreens (d). The horizontal line that forms the top of the box is the 75th percentile and the bottom of the box is the 25th percentile. The thick line that intersects the box is the median. Horizontal lines above and below the box represent maximum and minimum values that are no more than 1.5 times the span of the interquartile range. An open circle represents an outlier. Old growth forests have significantly greater abundance for all species (OG = 117.8 ± 6.1 ind./plot; MA = 75.3 ± 5.5 ind./plot; $p < 0.001$), spring ephemerals (OG = 40.6 ± 4.4 ind./plot; MA = 27.2 ± 3.8 ind./plot; $p = 0.005$) summer greens (Og = 56.7 ± 3.2 ind./plot; MA = 42.9 ± 3.2 ind./plot; $p < 0.001$), and evergreens (Og = 11.9 ± 1.1 ind./plot; MA = 5.2 ± 0.6 ind./plot; $p < 0.001$).
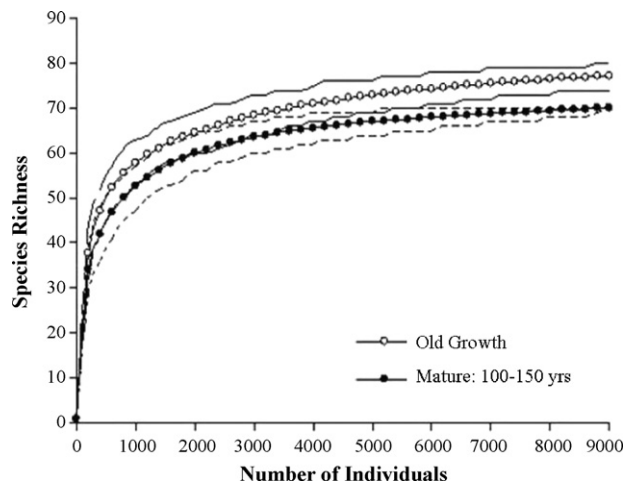
Fig. 5. Rarefaction analysis showing greater mean species richness for old growth (OG; open circles) than mature forests (MA; closed circles). Samples ranged from 200 to 9000 individuals with 200 individual increments. Each sample size was randomly sampled 10,000 from each forest community with 95% confidence intervals shown by the envelopes.

Fig. 6. Non-metric multidimensional scaling biplot axes 1 and 2 for forest age × herb-layer community composition sampled in 360 plots across six rich cove forests for all species.

than mature forests for all species (Og = 117.8 ± 6.1 ind./plot; Ma = 75.3 ± 5.5 ind./plot; $p < 0.001$) as well as each phenological group (Fig. 4a–d). As both species richness and number of individuals were greater in Og versus Ma plots, we used rarefaction to control for sampling effects on species richness. Species richness was greater in old growth compared to mature forests for all species when abundance was taken into account with rarefaction (Fig. 5).

3.1. Species composition

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 (MRPP test, chance-corrected within group agreement $A = 0.08$, $p < 0.001$) with forest age explaining 18.6% of variation in species composition along axis 1 (Fig. 6).

3.2. Partitioning

Differences in community composition among forest sites, and between old growth and mature forests were both significantly greater than expected by chance for the entire community and each phenology with all diversity metrics except the case of Simpson's index on spring ephemerals (Table 1). The greatest species richness for all herb species accumulates among 1 m² quadrats within sites (34.0%) closely followed by increases in diversity as one moves between sites (33.3%). Species richness differences between forest ages accounted for 11% of the total species richness (Fig. 7a). Within plot diversity contributes the greatest to overall diversity based on Shannon and Simpson indices, but does not differ from random ($H' = 50.4\%$; $\lambda = 81.6\%$). Diversity accumulates similarly across the four spatial scales in both mature and old growth forests with richness partitioned equally between the highest scales (among sites and among quadrats) for both old growth and mature forests (Fig. 7a). Significantly greater species richness than expected occurred between sites for both ages.

