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Temporal Change Within and Among Forest Communities of Great Smoky Mountains National Park: The Influence of Historic Disturbance and Environmental Gradients

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To the Graduate Council:

I am submitting herewith a thesis written by Windy A. Bunn entitled "Temporal Change Within and Among Forest Communities of Great Smoky Mountains National Park: The Influence of Historic Disturbance and Environmental Gradients." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology and Evolutionary Biology.

Nathan J. Sanders, Major Professor

We have read this thesis and recommend its acceptance:

Aimée T. Classen, Daniel Simberloff

Accepted for the Council:
Dixie L. Thompson

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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_Carolyn R. Hodges ______
Vice Provost and Dean of the
Graduate School

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Temporal change within and among forest communities of Great Smoky Mountains National Park: The influence of historic disturbance and environmental gradients

A Thesis Presented for
the Master of Science
Degree
The University of Tennessee, Knoxville

Windy A. Bunn
August 2008

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ABSTRACT

Understanding how ecological communities change over time is critical for biodiversity conservation. However, few long-term studies directly address decadal-scale changes in the ecological communities of protected areas. In this study, we take advantage of a network of permanent forest plots, established in Great Smoky Mountains National Park in 1978, to investigate temporal changes in plant communities. In particular, we examine the factors that influence temporal change in species richness and composition within communities and temporal change in compositional similarity among communities. In 2007, we revisited 15 permanent plots that were logged in the late 1920s and 15 permanent plots that have no documented history of intensive human disturbance. In addition to differences in disturbance history, these plots varied in elevation and a variety of edaphic parameters. We found that understory species richness decreased by an average of 4.3 species over the 30-year study period in the logged plots, while understory richness remained relatively unchanged in the unlogged plots. In addition, tree density decreased by an average of 145 stems/ha in the logged plots but was relatively stable in the unlogged plots. Historic logging had no effect on within-site understory or tree compositional turnover. However, sites with higher soil pH had higher understory turnover and higher tree turnover than did sites with lower soil pH. In addition, sites at lower elevations and sites with lower understory productivity in 1978 had higher understory turnover than did sites at higher elevations and sites with higher understory productivity in 1978. Among-community similarity was unchanged from 1978 to 2007 in the understory communities and in the tree communities of both the logged and unlogged plots. Taken together, our results indicate that human disturbance can affect plant communities for decades following the disturbance event but that the extent of temporal change in community composition may depend more on environmental gradients than on the legacy of large-scale but short-lived historic disturbances, such as logging. In addition, our results suggest that variation in temporal turnover within communities may not necessarily translate into changes in compositional similarity among communities over time.

PREFACE

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Throughout the manuscript the term “we” refers to myself and the coauthors listed above. My primary contributions to this manuscript include (1) selection of topic and design of research approach, (2) identification of study areas, (3) collection of vegetation data in 2007, (4) analysis of data, and (5) writing the majority of the manuscript. Other authors contributed to this research as follows: N.J.S. advised in the development of the research and assisted with writing the paper; M.A.J. provided historic vegetation data, provided soils data, and assisted with writing the paper; C.B.B. assisted with data collection and analysis.

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INTRODUCTION

Both within- and among-community attributes can change over time, and understanding these changes often requires long-term empirical data, perhaps over several decades in some systems (Magnuson 1990; Wardle *et al*. 2004). Within a community, the total number of species present as well as the abundance of particular species can change with time. These within-community changes can lead to temporal differences in similarity among communities within a region (Loreau 2000). Despite the potential for within-community changes to influence similarity among communities, few studies directly measure long-term changes in both the within- and among-community components of diversity (but see Chalcraft *et al*. 2004). In this study, we use long-term monitoring data from Great Smoky Mountains National Park to examine temporal changes in forest understory plant communities and tree communities across 30 years. Specifically, we examine the factors that influence temporal change in species richness and composition within communities and temporal change in compositional similarity among communities.

Temporal change within communities

Over time, the total number of species in a community can increase, decrease, or remain stable as new species are gained and lost from the community (Brown *et al*. 2001). In addition to temporal changes in species richness, the relative abundance of species in a community can change, though richness itself might not (Brown *et al*. 2001). Communities with little temporal change in species composition have low turnover, and communities with more extensive temporal change in composition have high turnover. Within-community change in species richness and temporal turnover can vary with a number of factors, including disturbance (Collins & Smith 2006), species invasions (Yurkonis & Meiners 2004), rainfall (Anderson 2008), elevation (Aplet & Vitousek 1994; Selmants & Knight 2003), soil fertility and productivity (Peet & Christensen 1988; Verheyen *et al*. 2003; Taverna *et al*. 2005; Clark & Tilman 2008), and species richness (Smart *et al*. 2006; White *et al*. 2006). However, the relative influence of these factors on temporal change in plant communities is poorly understood and likely varies by habitat type.

Temporal change among communities

Temporal change within communities can affect among-community similarity (Loreau 2000). Over time, communities within a region can become either more similar or less similar to one another depending on the extent of temporal change within individual communities of the region. Research aimed at understanding changes in community similarity with time is of increasing interest because contemporary habitat alteration, species invasions (McKinney & Lockwood 1999), intense herbivory (Rooney *et al*. 2004), and historic disturbance (Christensen & Peet 1984; Vellend *et al*. 2007) can homogenize communities across regions.

Though there is a growing interest in changes in among-community similarity in space and in time (Olden 2006), understanding the factors that influence this component of diversity can require long-term data. One way to investigate these long-term processes is to use space-for-time substitution (or chronosequence) studies of age-dependent differences in community composition. However, chronosequence studies are limited by the fact that site-to-site variability can confound patterns of temporal change (Fukami & Wardle 2005). To differentiate fully the mechanisms driving temporal change within and among communities, trends documented in chronosequence studies must be compared with data from long-term plot resampling schemes, especially in long-lived communities.

Temporal change in forests of the eastern U.S.

Recent studies of decadal-scale change in forest communities indicate that declines in species richness (Drayton & Primack 1996; Rooney & Dress 1997; Rooney *et al*. 2004; Taverna *et al*. 2005), shifts in plant community composition (Taverna *et al*. 2005), and changes in regional community similarity (Rooney *et al*. 2004) over time may be common in forests of the eastern United States. Since land-use history can have large effects on forest communities (Foster *et al*. 1998; Vellend *et al*. 2007), the legacy of human disturbance should be considered when evaluating temporal change in these long-lived communities.

In this study, we take advantage of a network of permanent forest plots, established in Great Smoky Mountains National Park in 1978, to investigate changes in forest understory plant communities as well as tree communities in historically logged and unlogged forests. Specifically, we ask: (1) Does historic logging affect temporal change in species richness and compositional turnover within communities? (2) Are within-community changes in species richness and compositional turnover related to topographic factors, edaphic factors, or community attributes? (3) Does historic logging affect temporal change in among-community similarity?

METHODS

We conducted this study in Great Smoky Mountains National Park (GSMNP) in eastern Tennessee, USA. GSMNP has one of the most complex vegetation patterns in North America (Whittaker 1956) and has been a center for plant community research since its establishment in the early 1930s. GSMNP ranges in elevation from 271 m to 2025 m, and climate and vegetation types vary considerably along the elevational gradient. Mean annual rainfall in low elevation sites is 140 cm with mean temperatures greater than 12 °C, while annual rainfall is > 200 cm and temperature averages 6 °C at high elevation peaks. GSMNP contains 79 vegetation associations that vary from low- to mid-elevation mixed hardwood forests and xeric *Pinus* and *Quercus* forests to high-elevation *Picea-Abies* forests and heath balds (White *et al*. 2003). Prior to GSMNP establishment, approximately 80% of the area within the current GSMNP boundary was subject to anthropogenic disturbance (Pyle 1988). Despite the history of disturbance, GSMNP is considered a center for diversity in North America and at 211,000 ha is one of the largest protected areas in the eastern United States.

Plot selection and field methods

In 2007, we resampled thirty 20 m × 50 m forest plots originally established in GSMNP in 1978 by the Uplands Field Research Laboratory (White & Busing 1993). Fifteen of the resampled plots are in historically logged forests and fifteen plots are in unlogged forests. We used detailed maps of historic anthropogenic disturbance in GSMNP (summarized in Pyle 1988) to identify areas that underwent historic logging and areas that had no known large-scale human disturbance in the past. Historically logged areas were defined using the “corporate logging” category of Pyle (1988), and included only those areas defined by Pyle as high intensity logging. Under Pyle’s definition, high intensity logging included the use of railroads and mechanized skidding, non-selective cutting practices, and highly extensive cutting on slopes. We defined unlogged areas using Pyle’s “high in virgin forest attributes” and “big trees with diffuse disturbance” categories.

In order to restrict our analysis to the effects of historic disturbance on community dynamics, we used 1978 field data and 2007 pre-sampling surveys to exclude areas with high levels of recent disturbance. Toward this end, we sampled only plots dominated by hardwood species (those defined by White *et al*. 2003 as Montane Oak-Hickory, Mountain Cove, and Northern Hardwood forests) in order to avoid potential disturbances caused by frequent fire, southern pine beetle, and balsam woolly adelgid in the last 30 years. We also excluded plots that had extensive loss of canopy trees due to the recent spread of hemlock woolly adelgid.

To examine whether environmental conditions affected community turnover, we chose plots that met the above disturbance criteria and were arrayed along an elevational gradient. Note that the mean elevation of logged plots did not differ from the mean elevation of unlogged plots (Table A.1; all tables located in the appendices). The 15 logged plots ranged in elevation from 727 m to 1402 m and occurred on north- (n = 8), east- (n = 4), and west- (n = 3) facing slopes. The 15 unlogged plots ranged in elevation from 664 m to 1400 m and occurred on north- (n = 10), east- (n = 1), and west- (n = 3) facing slopes. The underlying bedrock in the unlogged plots and the low elevation logged plots is metasandstone interbedded with metasiltstone layers, and the high elevation logged plots are underlain by a mix of slate, metasiltstone, and phyllite with thin beds of metasandstone (Southworth *et al*. 2005). Both the logged and unlogged plots are characterized by well-drained loamy soils classified as either Humic or Typic Dystrudepts (Anthony Khiel, NRCS, unpublished report).

Tree cores collected and analyzed as part of the GSMNP vegetation program were available for a subset of the sampling plots (M. A. Jenkins, unpublished data). Cores were taken from 2 – 4 dominant trees within each plot. Complete cores from three unlogged plots, cores without pith from three additional unlogged plots, and complete cores from three logged plots were used for age comparison. These cores indicate that dominant trees in unlogged plots were 150 – 228 years old (complete cores) or a minimum 132 – 147 years old (cores without pith) in 2007. As expected from logging history records, dominant trees in logged plots were 75 – 80 years old in 2007.

In 1978, the 20 m × 50 m forest plots were permanently marked with rebar and witness tree tags, which allowed us to identify the plots in 2007. In the 2007 resampling, we used the same sampling design used in the original 1978 sampling (Bratton 1978). Specifically, within each 20 m × 50 m plot, we recorded the presence and percent cover of understory shrub and tree seedling species < 1 m tall in 25 4-m^2 subplots and the presence and cover of understory herbaceous species in 25 1-m^2 subplots nested within the shrub and seedling subplots (Fig. A.1; all figures located in the appendices). We defined the understory community as the shrub, seedling, and herbaceous species recorded in all 25 subplots within the entire 20 m × 50 m plot. We also recorded the identity, density, and diameter at breast height (dbh) of all tree species (≥10 cm dbh) in the 20 m × 50 m plot and called these species the tree community. In 2007, we sampled plots at roughly the same time of year that they were sampled in 1978. Sampling was conducted between June 19 and August 26 in 1978 and between July 9 and August 26 in 2007. Sampling of plots was paired, as best as possible, within seasons. That is, if a plot was sampled late in the field season in 1978, we attempted to sample that plot late in the field season of 2007.

