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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.

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 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).

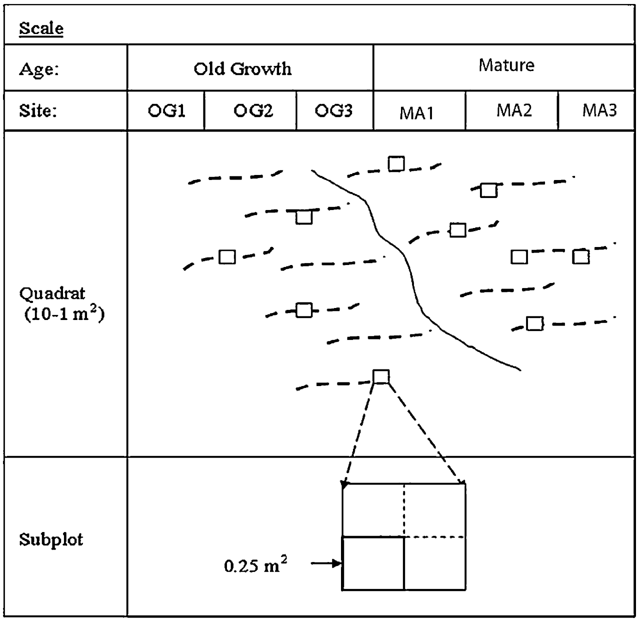

Fig. 1. Overview of study design. Nested sampling design with four hierarchical scales (age, forest site, quadrat and subplot) was established in six rich cove forests. Each of the three old growth sites and three mature sites has ten 1 m^2 quadrats randomly selected from the diversity sampling plots.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

2.2. Diversity and partitioning sampling

At each site, we established twelve transects consisting of five 0.25 m^2 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 m^2 plots to assess overall diversity. We used a subset of the diversity plots for abundance sampling, counting individual ramets. Ten randomly chosen 0.25 m^2 plots at each site were expanded to 1 m^2 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