3.3. Phenology

For all phenologies, diversity among quadrats within a forest site contributes the most to overall species richness (Fig. 7b–d).
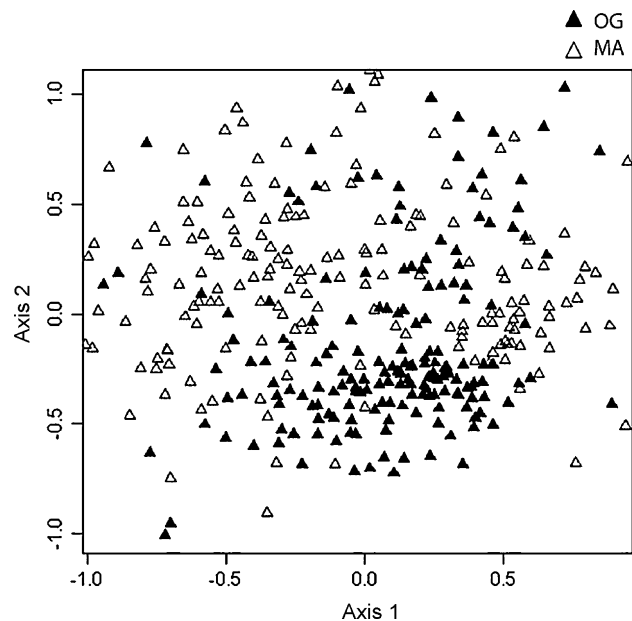
The two highest scales (between sites and between ages) have significantly more species richness than expected for all phenologies.

Of the phenologies, only evergreens show differences in how diversity is partitioned within old growth and mature forests. Old growth forests have most evergreen diversity accumulating among sites (species richness: 42.9%, Shannon's index: 40.2%). In mature forests, diversity accumulates among quadrats within sites (species richness: 53.3%, Shannon's index: 52.6%; Fig. 8d).

4. Discussion

Previously logged forests are not equivalent to remnant old growth stands even after 100–150 years of recovery in terms of herb-layer species richness, individual abundance or species composition. This is true when controlling for intersite heterogeneity. Old growth forests have greater species richness and abundance than previously logged forests along with a distinct species composition (Figs. 3, 4 and 6). Species diversity is 32% higher in the average old growth plot, and the number of individuals is more than 50% higher. The increased diversity in old growth plots is not a simple artifact of increased stem numbers, but rather shows a larger species pool (Fig. 8a).

These results support previous arguments that timber harvesting alters the herb layer (Brewer, 1980; Duffy and Meier, 1992; Meier et al., 1995; Vellend et al., 2007) and clearly refutes statements 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 (Duffy and Meier, 1992) and similar conclusions have been made in systems with much shorter harvesting intervals (Decocq et al., 2004). This study demonstrates that even timber harvesting intervals of 100–150 years is shorter than herb-layer recovery time.

Table 1
Results of randomization process to determine whether diversity[a] partitioned at each spatial scale is more or less than what would be expected by chance for all species and each phenological group.[b].

	All species			Spring ephemerals			Summer			Evergreens		
	N_o	H'	λ	N_o	H'	λ	N_o	H'	λ	N_o	H'	λ
All ages												
Within 1	ns	ns	ns	ns	ns	+	ns	ns	ns	ns	ns	ns
Among$_1$	ns	ns	+	ns	+	+	ns	ns	+	ns	ns	+
Among$_2$	ns	+	ns	+	ns	ns	ns	+	ns	+	ns	ns
Among$_3$	+	+	+	+	+	ns	+	+	+	+	+	+
Among$_4$	+	+	+	+	+	+	+	+	+	+	+	+
Mature												
Within$_1$	ns	ns	ns	ns	ns	+	ns	ns	ns	ns	ns	+
Among$_1$	ns	ns	+	ns	+	+	ns	ns	+	ns	ns	+
Among$_2$	ns	+	ns	+	ns	ns	ns	+	ns	+	ns	ns
Among$_3$	+	+	+	+	+	+	+	+	+	+	+	+
Old growth												
Within$_1$	ns	ns	ns	ns	ns	+	ns	ns	ns	ns	ns	ns
Among$_1$	ns	ns	+	ns	+	+	ns	ns	+	ns	ns	ns
Among$_2$	+	+	+	+	ns	ns	+	+	+	+	+	ns
Among$_3$	+	+	+	+	ns	ns	+	+	+	+	+	+

[a] Diversity indices are species richness (N_o), Shannon's index (H') and Simpson's index (λ).

[b] Significance was determined at the 0.05 level; + indicates significantly greater than expected diversity and ns indicates not significant.