The 1978 survey crew recorded cover values in 1% increments. But in 2007, we estimated percent cover according to the Carolina Vegetation Survey (CVS) scale with 10 cover classes (Peet *et al*. 1998) to reduce bias between individual recorders. In order to compare percent cover values between years, we converted the 1978 cover estimates to the 10-point CVS scale. To account for taxonomic changes over the past 30 years, we updated the 1978 species nomenclature according to Kartesz (1999).

To characterize the sampling plots, we estimated a suite of topographic and edaphic parameters (Table A.1). We calculated percent slope by averaging three slope measurements taken at the two end lines and along the centerline of each plot. We used field measurements of slope and aspect to calculate heat load, an integrative measure of a plot's yearly exposure to incident sunlight (Equation 3 from McCune & Keon 2002). Between 2002 and 2007, soil samples were collected from the top 10 cm of soil at five locations throughout each of the 30 plots with a hand spade. The five subsamples were combined into one composite sample per plot, dried at 43 °C for at least 8 hours, and sieved through a 2 mm mesh. The samples were analyzed for pH, cation exchange capacity (CEC), total phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg), and percent organic matter by A&L Analytical Laboratories, Memphis, TN (see Jenkins *et al*. 2007 for details of cation extraction procedures).

Influence of historic logging on forest communities

To determine the influence of historic logging on plant community attributes, we compared species richness and total species abundance in logged plots with species richness and abundance in unlogged plots using separate *t*-tests (JMP 6.0; SAS Institute Cary, NC, USA) for 1978 and 2007. For the analyses of tree species richness, we used both the observed number of species present in a plot and an estimate of species richness generated by individual-based rarefaction (PRIMER, Version 6, PRIMER-E Ltd., Plymouth Marine Laboratory, Plymouth, UK). Rarefaction allowed us to correct species richness values for differences in the number of individuals sampled in each plot by using a resampling procedure to generate estimated species richness values based on the number of individuals sampled in the plot with the fewest trees (Gotelli & Colwell 2001).

We used nonparametric, permutational multivariate analysis of variance (MANOVA) based on Bray-Curtis similarity values of species abundances to compare understory and tree community composition between logged and unlogged plots. Nonparametric MANOVA is appropriate for testing the simultaneous effects of a treatment on multiple non-independent variables (such as species abundances within a community) when the assumptions of the traditional MANOVA are not met

(Anderson 2001). We assessed differences in community composition between logged and unlogged plots using the FORTRAN program PERMANOVA (http://www.stat.auckland.ac.nz/~mja/Programs.htm; Anderson 2005). PERMANOVA compares the variability in species similarity between plots within a treatment to the variability in species similarity between plots from different treatments. The test statistic for PERMANOVA is the pseudo *F*-ratio, where a large pseudo *F*-ratio indicates that logged plots are closer to one another in multivariate space than they are to unlogged plots and that the logged and unlogged plots differ in community composition. The significance of the pseudo *F*-ratio is tested using a permutation test that shuffles the sample labels and calculates the pseudo *F*-ratio for 9999 arbitrary reassignments of the data. The pseudo *F*-ratios of these randomly assigned communities are then compared to the pseudo *F*-ratio of the observed community to calculate the significance level of the test (Anderson 2001). For the understory communities, we calculated species abundance both by calculating the average of the cover values for an individual species in the 25 subplots (cover-based estimate) and by calculating the percentage of the 25 subplots in which the species occurred (frequency-based estimate). For the tree communities, we used the number of individual trees of a species as the abundance value. Since the scale of abundance values in our study was small (ranging from 0 to 100 for understory species and 0 to 52 for tree species), we did not transform the data to reduce the influence of abundant species.

A significant pseudo *F*-ratio from the PERMANOVA can indicate a difference in community composition between treatments due either to differences in the location of the treatment communities in multivariate space or to differences in dispersion of communities in multivariate space within the treatments (Anderson 2001; Anderson 2004). To confirm that compositional differences between logged and unlogged communities were due to location differences rather than to dispersion differences, we used the FORTRAN program PERMDISP (http://www.stat.auckland.ac.nz/~mja/Programs.htm; Anderson 2004). PERMDISP calculates the centroid of each treatment (logged or unlogged) in multivariate space based on the chosen similarity measure (in this case, Bray-Curtis), and then calculates the distance of each plot within the treatment from the treatment centroid. To compare average dispersion values between treatments (logged understory communities vs. unlogged understory communities; logged tree communities vs. unlogged tree communities), PERMDISP performs a permutational ANOVA and calculates a pseudo *F*-statistic and *P*-value in the same manner as the PERMANOVA described above (Anderson 2004). A significant pseudo *F*-ratio from the PERMANOVA and a non-significant difference in dispersion between logged and unlogged plots from the PERMDISP analysis would suggest that logged and unlogged communities differ in multivariate composition and do not differ in variation around the mean composition within logged and unlogged communities.

To determine whether particular species accounted for the observed differences in community composition between logged and unlogged communities, we performed indicator species analysis (Dufrene & Legendre 1997) using PC-ORD 5.0 (MjM Software Design, Gleneden Beach, OR). The indicator analysis uses the relative abundance of each species (abundance in one group divided by abundance in all other groups) and the number of plots within each group in which the species occurs (relative frequency) to calculate an indicator value that ranges from 0 to 100. An indicator value of 100 indicates that the species was observed in only one group (in this case, logged or unlogged plots) and that each plot within that group contained at least one individual of that species. The significance of the indicator value is determined with a Monte Carlo test based on Bray-Curtis distance (Dufrene & Legendre 1997).

Temporal change within communities

We analyzed within-plot change in species richness and total abundance with paired *t*-tests, where the species richness and total abundance values for a plot in 1978 were compared with the species richness and total abundance values for the same plot in 2007. To determine whether topographic or edaphic factors influenced the change in species richness over time, we calculated the proportional difference in species richness between 1978 and 2007 for each plot. We then generated Pearson's correlation coefficients between proportional change in species richness and each factor listed in Table A.1 to examine whether any topographic or edaphic factors were correlated with the extent of change in richness.

To estimate temporal turnover in community composition, we calculated the similarity of each plot in 1978 to itself in 2007 using the Bray-Curtis index and the Chao-Sørensen incidence-based index in EstimateS (Colwell 2005). The Bray-Curtis index (also referred to as the Sørensen quantitative index or the Czekanowski coefficient; C_N) is widely used to assess similarity between two communities (Magurran 2004). The Chao-Sørensen incidence-based index (L_{inc}) is a modified form of the traditional Sørensen similarity index that accounts for both the frequency of individual species in the community and for the effects of "unseen shared species" (species that are missing from the sample data but are likely present in the community) on community similarity (Chao *et al*. 2005). The Chao-Sørensen index is useful for assessing similarity between diverse communities that contain many rare species, such as the forest understory community. For both the Bray-Curtis and the Chao-Sørensen indices, values near 1 indicate nearly identical community composition between time periods and values near 0 indicate that communities have very little compositional overlap between time periods.

We defined temporal turnover as the degree of compositional dissimilarity between 1978 and 2007 within an individual plot. Therefore, we calculated turnover as $1 - C_N$ and $1 - L_{inc}$. To evaluate whether historic logging influenced temporal turnover, we performed *t*-tests to compare mean logged and unlogged community turnover for both the $1 - C_N$ and $1 - L_{inc}$ dissimilarity values. We generated Pearson's correlation coefficients to determine whether temporal turnover was related to the topographic or edaphic factors listed in Table A.1 or to community attributes. We used JMP 6.0 for all analyses of within-plot temporal turnover.

Temporal change among communities

To examine whether similarity among communities changed over time in logged and unlogged plots, we used a test for homogeneity of multivariate dispersions (Anderson *et al*. 2006) based on Bray-Curtis dissimilarity. Traditionally, overall among-community similarity within a group has been described as the mean similarity of each community to all other communities within that group. However, direct statistical tests cannot be performed on these average similarity values because the values are not independent of one another (Anderson *et al*. 2006). Here, we describe among-community similarity as the average distance of plots within a group to the group centroid in multivariate space (i.e. multivariate dispersion as in Anderson *et al*. 2006), and use a permutational ANOVA (described above) in the PERMDISP program to statistically test for differences in among-community similarity between years. Using this approach, a significant *P*-value indicates that plots within a treatment (logged or unlogged) became either more homogeneous (had lower multivariate dispersion in 2007 than in 1978) or more dissimilar to one another (had higher multivariate dispersion in 2007 than in 1978) over time. For our study plots, average distance of individual plots to the group centroid is directly comparable to traditional measures that calculate mean similarity of each plot to all other plots within the group. For understory communities, average Bray-Curtis similarity and average Chao-Sørensen similarity were highly correlated with average distance to the group centroid in 1978 ($r = 0.99$, $P < 0.001$; $r = 0.97$, $P < 0.001$, respectively) and in 2007 ($r = 0.99$, $P < 0.0001$; $r = 0.96$, $P < 0.0001$, respectively). For tree communities, average Bray-Curtis similarity was highly correlated with average distance to the group centroid in 1978 ($r = 0.99$, $P < 0.001$) and in 2007 ($r = 0.87$, $P < 0.0001$).

RESULTS

Influence of historic logging on forest communities

In 1978 (50 years after logging), historically logged plots contained a total of 132 understory species and 29 tree species while unlogged plots contained 157 understory species and 25 tree species (Appendix B). In 2007 (80 years after logging), historically logged plots contained a total of 110 understory species and 24 tree species while unlogged plots contained 134 understory species and 26 tree species (Appendix C). Across both sampling periods, historically logged plots contained 25 understory species and 5 tree species that were not found in unlogged plots, and unlogged plots contained 48 understory species and 2 tree species that were unique to unlogged plots (Appendix D). Overall, 39 species recorded in 1978 were not seen in 2007, and 9 new species were encountered in 2007 that were not recorded in 1978 (Appendix D).

Neither mean understory species richness ($t = 1.59$, df = 27, $P = 0.12$) nor mean tree species richness (observed: $t = 1.65$, df = 24, $P = 0.11$, rarefied: $t = 1.0$, df = 25, $P = 0.33$) differed between logged and unlogged plots in 1978. In 2007, however, understory species richness was 1.4× greater in unlogged plots than in logged plots ($t = 2.25$, df = 27, $P = 0.03$). Tree species richness did not differ between logged and unlogged plots in 2007 (observed: $t = 1.26$, df = 23, $P = 0.22$, rarefied: $t = 0.83$, df = 25, $P = 0.42$).

Understory percent cover did not differ between logged and unlogged plots in 1978 ($t = 1.13$, df = 27, $P = 0.27$). But in 2007, understory cover was 1.8× greater in unlogged plots than in logged plots ($t = 2.89$, df = 27, $P = 0.007$). Tree density was 1.7× higher in logged plots than in unlogged plots in 1978 ($t = 4.9$, df = 27, $P < 0.0001$) and 1.4× higher in logged plots than in unlogged plots in 2007 ($t = 2.69$, df = 21, $P = 0.01$).

Using frequency-based estimates of species abundance, we found slight differences in understory community composition between logged and unlogged plots in both 1978 (PERMANOVA: $F_{1,28} = 1.84$, $P = 0.05$) and 2007 (PERMANOVA: $F_{1,28} = 1.80$, $P = 0.05$). Using percent cover-based estimates of species abundance, we also found differences in understory community composition between logged and unlogged plots in 1978 (PERMANOVA: $F_{1,28} = 1.81$, $P = 0.02$) and in 2007 (PERMANOVA: $F_{1,28} = 1.85$, $P = 0.03$). The differences in understory community composition were due to differences in the location of the logged and unlogged plots in multivariate space rather than to differences in the relative dispersion of plots within the logged and unlogged groups (1978 PERMDISP: $F = 0.54$, $P = 0.52$ (frequency-based), $F = 0.08$, $P = 0.80$ (cover-based); 2007 PERMDISP: $F = 0.40$, $P = 0.59$ (frequency-based), $F = 0.32$, $P = 0.64$ (cover-based)). Overall, fourteen understory species had significantly higher indicator values (a combination of relative abundance and relative frequency) in unlogged plots in at least one of the years and five understory species had significantly higher indicator values in logged plots (Table A.2). Indicators of unlogged plots included tree seedlings, small shrubs, and slow-dispersing forest interior herbs, such as *Trillium* spp., *Viola hastata*, *Arisaema triphyllum*, and *Eurbyia divaricatus*. Four of the five significant indicators of logged plots were woody seedlings or shrubs.

Composition of tree communities differed between the logged and unlogged plots in both 1978 (PERMANOVA: $F_{1, 28} = 2.11$, $P = 0.03$) and 2007 (PERMANOVA: $F_{1, 28} = 2.37$, $P = 0.02$). Differences in tree community composition were due to differences in the location of the logged and unlogged plots in multivariate space rather than to differences in the relative dispersion of plots within the logged and unlogged groups (1978 PERMDISP: $F = 0.02$, $P = 0.89$; 2007 PERMDISP: $F = 0.36$, $P = 0.59$). *Betula lenta* and *Prunus serotina* had significantly higher indicator values in logged plots than in unlogged plots in both years. In addition, *Prunus pensylvanica* had a significantly higher indicator value in logged plots than in unlogged plots in 1978 and *Magnolia fraseri* had a significantly higher indicator value in logged plots than in unlogged plots in 2007. *Acer saccharum* was the only tree species with a significantly higher indicator value in unlogged plots than in logged plots (Table A.3).

Overall, logged and unlogged plots had similar topographic properties, but differed in some edaphic parameters (Table A.1). Soil cation exchange capacity was 1.3× higher, soil Ca was 2× higher, and soil organic matter was 1.7× higher in logged plots than in unlogged plots. Soil pH was 1.1× higher in unlogged plots than in logged plots and higher elevation plots tended to have significantly lower soil pH than did lower elevation plots (Table A.4).

Effects of historic logging on temporal change within communities

Understory species richness decreased by an average of 13% over the 30-year study period in the historically logged plots ($t = 2.35$, df = 14, $P = 0.03$), but did not change in the unlogged plots ($t = 1.06$, df = 14, $P = 0.31$). The decrease in overall understory species richness in the logged plots resulted from decreased richness of herbaceous species (Table A.5; Fig. A.2). Shrub, seedling, and tree species richness did not change over time in either logged or unlogged plots ($P > 0.08$ in all cases; Table A.5; Fig. A.2).

Over the 30-year study period, stem density of trees decreased by an average of 21% in the historically logged plots ($t = 6.14$, df = 14, $P < 0.0001$) but did not change in unlogged plots ($t = 0.30$, df = 14, $P = 0.77$) (Table A.5, Fig. A.3). Tree basal area increased slightly over 30 years in the historically logged plots ($t = 2.0$, df = 14, $P = 0.07$) but did not change over time in the unlogged plots ($t = 1.07$, df = 14, $P = 0.30$).

Historic logging had no effect on within-plot understory compositional turnover measured using the Bray-Curtis ($t = 0.08$, df = 28, $P = 0.94$) or the Chao-Sørensen ($t = 0.45$, df = 26, $P = 0.65$) indices. Similarly, there was no effect of historic logging on within-plot tree compositional turnover (Bray-Curtis: $t = 1.4$, df = 27, $P = 0.17$).

Effects of topographic and edaphic factors on temporal change within communities

The topographic and edaphic factors listed in Table A.1 were not correlated with proportional change in understory species richness within individual plots (all $P > 0.18$). Within-plot understory compositional turnover, however, was negatively correlated with elevation and positively correlated with soil pH (Table A.6). Overall, plots at higher elevations had lower understory compositional turnover over the 30-year period than did plots at lower elevations (Bray-Curtis: $r = -0.46$, $P = 0.01$; Chao- Sørensen: $r = -0.41$, $P = 0.02$; Fig. A.4). In addition, plots with high soil pH had higher understory turnover than did plots with low soil pH (Bray-Curtis: *r* = 0.37, *P* = 0.04; Chao- Sørensen: *r* = 0.31, *P* = 0.09; Fig. A.4).

Temporal turnover in understory community composition was not related to tree compositional turnover (*r* = 0.19, *P* = 0.32). Tree compositional turnover was negatively correlated with soil cation exchange capacity (CEC; *r* = -0.57, *P* = 0.001) and positively correlated with soil pH (*r* = 0.41, *P* = 0.03). Plots with high CEC and low pH had lower compositional turnover in the tree community than plots with low CEC and high pH (Fig. A.5). No other topographic or edaphic factors listed in Table A.1 were correlated with proportional changes in tree species richness or with tree compositional turnover (all *P* > 0.08; Table A.6).

Effects of community attributes on temporal change within communities

Neither proportional change in understory species richness (*r* = -0.25, *P* = 0.18) nor understory compositional turnover (Bray-Curtis: *r* = 0.32, *P* = 0.09; Chao-Sørensen: *r* = 0.18, *P* = 0.35) was related to 1978 understory species richness. However, plots with high tree species richness in 1978 lost a greater proportion of species over time than did plots with low tree species richness in 1978 (*r* = -0.45, *P* = 0.01). Tree species richness in 1978 was not correlated with compositional change in the tree community (*r* = 0.18, *P* = 0.33).

With the exception of one statistical outlier (determined using Cook's D and hat matrix analyses) that contained approximately 55% cover of two fern species (*Phegopteris hexagonoptera* and *Dennstaedtia punctilobula*), plots with high understory productivity in 1978 (estimated using percent cover values) had lower understory turnover than did plots with low understory productivity in 1978 (Bray-

Curtis: $r = -0.49$, $P = 0.007$; Chao-Sørensen: $r = -0.45$, $P = 0.01$; Fig. A.4). Change in understory species richness was not related to 1978 understory productivity ($r = -0.23$, $P = 0.22$). Tree productivity in 1978 (estimated using stand basal area values) was not significantly correlated with change in tree species richness ($r = -0.03$, $P = 0.87$) or with tree compositional turnover ($r = -0.33$, $P = 0.08$). Understory percent cover and tree basal area were not correlated with any measured topographic or edaphic factors (Table A.7).

Effects of historic logging on temporal change among communities

Among-community similarity was unchanged from 1978 to 2007 in both the logged and unlogged plots (Table A.8). We found no differences in the multivariate dispersion of understory communities in 2007 compared with 1978 in either the logged (PERMDISP: $F = 0.18$, $P = 0.74$ (frequency-based), $F = 0.04$, $P = 0.88$ (cover-based)) or unlogged (PERMDISP: $F = 0.19$, $P = 0.69$ (frequency-based), $F = 1.25$, $P = 0.34$ (cover-based)) plots. Similarly, multivariate dispersion of tree communities did not change between 1978 and 2007 in logged (PERMDISP: $F = 0.06$, $P = 0.82$) or unlogged (PERMDISP: $F = 1.17$, $P = 0.35$) plots.

DISCUSSION

By resampling permanently marked forest plots, we investigated whether the legacy of historic logging influenced temporal change within and among forest communities and whether topographic factors, edaphic factors, or community attributes were correlated with temporal change in these communities. We found that logging history affected temporal change in understory species richness and tree density within communities. However, logging history did not affect the extent of within-community compositional turnover for either the understory or tree community. Instead, factors such as topography, soil properties, the number of species within a community, and community productivity were related to within-community compositional change. Among-community similarity was unchanged from 1978 to 2007 in the understory communities and in the tree communities of both the logged and unlogged plots.

Effects of historic logging on temporal change within communities

In 1978 (50 years after logging), understory community composition differed only slightly between historically logged and unlogged plots. Historically logged and unlogged plots also differed only slightly in understory composition in 2007 (80 years after logging). These results are similar to some chronosequence studies comparing understory communities in recently (< 50 years) logged forests with understory communities of older (> 80 years) forests (Gilliam *et al*. 1995; Ford *et al*. 2000). However, other studies have found larger and more persistent differences in the understory communities of anthropogenically disturbed and undisturbed forests (Duffy & Meier 1992; Meier *et al*. 1995; Bellemare *et al*. 2002; Flinn & Vellend

2005; Harrelson & Matlack 2006). There are at least two reasons for the discrepancies among previous studies. First, evidence for large differences in understory composition between human-disturbed and undisturbed forests generally comes from studies of abandoned agricultural land (Bellemare *et al*. 2002; Flinn & Vellend 2005; Harrelson & Matlack 2006). Agricultural disturbance can last for many decades and deplete forest species from the seedbank, leaving only a subset of the forest understory species to recolonize abandoned sites (Bellemare *et al*. 2002; Flinn & Vellend 2005; Harrelson & Matlack 2006). Second, it is possible that the effects of historic logging are stronger on vernal understory species (Duffy & Meier 1992; Meier *et al*. 1995) than on late-season (summer) species. In our study site, the relatively small differences we observed in community composition between logged and unlogged plots could be due to the short duration of logging activities or to our focus on late-season species. Logging activities lasted for four years in our study area (Schmidt & Hooks 1994), and understory species may have persisted in the soil seedbank and subsequently recolonized logged areas or survived as scattered mature individuals in the logged areas. In addition, our 1978 and 2007 sampling data were collected between mid-June and late-August and included only late-season understory species, which may be more resistant to logging effects than vernal species.

We found that temporal change in understory species richness differed between logged and unlogged plots, but that temporal change in tree species richness did not. Logged plots lost, on average, 4.3 understory species over the 30-year study period, while understory species richness in unlogged plots did not change significantly over the same time interval. Species loss in other protected areas of the eastern U.S. has been attributed to increases in white-tailed deer populations (Rooney & Dress 1997; Rooney *et al*. 2004; Taverna *et al*. 2005). However, deer impacts to vegetation in GSMNP are generally concentrated near historic agricultural fields (Webster *et al*. 2005) that do not intersect our study sites, and there is no reason to suspect that deer herbivory differentially affects logged and unlogged plots in this area. The loss of understory species in individual logged plots is more likely due to the loss of early colonizing herbs or to the changing light regime caused by changes in overstory stem density, though we did not explicitly test either of these hypotheses.

Consistent with other studies in this area (e.g., Clebsch & Busing 1989), tree species richness did not differ between logged and unlogged plots in either 1978 or 2007. However, tree species composition did differ between logged and unlogged plots in 1978 and also in 2007. Overall, we encountered five tree species in the logged plots that were not encountered in the unlogged plots and two tree species in the unlogged plots that were not encountered in the logged plots. In addition, tree density was higher in logged plots than in unlogged plots in both years.

Over the 30-year study period, tree density decreased by 21% in the logged plots though it remained relatively stable in the unlogged plots. The decrease in tree density in the logged plots was driven by a decrease in the number of trees smaller than 30 cm dbh (data not shown). The decrease in tree density in the logged plots suggests that these plots were in the stem exclusion stage of forest development, when trees established after the logging event compete most intensely with one another for growing space (Oliver & Larson 1996), and those individuals that grew more slowly had less access to light and died. The relative stability of tree density in the unlogged plots indicates that these plots have entered the later stages of forest development when the loss of individual trees is more idiosyncratic (Oliver & Larson 1996).