4.1. 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). This study demonstrates that there is greater species turnover than expected at large spatial and temporal 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 accumulation of species over spatial scales is similar within mature and old growth forests. The greatest number of species accumulates among forest sites and among plots at the forest site scale for both forest ages. High turnover in 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 can drive spatial patterns of diversity (Jacquemyn et al., 2001; Small and McCarthy, 2002; Freestone and Inouye, 2006). Species turnover at large-scales was greater than expected (Fig. 7a). Spatial turnover among sites could be due limited dispersal and niche specificity combined with environmental differences (e.g., substrate). 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). Distinguishing between dispersal limitation and environmental correlations at large spatial scales is difficult, but can be done by looking for
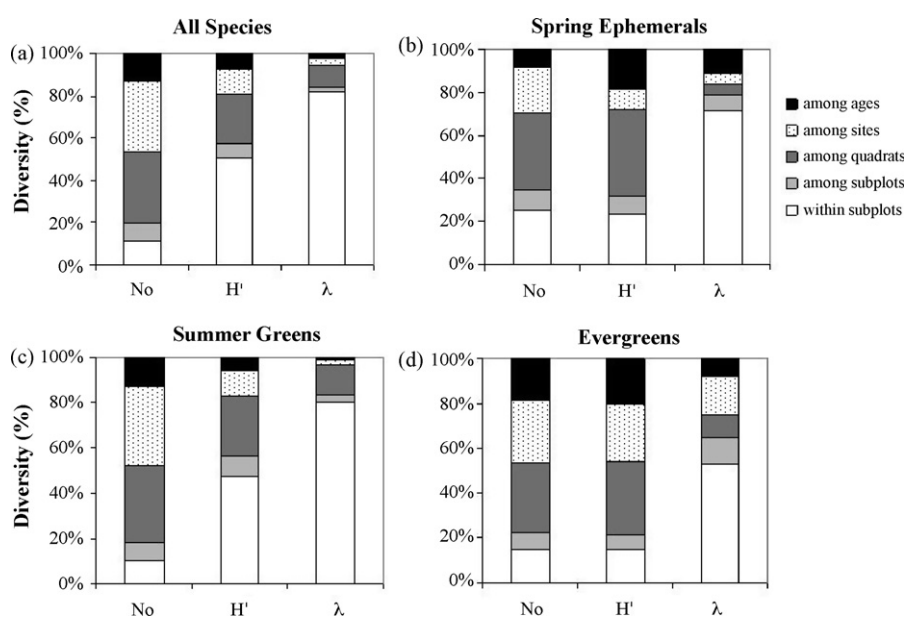

Fig. 7. Percent of diversity partitioned into within and among components for all species (a), spring ephemerals (b), summer greens (c) and evergreens (d) with three diversity indices: species richness (N_o), Shannon's diversity index (H') and Simpson's index (λ).
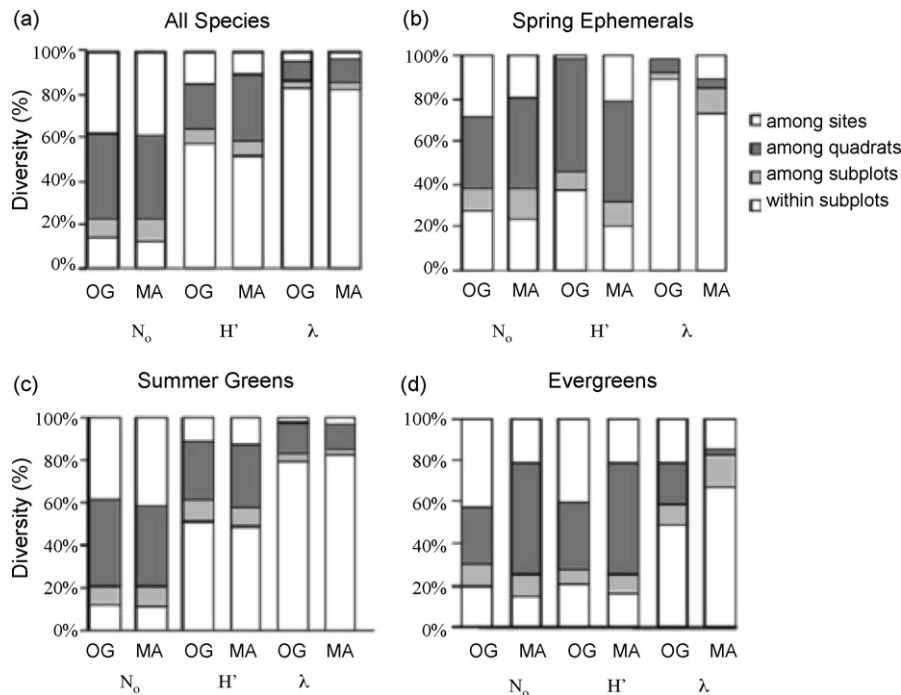
Fig. 8. Percent of diversity partitioned into within and among components within old growth (Og) and mature (Ma) forests for all species (a), spring ephemerals (b), summer greens (c) and evergreens (d) with three diversity indices: species richness (N_o), Shannon's index (H') and Simpson's index (λ).

non-random trait distributions with respect to sampling. A comprehensive study of trait–environment correlations in Appalachian forests, however, has yet to be conducted.