Contrary to our expectations, the occurrence of historic logging did not affect the extent of compositional turnover in the understory community or the extent of tree compositional turnover during our 30-year study period. We expected greater compositional change in the understory of logged plots than in unlogged plots during this period due to the changing understory light environment as the logged plots moved through the stem exclusion and understory reinitiation stages of development (Oliver & Larson 1996). While we did expect some change in understory species composition over time in the unlogged plots (Taverna *et al*. 2005), we expected this change to be small relative to understory change in logged plots. It may be that we found no difference in the extent of compositional change in the understory of logged and unlogged plots because logging events that occurred greater than 50 years ago no longer affect understory dynamics in these forests.

For tree communities, we expected the logged plots to have a higher compositional turnover than the unlogged plots due to the expected decrease in small trees over time and the presence of early successional tree species in the logged plots. However, we found that the extent of tree compositional turnover in unlogged plots was similar to tree turnover in logged plots. Given that tree density in the logged plots was almost twice as high as tree density in the unlogged plots in 1978, the loss of individual trees likely had a smaller effect on compositional turnover in the logged plots than in the unlogged plots. Since each tree species is represented by fewer individuals in the unlogged plots, a small change in tree density could result in a proportionally larger change in community composition. The different responses of logged and unlogged tree communities to the loss of individual trees could explain the similar extent of compositional turnover we observed in logged and unlogged plots.

Effects of topographic and edaphic factors on temporal change within communities

Topography, edaphic parameters, and community productivity were all correlated with temporal turnover in the forest understory community. However, only edaphic parameters were correlated with turnover in the tree community. Overall, the extent of temporal turnover in understory community composition was not related to the extent of tree compositional turnover during the 30-year study period.

Consistent with other studies (Aplet & Vitousek 1994; Selmants & Knight 2003), we found that the extent of temporal turnover in the understory community decreased along the elevational gradient, with greater change in plots at low elevations than in plots at higher elevations. Mean annual temperature decreases about 4 °C and mean annual precipitation increases about 50 cm over the 740 m elevational gradient in our study site (Garten & Hanson 2006). The lower temperatures at higher elevation could slow decomposition, decrease nutrient availability, and reduce overall plant growth (Vitousek *et al*. 1992; Aplet & Vitousek 1994), which might result in lower temporal turnover at high elevations. In Great Smoky Mountains National Park, decomposition rates generally decrease with elevation, but nitrogen availability increases due to low soil C-to-N ratios at high elevations (Garten 2004). We did not measure decomposition rates or nitrogen availability directly on our study plots; therefore, it is unclear whether reduced plant growth at high elevations is responsible for the smaller changes in understory composition over time that we observed here.

Differences in precipitation could also lead to differences in compositional turnover (Anderson 2008) along the elevational gradient. Anderson (2008) showed that areas with higher mean annual precipitation have greater compositional change over time. Our results show the opposite trend—forest understory turnover is lower at high elevation sites that have higher mean annual precipitation. However, our observational study does not allow us to separate the effects of precipitation, *per se*, from the effects of other elevational covariates on understory turnover. On average, annual precipitation in our forested sites is more than 2.5× higher than annual precipitation in Anderson's (2008) grassland study, and precipitation may not be the limiting resource that controls community dynamics in our study area.

In addition to temperature and precipitation, soil pH also varies with elevation in our study sites, with more acidic soils at higher elevation sites. Consistent with our result of higher temporal turnover in the understory communities at low elevations compared with high elevations, we found higher temporal turnover in the understory communities of plots with high soil pH than in those with low soil pH. We also found that temporal turnover in tree communities was positively related to soil pH. Tree compositional turnover was higher in plots with high soil pH and low cation exchange capacity compared with plots that had low soil pH and high cation exchange capacity. Temporal change in understory community composition is also correlated with soil fertility gradients in other southeastern U.S. temperate forests (Peet & Christensen 1988; Taverna *et al*. 2004). In the acidic soils of this region, higher soil pH can indicate greater nutrient availability to plants. In the understory, greater nutrient availability could lead to increased temporal turnover either by increasing the likelihood that newly arriving species will establish in a community (Peet & Christensen 1988) or by increasing the growth of dominant species that could outcompete other species in the community. In addition, the large regional species pool of high pH sites (Peet *et al*. 2003) could increase the chance that new species would colonize these sites over time or that more species would be present in the initial community (see discussion below). A larger pool of potential colonizers could increase understory compositional change in high pH communities compared to low pH communities. For trees, it may be that fertile sites allow faster tree growth, which could increase recruitment into the overstory or increase mortality through competitive exclusion. Either increased recruitment or mortality could lead to greater tree compositional turnover in more fertile plots.

Unlike understory temporal turnover, tree compositional turnover was not related to elevation. Given that turnover of individual tree stems can be a function of elevation, latitude, and productivity in some forest systems (Phillips *et al*. 2004; Bellingham *et al*. 1999; Stephenson & van Mantgem 2005), we expected to see more temporal turnover in the tree community in low elevation plots than in high elevation plots. However, elevation was not correlated with overall change in tree community composition, stem density, or tree species richness over time in our study. We did not directly measure turnover of individual trees in this study and cannot say whether the rate of stem recruitment or mortality changed with elevation. While variation in tree population dynamics based on elevation may occur in our system, this potential variation has not led to differences in compositional turnover in the tree community.

Effects of community attributes on temporal change within communities

In addition to topographic and edaphic parameters, community attributes such as species richness and productivity could influence temporal change in community composition (Chalcraft *et al*. 2004; White *et al*. 2006). Based on multi-taxon analyses of species-time relationships, White *et al*. (2006) proposed that the mechanisms generating high species richness in a community could also lead to low species turnover in that community. Our study does not provide support for this hypothesis. Instead, plots with higher understory species richness in 1978 lost more total species over time in our study, but the proportion of understory species lost did not differ between plots with high species richness in 1978 and those with low species richness in 1978. For trees, plots with high species richness in 1978 lost proportionally more species than did plots with low species richness in 1978. While we did not find a direct relationship between understory compositional turnover and understory species richness in 1978, plots at low elevation and with high soil pH supported more understory species in 1978 and had more understory turnover than did plots at high elevation and low pH. This suggests that in forested systems, such as our study sites, mechanisms leading to high species richness may lead to higher, rather than lower, temporal turnover.

Based on observations in aquatic systems, Chase & Leibold (2002) hypothesized that compositional turnover might be greater in sites with high primary productivity than in sites with low primary productivity. Chalcraft *et al*. (2004) found no support for this hypothesis in grassland plant communities. In our study, understory productivity in 1978 was correlated with understory compositional turnover, but tree productivity in 1978 was not related to tree compositional turnover. Plots with high understory percent cover (an estimate of understory productivity; Gilliam & Turrill 1993) in 1978 had lower compositional turnover than did plots with low understory cover in 1978. We found that both 1978 understory biomass estimates (equations from Gilliam & Turrill 1993) and understory biomass estimates averaged across the two survey periods (1978 and 2007) were negatively related to change in understory community composition (data not shown). The proportion of a plot initially occupied by understory species might affect community change in these forests over time due to resident species excluding new species from establishing or limiting the population growth of other resident species.

Effects of historic logging on temporal change among communities

We documented a wide-range of temporal changes in species composition within communities, but these within-community changes did not translate into a temporal change in among-community similarity. We found no change in among-community similarity from 1978 to 2007 in either the logged and unlogged plots. Evidence that among-community similarity is lower in forests formerly disturbed by agriculture compared with older forests (Christensen & Peet 1984; Vellend *et al*. 2007) suggests that younger forests may become more dissimilar to one another over time. We did not find support for that hypothesis here. Between 50 and 80 years after logging, we found no change in among-community similarity in either the understory or the tree community of the logged plots. We also found no change in among-community similarity in the plant communities of the unlogged plots over this same 30-year time period. However, the theoretical expectation for temporal change in among-community similarity in undisturbed forests is unclear. It may be that our 30-year study period was a relatively stable period within larger cycles of among-community heterogeneity in forest development or perhaps among-community heterogeneity has reached a static point and will remain unchanged in the absence of further disturbance (Rejmánek & Rosen 1992). While our study suggests that among-community similarity in both young and old forests can remain stable for decades, we cannot speculate on the long-term trends in spatial heterogeneity across these communities or on the mechanisms maintaining this stability.

CONCLUSIONS

In this study, we added to insights gained from chronosequence analyses of long-term community dynamics by using permanent plots to directly measure compositional changes both within and among forest communities over 30 years. In addition, we compared temporal changes within and among historically disturbed communities to changes within and among communities with no evidence of large-scale historic disturbance. We expected greater temporal change in community composition both within and among disturbed communities than we expected within and among undisturbed communities (Christensen & Peet 1984; Vellend *et al*. 2007). However, we found that the extent of temporal change in community composition was not related to historic disturbance, and that among-community similarity did not change over time in either historically disturbed or undisturbed plots. We recorded a wide range of compositional turnover values within both disturbed and undisturbed communities, but these within-plot changes did not affect similarity among communities over time.

With this long-term observational dataset, we could not test the mechanisms driving temporal change within these forest communities directly. However, we found correlations between the extent of compositional turnover within communities and some topographic and edaphic factors as well as community attributes. Consistent with chronosequence studies (Aplet & Vitousek 1994; Selmants & Knight 2003), we found that elevation was correlated with temporal turnover in forest understory communities. In addition, we found that soil pH was correlated with temporal turnover in both understory and tree communities and that community productivity was correlated with temporal turnover in understory communities.

Overall, our results indicate that the extent of temporal change in community composition may depend more on environmental gradients than on the legacy of large-scale but short-lived historic disturbances, such as logging. In addition, our results suggest that variation in temporal turnover within communities may not necessarily translate into changes in compositional similarity among communities over time. Additional long-term studies that directly measure temporal change both within and among communities are needed in order to increase our understanding of the factors that control multi-scale diversity across time.

REFERENCES

REFERENCES

Anderson, M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, **26**, 32-46.

Anderson, M.J. (2004) PERMDISP: a FORTRAN computer program for permutational analysis of multivariate dispersions (for any two-factor ANOVA design) using permutation tests. Department of Statistics, University of Auckland, New Zealand.

Anderson, M.J. (2005) PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance. Department of Statistics, University of Auckland, New Zealand.

Anderson, M.J., Ellingsen, K.E., & McArdle, B.H. (2006) Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, **9**, 683-693.

Anderson, T.M. (2008) Plant compositional change over time increases with rainfall in Serengeti grasslands. *Oikos*, **117**, 675-682.

Aplet, G.H. & Vitousek, P.M. (1994) An age-altitude matrix analysis of Hawaiian rain forest succession. *Journal of Ecology*, **82**, 137-147.

Bellemare, J., Motzkin, G., & Foster, D.R. (2002) Legacies of the agricultural past in the forested present: An assessment of historical land-use effects on rich mesic forests. *Journal of Biogeography*, **29**, 1401-1420.

Bellingham, P.J., Stewart, G.H., & Allen, R.B. (1999) Tree species richness and turnover throughout New Zealand forests. *Journal of Vegetation Science*, **10**, 825-832.

Bratton, S.P. (1978). Vegetation survey Great Smoky Mountains National Park. National Park Service, Southeast Regional Office, Atlanta.

Brown, J.H., Ernest, S.K.M., Parody, J.M., & Haskell, J.P. (2001) Regulation of diversity: Maintenance of species richness in changing environments. *Oecologia*, **126**, 321-332.

Chalcraft, D.R., Williams, J.W., Smith, M.D., & Willig, M.R. (2004) Scale dependence in the species-richness-productivity relationship: The role of species turnover. *Ecology*, **85**, 2701-2708.

Chao, A., Chazdon, R.L., Colwell, R.K., & Shen, T.J. (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters*, **8**, 148-159.

Chase, J.M. & Leibold, M.A. (2002) Spatial scale dictates the productivity-biodiversity relationship. *Nature*, **416**, 427-430.

Christensen, N.L. & Peet, R.K. (1984) Convergence during secondary forest succession. *Journal of Ecology*, **72**, 25-36.

Clark, C.M. & Tilman, D. (2008) Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. *Nature*, **451**, 712-715.

Clebsch, E.E.C. & Busing, R.T. (1989) Secondary succession, gap dynamics, and community structure in a southern Appalachian cove forest. *Ecology*, **70**, 728-735.

Collins, S.L. & Smith, M.D. (2006) Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. *Ecology*, **87**, 2058-2067.

Colwell, R.K. (2005) EstimateS: Statistical estimation of species richness and shared species from samples. User's Guide and application published at: http://purl.oclc.org/estimates.

Drayton, B. & Primack, R.B. (1996) Plant species lost in an isolated conservation area in Metropolitan Boston from 1894 to 1993. *Conservation Biology*, **10**, 30-39.

Duffy, D.C. & Meier, A.J. (1992) Do Appalachian herbaceous understories ever recover from clearcutting. *Conservation Biology*, **6**, 196-201.

Dufrene, M. & Legendre, P. (1997) Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs*, **67**, 345-366.

Flinn, K.M. & Vellend, M. (2005) Recovery of forest plant communities in post-agricultural landscapes. *Frontiers in Ecology and the Environment*, **3**, 243-250.

Ford, W.M., Odom, R.H., Hale, P.E., & Chapman, B.R. (2000) Stand-age, stand characteristics, and landform effects on understory herbaceous communities in southern Appalachian cove-hardwoods. *Biological Conservation*, **93**, 237-246.

Foster, D.R., Motzkin, G., & Slater, B. (1998) Land-use history as long-term broad-scale disturbance: Regional forest dynamics in central New England. *Ecosystems*, **1**, 96-119.

Fukami, T. & Wardle, D.A. (2005) Long-term ecological dynamics: Reciprocal insights from natural and anthropogenic gradients. *Proceedings of the Royal Society B-Biological Sciences*, **272**, 2105-2115.

Garten, C.T. (2004) Potential net soil N mineralization and decomposition of glycine-C-13 in forest soils along an elevation gradient. *Soil Biology & Biochemistry*, **36**, 1491-1496.

Garten, C.T. & Hanson, P.J. (2006) Measured forest soil C stocks and estimated turnover times along an elevation gradient. *Geoderma*, **136**, 342-352.

Gilliam, F.S. & Turrill, N.L. (1993) Herbaceous layer cover and biomass in a young versus a mature stand of a Central Appalachian hardwood forest. *Bulletin of the Torrey Botanical Club*, **120**, 445-450.

Gilliam, F.S., Turrill, N.L., & Adams, M.B. (1995) Herbaceous-layer and overstory species in clear-cut and mature central Appalachian hardwood forests. *Ecological Applications*, **5**, 947-955.

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379-391.

Harrelson, S.M. & Matlack, G.R. (2006) Influence of stand age and physical environment on the herb composition of second-growth forest, Strouds Run, Ohio, USA. *Journal of Biogeography*, **33**, 1139-1149.

Jenkins, M.A., Jose, S., & White, P.S. (2007) Impacts of an exotic disease and vegetation change on foliar calcium cycling in Appalachian forests. *Ecological Applications*, **17**, 869-881.

Kartesz, J.T. (1999). A synonymized checklist and atlas with biological attributes for the vascular flora of the United States, Canada, and Greenland, first ed. In *Synthesis of the North American Flora, Version 1.0.* (eds J.T. Kartesz & C.A. Meacham). North Carolina Botanical Garden, Chapel Hill.

Loreau, M. (2000) Are communities saturated? On the relationship between alpha, beta and gamma diversity. *Ecology Letters*, **3**, 73-76.

Magnuson, J.J. (1990) Long-term ecological research and the invisible present. *Bioscience*, **40**, 495-501.

Magurran, A.E. (2004) *Measuring biological diversity* Blackwell, Oxford.

McCune, B. & Keon, D. (2002) Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science*, **13**, 603-606.

McKinney, M.L. & Lockwood, J.L. (1999) Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, **14**, 450-453.

Meier, A.J., Bratton, S.P., & Duffy, D.C. (1995) Possible ecological mechanisms for loss of vernal-herb diversity in logged Eastern deciduous forests. *Ecological Applications*, **5**, 935-946.

Olden, J.D. (2006) Biotic homogenization: A new research agenda for conservation biogeography. *Journal of Biogeography*, **33**, 2027-2039.

Oliver, C.D. & Larson, B.C. (1996) *Forest stand dynamics* Wiley, New York.

Peet, R.K. & Christensen, N.L. (1988). Changes in species diversity during secondary forest succession on the North Carolina Piedmont. In *Diversity and*

Pattern in Plant Communities (eds H.J. During, M.J.A. Werner & J.W. Williams), pp. 233-245. SPB Academic Publishing, The Hague.

Peet, R.K., Fridley, J.D., & Gramling, J.M. (2003) Variation in species richness and species pool size across a pH gradient in forests of the southern Blue Ridge Mountains. *Folia Geobotanica*, **38**, 391-401.

Peet, R.K., Wentworth, T.R., & White, P.S. (1988) A flexible multipurpose method for recording vegetation composition and structure. *Castanea*, **63**, 262-274.

Phillips, O.L., Baker, T.R., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, W.F., Lewis, S.L., Lloyd, J., Malhi, Y., Monteagudo, A., Neill, D.A., Vargas, P.N., Silva, J.N.M., Terborgh, J., Martinez, R.V., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, J.A., Czimczik, C.I., Di Fiore, A., Erwin, T., Kuebler, C., Laurance, S.G., Nascimento, H.E.M., Olivier, J., Palacios, W., Patino, S., Pitman, N.C.A., Quesada, C.A., Salidas, M., Lezama, A.T., & Vinceti, B. (2004) Pattern and process in Amazon tree turnover, 1976-2001. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **359**, 381-407.

Pyle, C. (1988) The type and extent of anthropogenic vegetation disturbance in the Great Smoky Mountains before National Park Service acquisition. *Castanea*, **53**, 183-196.

Rejmanek, M. & Rosen, E. (1992) Cycles of heterogeneity during succession - a premature generalization. *Ecology*, **73**, 2329-2331.

Rooney, T.P. & Dress, W.J. (1997) Species loss over sixty-six years in the ground-layer vegetation of Heart's Content, an old-growth forest in Pennsylvania USA. *Natural Areas Journal*, **17**, 297-305.

Rooney, T.P., Wiegmann, S.M., Rogers, D.A., & Waller, D.M. (2004) Biotic impoverishment and homogenization in unfragmented forest understory communities. *Conservation Biology*, **18**, 787-798.

Schmidt, R.G. & Hooks, W.S. (1994) Whistle over the mountain: Timber, track & trails in the Tennessee Smokies: An historical and field guide to the Little River Lumber Company and the Little River Railroad in the Great Smoky Mountains National Park in Tennessee. Graphicom Press, Yellow Springs, Ohio.

Selmants, P.C. & Knight, D.H. (2003) Understory plant species composition 30-50 years after clearcutting in southeastern Wyoming coniferous forests. *Forest Ecology and Management*, **185**, 275-289.

Smart, S.M., Thompson, K., Marrs, R.H., Le Duc, M.G., Maskell, L.C., & Firbank, L.G. (2006) Biotic homogenization and changes in species diversity across human-modified ecosystems. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 2659-2665.

Southworth, S., Schultz, A., & Denenny, D. (2005). Generalized geologic map of bedrock lithologies and surficial deposits in the Great Smoky Mountains National Park region, Tennessee and North Carolina, Rep. No. Open-File Report 2004-1410. U.S. Department of the Interior, U.S. Geological Survey.

Stephenson, N.L. & van Mantgem, P.J. (2005) Forest turnover rates follow global and regional patterns of productivity. *Ecology Letters*, **8**, 524-531.

Taverna, K., Peet, R.K., & Phillips, L.C. (2005) Long-term change in ground-layer vegetation of deciduous forests of the North Carolina Piedmont, USA. *Journal of Ecology*, **93**, 202-213.

Vellend, M., Verheyen, K., Flinn, K.M., Jacquemyn, H., Kolb, A., Van Calster, H., Peterken, G., Graae, B.J., Bellemare, J., Honnay, O., Brunet, J., Wulf, M., Gerhardt, F., & Hermy, M. (2007) Homogenization of forest plant communities and weakening of species-environment relationships via agricultural land use. *Journal of Ecology*, **95**, 565-573.

Verheyen, K., Bossuyt, B., Honnay, O., & Hermy, M. (2003) Herbaceous plant community structure of ancient and recent forests in two contrasting forest types. *Basic and Applied Ecology*, **4**, 537-546.

Vitousek, P.M., Aplet, G., Turner, D., & Lockwood, J.J. (1992) The Mauna-Loa environmental matrix - foliar and soil nutrients. *Oecologia*, **89**, 372-382.

Wardle, D.A., Walker, L.R., & Bardgett, R.D. (2004) Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science*, **305**, 509-513.

Webster, C.R., Jenkins, M.A., & Rock, J.H. (2005) Long-term response of spring flora to chronic herbivory and deer exclusion in Great Smoky Mountains National Park, USA. *Biological Conservation*, **125**, 297-307.

White, E.P., Adler, P.B., Lauenroth, W.K., Gill, R.A., Greenberg, D., Kaufman, D.M., Rassweiler, A., Rusak, J.A., Smith, M.D., Steinbeck, J.R., Waide, R.B., & Yao, J. (2006) A comparison of the species-time relationship across ecosystems and taxonomic groups. *Oikos*, **112**, 185-195.

White, P.S. & Busing, R.T. (1993). LTERM: Long-term monitoring and research in Great Smoky Mountains National Park, vegetation monitoring and an assessment of past studies, Rep. No. Technical Report NPS/sergrsm/nrtr-93/10. National Park Service, Southeast Region, Atlanta.

White, R.D., Patterson, K.D., Weakley, A., Ulrey, C.J., & Drake, J. (2003). Vegetation classification of Great Smoky Mountains National Park: Unpublished report submitted to BRD-NPS Vegetation Mapping Program. NatureServe, Durham.

Whittaker, R.H. (1956) Vegetation of the Great Smoky Mountains. *Ecological Monographs*, **26**, 1-69.

Yurkonis, K.A. & Meiners, S.J. (2004) Invasion impacts local species turnover in a successional system. *Ecology Letters*, **7**, 764-769.

APPENDIX A

Table A.1. Comparison of topographic and edaphic variables in historically logged and unlogged plots.

The logged vs. unlogged columns illustrate the mean difference between logged and unlogged plots and the P-value from t-tests of these differences. One asterisk (*) indicates P ≤ 0.05 and two asterisks (**) indicate P ≤ 0.01.