Previous studies have addressed partitioning of diversity for several taxa across landscape and ecoregion scales (Wagner et al., 2000; Gering et al., 2003; Chandy et al., 2006; Gabriel 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. 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). We found that herbaceous layer diversity was partitioned primarily at the intermediate-scale (within forest site) and landscape-scale (among forest sites).

4.2. Diversity indices

Multiple diversity indices that take into account proportional abundance of species were used to address how abundant and rare species are distributed across spatial scales (Appendix C). 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 (Fig. 7). Brown (1984) established this general relationship between abundance and distribution, which has been supported in other partitioning studies (Wagner et al., 2000; Gering et al., 2003). Contrasting partition between species richness and Shannon's index was not seen for spring ephemerals or evergreens (Fig. 7b and d). Taxa in these phenologies do not have a strong distinction between domi-

nant and rare species, with spring ephemerals and evergreens being more evenly distributed across the landscape at all spatial scales.

4.3. Timbering effects and phenological guilds

All phenological guilds are affected by past timber harvesting in terms of 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 seemingly mature forests, spring ephemerals and summer greens occur in fewer plots, have fewer species occurring in a single plot, and species have lower total site abundances compared to old growth. 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 by clonal growth or by sexual reproduction with dispersal distances generally less than a meter (Bierzychudek, 1982; 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 (Fig. 8). 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.

5. Conclusions

Logging is a ubiquitous disturbance in forests and understanding the successional trajectory of recovering forests is critical for conservation. We demonstrate that forests < 100 years old should not be used as a baseline for understanding herb-layer diversity; even 100–150 years is not enough time for the herb layer to recover from timber harvesting in a diverse community. Species richness, abundance and composition in these mature forests are still changing along a successional trajectory and have not recovered to old growth levels. Spring ephemeral and evergreen herbs are most affected by harvesting, but respond in different ways due to their life history characteristics. Evergreens have altered spatial patterns while spring ephemerals differ in species richness and composition.

The greatest species accumulation occurs across a forest site and between forest sites, suggesting that a landscape-scale perspective is required for conservation of these high biodiversity communities. Current forest management neglects the understory herb layer, even though biodiversity in the herb-layer dwarfs that of trees in Appalachian cove forest. Because species diversity accrues even at large (>10 km) spatial scales, multiple forest stands in the landscape need to be removed from the logging rotation along with the preservation of all remnant old growth forests. Forests set-aside from logging will also act as a propagule source for nearby logged forests.

Previous studies have shown that the herb layer found in mature 100-year-old forests can be reached rapidly (20–25 years) following timber harvesting (Ford et al., 2000). However, we show that the rate at which these mature forests recover to old growth standards is not rapid and takes >100 years. Given that the majority of forested land in eastern North American has been logged in the past 100–150 years (USFS), we need long-terming monitoring of the herb layer and management practices that enhance recovery. Long-term monitoring is essential for knowing if and when mature forests recover to the same diversity, abundance and species composition found in old growth forests. Active management of mature forests to enhance old growth characteristics in stand structure and complexity (tree fall gaps, snags, coarse woody debris, etc.) has been shown to improve biodiversity (Bauhus et al., 2009). Research on understory diversity has found that certain silviculture techniques (single tree selection, group selection and reserve management) enhance species richness (Battles et al., 2001). Studies addressing the impact of active management practices (single tree selection and group selection) or passive reserve management on herb-layer recovery need to be implemented within these mature forests to assess their affect on herb-layer recovery.

Current forestry management is not conducive to long-term maintenance of herb-layer diversity in Appalachian forests. Mature forest herb layers have fewer species, fewer individuals, and altered community composition compared to herb layers in old growth forest, even when examined at large spatial scales. Given the importance of the herb layer to higher trophic levels in these communities, as well as competition with trees, current forest management will lead to a steady erosion of both biodiversity and ecosystem function in the highest biodiversity component of Appalachian forests.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2010.04.010.

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