	Range (min - max)		Mean ± SE		Logged vs. Unlogged	
Variable	logged	unlogged	logged	unlogged	difference	*P*-value
Elevation (m)	727 - 1402	664 - 1400	1104 ± 61.6	1034 ± 67.3	70.70	0.45
slope (%)	0.3 - 35	2.0 - 31.7	19.0 ± 3.26	19.8 ± 2.42	0.89	0.83
heat load (ln(MJ cm^{-2} yr^{-1}))	0.8 - 0.99	0.8 - 0.99	0.9 ± 0.02	0.9 ± 0.01	0.01	0.58
Soil pH	3.7 - 5.3	3.9 - 5.3	4.2 ± 0.11	4.5 ± 0.12	0.36	0.03*
soil cation exchange capacity (meq/100g)	7.3 - 12.2	6.2 - 8.4	9.4 ± 0.40	7.1 ± 0.16	2.28	< 0.0001**
soil K (ppm)	40 - 176	38 - 113	68.5 ± 9.04	64.8 ± 4.93	3.67	0.73
soil Ca (ppm)	61 - 971	25 - 384	326 ± 71.9	165 ± 27.1	161	0.05*
soil Mg (ppm)	18 - 121	11 - 58	44.9 ± 6.63	32.3 ± 3.45	12.53	0.11
soil P (ppm)	7 - 34	6 - 40	14.3 ± 1.70	15.4 ± 2.46	1.07	0.72
soil organic matter (%)	4.1 - 8.5	1.2 - 5.2	5.1 ± 0.28	3.1 ± 0.33	2.00	< 0.0001**

Table A.2. Understory indicator species analysis for logged and unlogged plots. Understory species include herbs, shrubs, and seedlings < 1 m tall. Indicator values (IV) represent the degree to which a species is an indicator of the listed group, with 100 representing perfect indication. Species with significant IV in at least one year are listed alphabetically. One asterisk (*) indicates P ≤ 0.05 and two asterisks (**) indicate P ≤ 0.01.

	1978 understory frequency			2007 understory frequency		
Species	Group	IV	*P*	Group	IV	*P*
Acer saccharum	unlogged	44.6	0.16	unlogged	55.0	0.03*
Amphicarpaea bracteata	unlogged	31.7	0.04*	unlogged	18.7	0.45
Arisaema triphyllum	unlogged	63.6	0.001**	unlogged	45.1	0.02*
Athyrium filix-femina	unlogged	12.6	0.91	unlogged	44.6	0.02*
Betula alleghaniensis	logged	44.9	0.03*	logged	20.0	0.25
Betula lenta	unlogged	10.0	0.87	unlogged	40.0	0.02*
Calycanthus floridus	unlogged	53.3	0.002**	unlogged	37.0	0.06
Collinsonia canadensis	unlogged	60.0	0.002**	unlogged	6.7	1.00
Dioscorea villosa	unlogged	48.0	0.01*	unlogged	20.0	0.25
Eurbyia divaricatus	unlogged	51.2	0.16	unlogged	59.3	0.04*
Liriodendron tulipifera	unlogged	51.2	0.02*	unlogged	37.2	0.29
Osmunda claytoniana	logged	40.0	0.02*	--	--	--
Prunus serotina	logged	72.5	0.001**	logged	51.4	0.15
Quercus rubra	unlogged	58.9	0.01**	unlogged	31.7	0.63
Rhododendron maximum	logged	42.9	0.02*	logged	49.9	0.01*
Rubus spp.	logged	55.7	0.02*	unlogged	33.7	0.97
Thalictrum thalictroides	unlogged	22.2	0.23	unlogged	36.7	0.05*
Trillium spp.	unlogged	29.2	0.15	unlogged	72.3	0.002**
Viola hastata	unlogged	49.6	0.07	unlogged	58.4	0.003**

Table A.3. Tree (≥ 10 cm) indicator species analysis for logged and unlogged plots. Indicator values (IV) represent the degree to which a species is an indicator of the listed group, with 100 representing perfect indication. All observed tree species are listed alphabetically. One asterisk (*) indicates P ≤ 0.05 and two asterisks (**) indicate P ≤ 0.01.

	1978 tree density			2007 tree density		
Species	Group	IV	*P*	Group	IV	*P*
Acer pensylvanicum	logged	17.6	0.81	logged	31.1	0.31
Acer rubrum	logged	45.5	0.29	logged	57.4	0.12
Acer saccharum	unlogged	39.2	0.24	unlogged	62.2	0.03*
Aesculus flava	unlogged	18.7	0.83	unlogged	26.9	0.59
Betula alleghaniensis	logged	55.3	0.17	logged	31.1	0.54
Betula lenta	logged	68.3	0.005**	logged	60.4	0.02*
Carya spp.	unlogged	16.0	0.52	unlogged	17.1	0.47
Castanea dentata	--	--	--	unlogged	6.7	1.00
Cornus florida	unlogged	30.6	0.12	unlogged	13.3	0.48
Fagus grandifolia	unlogged	28.8	0.44	unlogged	37.3	0.16
Fraxinus americana	unlogged	24.2	0.23	unlogged	11.1	0.74
Halesia tetraptera	logged	41.7	0.85	unlogged	45.7	0.59
Hamamelis virginiana	logged	10.0	0.75	--	--	--
Ilex montana	logged	13.3	0.49	logged	6.7	1.00
Ilex opaca	logged	6.7	1.00	logged	6.7	1.00
Liriodendron tulipifera	logged	22.2	0.73	logged	20.0	0.86
Magnolia acuminata	logged	13.3	0.74	logged	23.8	0.39
Magnolia fraseri	logged	40.0	0.05	logged	43.9	0.05*
Nyssa sylvatica	logged	9.9	0.73	logged	13.3	0.50
Oxydendrum arboreum	logged	22.8	0.41	logged	11.7	0.80
Pinus pungens	logged	6.7	1.00	logged	6.7	1.00
Prunus pensylvanica	logged	33.3	0.03*	--	--	--
Prunus serotina	logged	56.9	0.02*	logged	50.0	0.02*
Quercus alba	unlogged	13.3	0.45	unlogged	13.3	0.48
Quercus coccinea	logged	6.7	1.00	logged	6.7	1.00
Quercus prinus	unlogged	7.7	1.00	unlogged	7.2	1.00
Quercus rubra	unlogged	26.1	0.58	unlogged	22.2	0.51
Robinia pseudoacacia	logged	15.4	0.70	logged	12.7	0.59
Sassafras albidum	logged	16.7	0.59	logged	5.1	1.00
Tilia americana	logged	30.8	0.34	logged	33.6	0.21
Tsuga canadensis	logged	51.5	0.19	logged	55.7	0.12

Table A.4. Correlation matrix between measured topographic and edaphic variables in historically logged and unlogged plots. Values are Pearson's correlation coefficients. One asterisk (*) indicates $P \leq 0.05$.

	elevation	slope	heat load	soil pH	soil CEC	soil K	soil Ca	soil Mg	soil P
slope	-0.08								
heat load	0.07	-0.94*							
soil pH	-0.55*	-0.07	0.03						
soil CEC	-0.05	-0.11	0.28	-0.26					
soil K	-0.52*	-0.20	0.19	0.54*	0.42*				
soil Ca	-0.28	-0.22	0.38	0.32	0.69*	0.75*			
soil Mg	-0.14	-0.40*	0.44*	0.35	0.56*	0.73*	0.83*		
soil P	0.51*	-0.13	0.11	-0.20	0.01	-0.03	0.08	0.19	
soil organic matter	0.24	-0.06	0.01	-0.41*	0.51*	0.02	0.12	0.18	-0.04

Table A.5. Change in species richness and abundance over 30 years in historically logged and unlogged plots. All understory includes herbs, shrubs, and seedlings. Understory abundance is the total percent cover of all species in each category and tree abundance is stem density (stems ha^{-1}). *P*-values represent differences in species richness or abundance across years within a disturbance type. One asterisk (*) indicates $P \leq 0.05$ and two asterisks (**) indicate $P \leq 0.01$.

	Herbs		Shrubs		Seedlings		All understory		Trees	
	logged	unlogged	logged	unlogged	logged	unlogged	logged	unlogged	logged	unlogged
Species richness										
Plots with increase	3	6	7	7	5	5	4	4	2	5
Plots with no change	1	1	1	3	4	1	1	2	6	2
Plots with decrease	11	8	7	5	6	9	10	9	7	8
1978 mean	18.2	24.5	5.3	4.8	8.8	10.5	32.3	39.9	9.7[1]	8[2]
2007 mean	14.3	21.9	4.9	5.3	8.7	10	27.9	37.4	8.9[1]	7.8[2]
Mean difference	-3.9	-2.7	-0.3	0.5	0.1	-0.5	-4.3	-2.5	-0.7[1]	-0.2[2]
P-value (paired *t*-test)	0.0004**	0.1	0.48	0.31	0.89	0.65	0.03*	0.31	0.08[1]	0.76[2]
Abundance										
Plots with increase	9	12	10	12	13	13	10	13	4	3
Plots with no change	0	0	0	1	0	0	0	0	2	0
Plots with decrease	6	3	5	2	2	2	5	2	9	12
1978 mean	23.7	27.4	3.2	5.6	2.4	5.9	29.3	39	700	411
2007 mean	34.4	60.7	6.7	11.5	5.6	13.6	46.7	85.8	555	399
Mean difference	10.6	33.3	3.5	5.9	3.2	7.8	17.4	46.9	-145	-11
P-value (paired *t*-test)	0.08	0.002**	0.08	0.009**	0.0006**	0.002**	0.02*	0.0003**	<0.0001**	0.77

[1] observed richness; rarefied values for logged plots are: 1978 mean = 6.3, 2007 mean = 6.2, mean difference = 0.1, *P*-value = 0.65.

[2] observed richness; rarefied values for unlogged plots are: 1978 mean = 5.8, 2007 mean = 5.8, mean difference = 0.04, *P*-value = 0.91.

Table A.6. Correlation between topographic and edaphic variables and change in species richness and compositional turnover. Understory includes herbs, shrubs, and seedlings < 1 m tall and trees includes trees ≥ 10 cm dbh. Values are Pearson's correlation coefficients. One asterisk (*) indicates $P \leq 0.05$ and two asterisks (**) indicate $P \leq 0.01$. All variables listed in Table 1 were tested for correlations with richness change and turnover, but only those variables with correlations significant at $P \leq 0.05$ are listed here.

	Richness change		Turnover (1 - Bray Curtis)		Turnover (1 - Chao Sørensen)	
Variable	Understory	Tree	Understory	Tree	Understory	Tree
Logging history						n/a
Elevation			-0.46*		-0.41*	n/a
soil pH			0.37*	0.41*		n/a
soil CEC				-0.57**		n/a
soil organic matter						n/a
1978 understory cover		n/a	-0.49**	n/a	-0.45*	n/a
1978 understory richness		n/a		n/a		n/a
1978 tree richness	n/a	-0.45**	n/a		n/a	n/a

Table A.7. Correlation matrix between topographic and edaphic variables and understory and tree community attributes. Values are Pearson's correlation coefficients. One asterisk (*) represents significant correlation at $P \leq 0.05$.

	understory richness		understory % cover		tree richness		tree basal area (m^2ha^{-1})	
Variable	1978	2007	1978	2007	1978	2007	1978	2007
elevation	-0.38*	-0.31	0.27	0.08	-0.20	-0.07	-0.15	0.05
slope	0.07	0.02	0.16	0.14	0.19	0.04	0.18	-0.12
heat load	-0.08	-0.09	-0.19	-0.23	-0.24	-0.05	-0.23	0.20
soil pH	0.75*	0.58*	0.28	0.15	0.08	0.17	-0.11	-0.15
soil CEC	-0.12	-0.12	-0.35	-0.34	0.08	0.01	-0.002	0.46*
soil K	0.51*	0.50*	-0.07	0.11	-0.01	-0.06	-0.07	-0.02
soil Ca	0.37*	0.26	-0.05	-0.06	-0.12	-0.04	-0.06	0.29
soil Mg	0.24	0.21	0	-0.11	-0.20	-0.1	0.01	0.34
soil P	-0.16	0.01	0.04	0.11	-0.39*	-0.21	-0.14	0.02
soil organic matter	-0.34	-0.28	-0.29	-0.32	0.13	-0.09	0.19	0.17

Table A.8. Among-community similarity (multivariate dispersion) in logged and unlogged plots in 1978 and 2007.

Mean distance of plots within a group from the group centroid (multivariate dispersion) in multivariate space is defined by Bray-Curtis dissimilarity. The pseudo *F*-statistics and *P*-values were generated from permutational ANOVA tests of differences in among-community similarity between 1978 and 2007. Understory frequency is an abundance measure based on the percentage of the 25 subplots within a 20 m × 50 m forest plot in which each species occurred. Understory cover is an abundance measure based on the average of the cover values for an individual species within a 20 m × 50 m forest plot. Tree density is an abundance measure based on the number of individual trees of a species within a 20 m × 50 m forest plot.

		Mean ± SE distance to centroid			
Abundance variable	Group	1978	2007	*F*	*P*-value
understory frequency	logged	53.05 ± 2.14	51.68 ± 2.39	0.18	0.74
	unlogged	50.92 ± 2.09	49.59 ± 2.21	0.19	0.69
understory cover	logged	58.01 ± 2.02	57.44 ± 2.14	0.04	0.88
	unlogged	58.83 ± 1.44	55.57 ± 2.53	1.25	0.34
tree density	logged	51.70 ± 2.22	50.87 ± 2.41	0.06	0.82
	unlogged	51.16 ± 2.58	47.72 ± 1.87	1.17	0.35

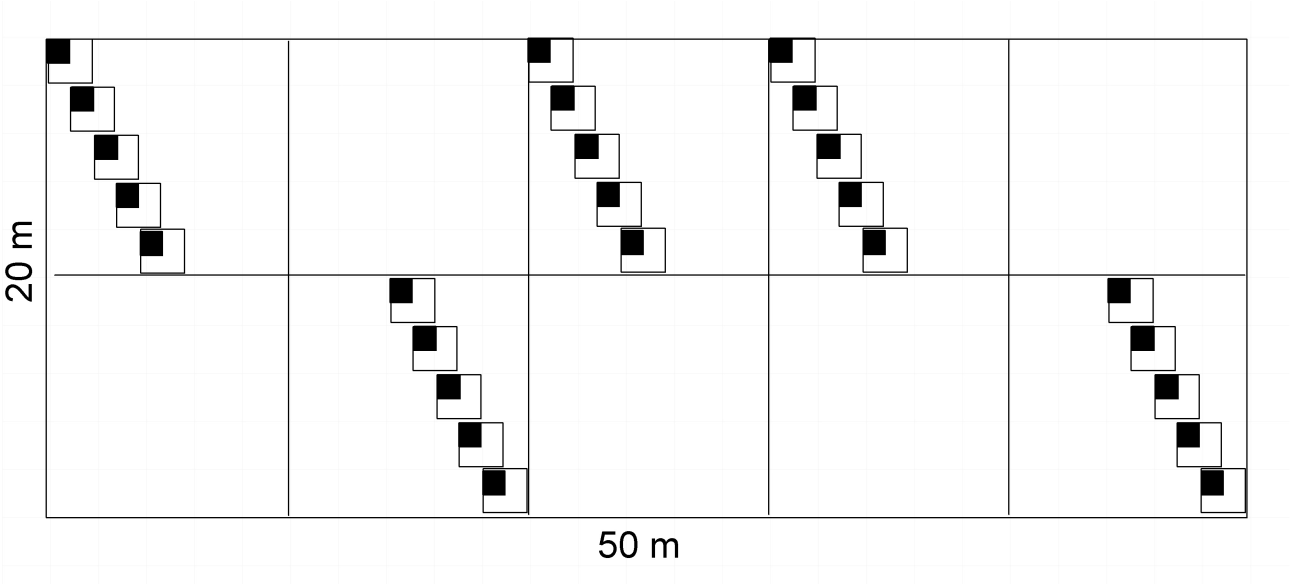

Figure A.1. Layout of 20 m × 50 m forest plots in Great Smoky Mountains National Park.

Trees ≥ 10 cm dbh were measured in the entire plot. Understory (< 1 m tall) woody shrubs and seedlings were recorded in 2 m × 2 m subplots, represented by white boxes. Understory herbaceous species were recorded in 1 m × 1 m subplots, represented by black boxes, nested within the woody species subplots.

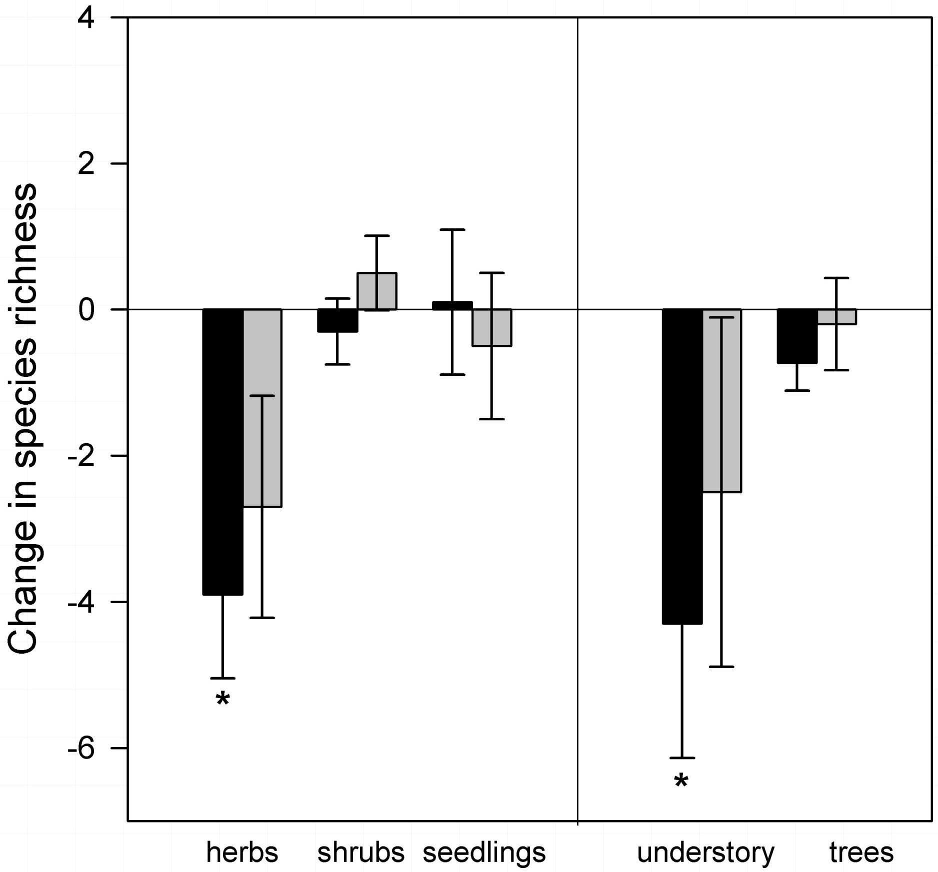

Figure A.2. Mean (±SE) change in species richness over 30 years in historically logged (black bars) and unlogged (gray bars) plots.

All understory includes herbs, shrubs, and seedlings < 1 m tall and trees includes trees ≥ 10 cm dbh. Asterisk (*) indicates significant differences at $P < 0.05$.

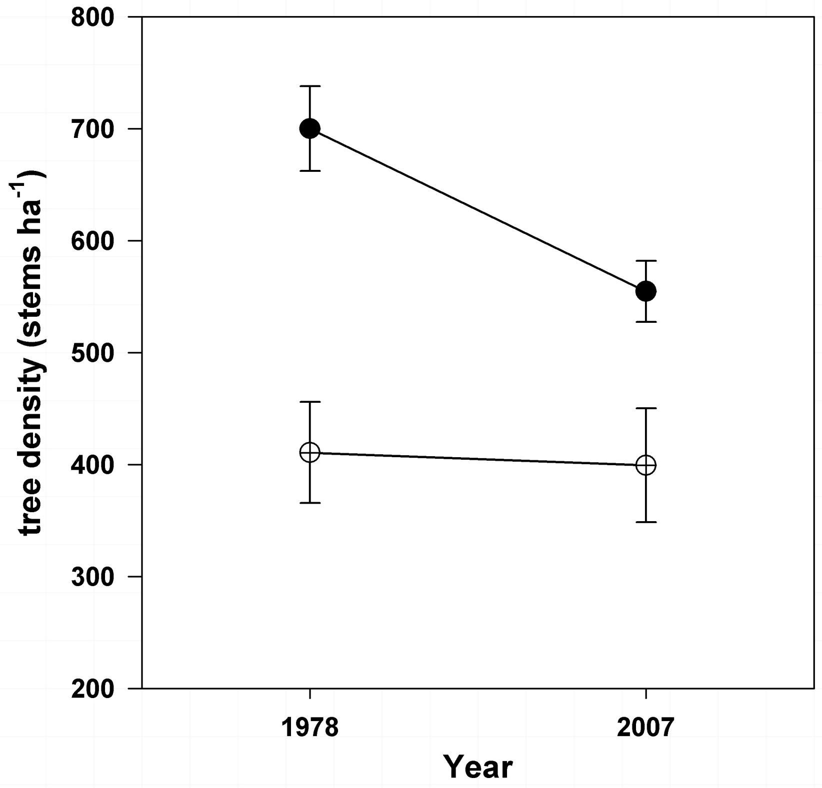

Figure A.3. Change in mean (±SE) tree (≥ 10 cm dbh) density over 30 years in historically logged and unlogged plots.

Filled circles represent logged plots and unfilled circles represent unlogged plots.

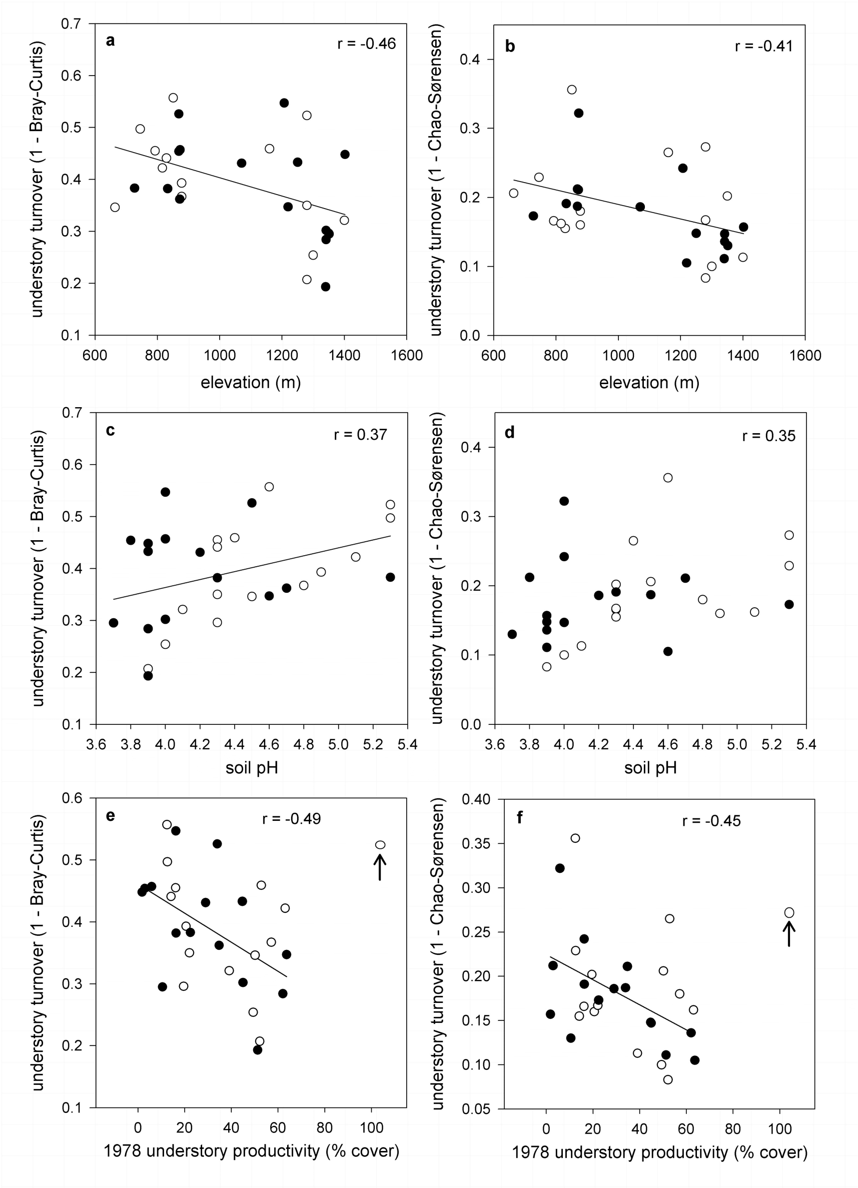

Figure A.4. Correlation between two measures of understory temporal turnover across 30 years and elevation (a, b), soil pH (c, d), and 1978 understory productivity measured as total percent cover (e, f).

Regression lines indicate significant correlations at $P < 0.05$. Filled circles represent logged plots and unfilled circles represent unlogged plots. Arrows in panels e and f point to an outlying data point that was excluded from the correlation.

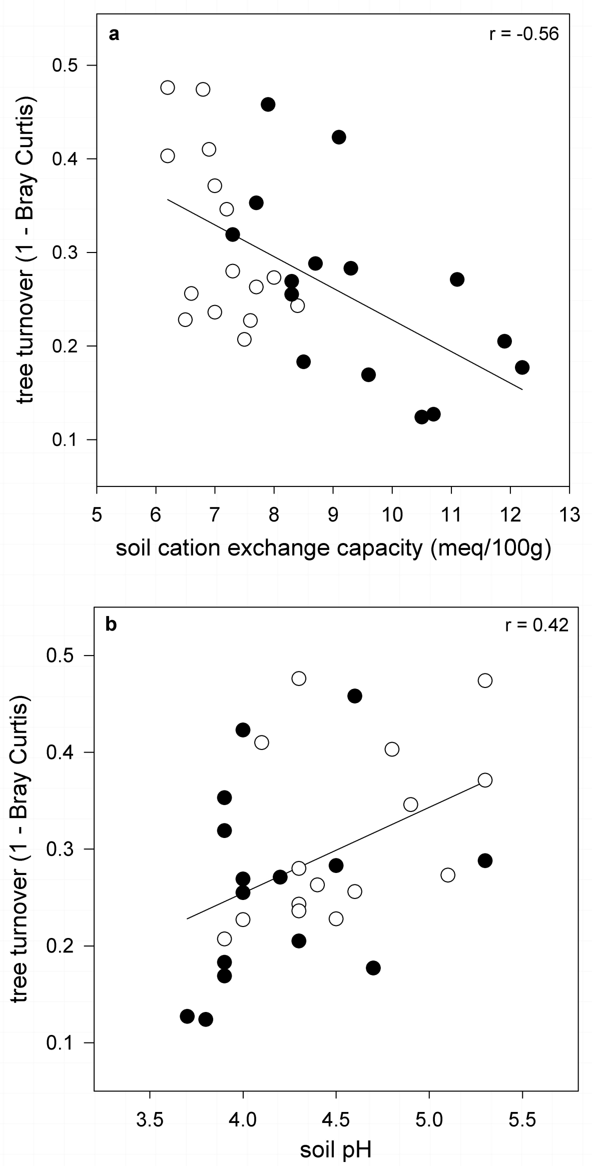

Figure A.5. Correlation between tree temporal turnover and soil cation exchange capacity (a) and soil pH (b).

Regression lines indicate significant correlations at $P < 0.05$. Filled circles represent logged plots and unfilled circles represent unlogged plots.

APPENDIX B

Table B.1. Number of logged (n = 15) and unlogged (n = 15) plots in which each understory species was recorded in 1978.

		# plots present	
Family	Species	logged	unlogged
Aceraceae	*Acer pensylvanicum*	11	10
Aceraceae	*Acer rubrum*	12	8
Aceraceae	*Acer saccharum*	7	10
Aceraceae	*Acer spicatum*	0	2
Apiaceae	*Osmorhiza claytonii*	2	6
Apiaceae	*Osmorhiza longistylis*	2	0
Apiaceae	*Sanicula* spp.	2	4
Apiaceae	*Thaspium trifoliatum*	0	1
Aquifoliaceae	*Ilex montana*	2	4
Aquifoliaceae	*Ilex opaca*	1	2
Araceae	*Arisaema triphyllum*	3	11
Araliaceae	*Panax quinquefolius*	1	2
Aristolochiaceae	*Aristolochia macrophylla*	6	2
Aristolochiaceae	*Asarum canadense*	1	0
Aspleniaceae	*Asplenium platyneuron*	2	0
Asteraceae	*Achillea millefolium var. occidentalis*	0	1
Asteraceae	*Ageratina altissima*	9	8
Asteraceae	*Aster* spp.	0	2
Asteraceae	*Eupatorium maculatum*	2	0
Asteraceae	*Eupatorium purpureum*	1	3
Asteraceae	*Eurbyia divaricatus*	10	12
Asteraceae	*Helianthus decapetalus*	1	0
Asteraceae	*Prenanthes* spp.	7	10
Asteraceae	*Solidago curtisii*	10	13
Asteraceae	*Solidago* spp.	1	3
Asteraceae	*Symphyotrichum lateriflorum var. lateriflorum*	0	1
Asteraceae	*Symphyotrichum lowrieanum*	3	0
Asteraceae	*Symphyotrichum undulatum*	0	1
Balsaminaceae	*Impatiens pallida*	2	3
Berberidaceae	*Caulophyllum thalictroides*	5	7
Berberidaceae	*Diphylleia cymosa*	3	1
Betulaceae	*Betula alleghaniensis var. alleghaniensis*	8	2
Betulaceae	*Betula lenta*	2	2
Brassicaceae	*Cardamine concatenata*	0	1
Brassicaceae	*Cardamine diphylla*	4	7
Calycanthaceae	*Calycanthus floridus var. glaucus*	0	8
Campanulaceae	*Campanula divaricata*	1	0
Caprifoliaceae	*Viburnum acerifolium*	3	5
Caprifoliaceae	*Viburnum lantana*	2	2
Caryophyllaceae	*Silene stellata*	1	2
Caryophyllaceae	*Stellaria pubera*	10	11

Table B.1. Continued.

		# plots present	
Family	Species	logged	unlogged
Celastraceae	*Euonymus americana*	3	2
Celastraceae	*Euonymus obovata*	2	1
Clethraceae	*Clethra acuminata*	0	1
Cornaceae	*Cornus alternifolia*	3	3
Cornaceae	*Cornus florida*	3	6
Cuscutaceae	*Cuscuta* spp.	2	1
Cyperaceae	*Carex debilis*	0	1
Cyperaceae	*Carex pensylvanica*	1	0
Cyperaceae	*Carex plantaginea*	2	0
Cyperaceae	*Carex* spp.	4	3
Dennstaedtiaceae	*Dennstaedtia punctilobula*	0	2
Diapensiaceae	*Galax urceolata*	2	2
Dioscoreaceae	*Dioscorea villosa*	1	8
Dryopteridaceae	*Athyrium filix-femina ssp. asplenioides*	4	3
Dryopteridaceae	*Cystopteris protrusa*	0	2
Dryopteridaceae	*Deparia acrostichoides*	3	7
Dryopteridaceae	*Dryopteris intermedia*	12	11
Dryopteridaceae	*Dryopteris marginalis*	3	0
Dryopteridaceae	*Polystichum acrostichoides*	8	9
Ericaceae	*Gaylussacia ursina*	2	3
Ericaceae	*Kalmia latifolia*	2	1
Ericaceae	*Leucothoe fontanesiana*	3	0
Ericaceae	*Oxydendrum arboreum*	2	2
Ericaceae	*Rhododendron calendulaceum*	1	2
Ericaceae	*Rhododendron maximum*	7	1
Ericaceae	*Vaccinium corymbosum*	1	0
Ericaceae	*Vaccinium erythrocarpum*	3	0
Ericaceae	*Vaccinium pallidum*	0	1
Ericaceae	*Vaccinium stamineum*	0	1
Fabaceae	*Amphicarpaea bracteata*	1	5
Fabaceae	*Cercis canadensis*	0	1
Fabaceae	*Desmodium* spp.	1	0
Fabaceae	*Robinia pseudoacacia*	4	3
Fagaceae	*Castanea dentata*	1	5
Fagaceae	*Fagus grandifolia*	4	5
Fagaceae	*Quercus alba*	0	1
Fagaceae	*Quercus prinus*	1	2
Fagaceae	*Quercus rubra*	4	11
Gentianaceae	*Gentiana decora*	0	1
Hamamelidaceae	*Hamamelis virginiana*	3	5
Hippocastanaceae	*Aesculus flava*	8	9
Hydrangeaceae	*Hydrangea arborescens*	6	5
Hydrophyllaceae	*Hydrophyllum canadense*	1	0
Hydrophyllaceae	*Hydrophyllum virginianum var. atranthum*	0	1
Iridaceae	*Iris cristata*	0	1

Table B.1. Continued.

		# plots present	
Family	Species	logged	unlogged
Juglandaceae	*Carya cordiformis*	1	3
Juglandaceae	*Carya glabra*	3	2
Juncaceae	*Luzula* spp.	0	1
Lamiaceae	*Collinsonia canadensis*	0	9
Lamiaceae	*Monarda didyma*	0	1
Lamiaceae	*Pycnanthemum montanum*	1	1
Lamiaceae	*Stachys clingmanii*	0	1
Lauraceae	*Lindera benzoin*	4	2
Lauraceae	*Sassafras albidum*	3	4
Liliaceae	*Allium tricoccum*	1	1
Liliaceae	*Clintonia umbellulata*	3	2
Liliaceae	*Lilium superbum*	0	1
Liliaceae	*Maianthemum racemosum ssp. racemosum*	7	3
Liliaceae	*Medeola virginiana*	3	7
Liliaceae	*Melanthium parviflorum*	0	2
Liliaceae	*Polygonatum biflorum*	10	6
Liliaceae	*Polygonatum pubescens*	0	2
Liliaceae	*Prosartes lanuginosa*	6	8
Liliaceae	*Stenanthium gramineum*	1	0
Liliaceae	*Trillium* spp.	3	7
Liliaceae	*Uvularia grandiflora*	0	4
Liliaceae	*Uvularia perfoliata*	0	2
Liliaceae	*Uvularia sessilifolia*	1	2
Liliaceae	*Veratrum viride*	0	1
Lycopodiaceae	*Huperzia lucidula*	4	0
Lycopodiaceae	*Lycopodium obscurum*	1	0
Magnoliaceae	*Liriodendron tulipifera*	4	9
Magnoliaceae	*Magnolia acuminata*	3	5
Magnoliaceae	*Magnolia fraseri*	5	7
Monotropaceae	*Monotropa uniflora*	0	1
Nyssaceae	*Nyssa sylvatica*	0	4
Oleaceae	*Fraxinus americana*	3	6
Onagraceae	*Circaea alpina*	0	1
Onagraceae	*Circaea lutetiana ssp. canadensis*	0	1
Ophioglossaceae	*Botrychium dissectum*	1	1
Ophioglossaceae	*Botrychium virginianum*	2	4
Orchidaceae	*Galearis spectabilis*	0	1
Orchidaceae	*Goodyera pubescens*	1	2
Osmundaceae	*Osmunda cinnamomea*	0	1
Osmundaceae	*Osmunda claytoniana*	6	0
Oxalidaceae	*Oxalis montana*	4	2
Papaveraceae	*Sanguinaria canadensis*	2	4
Pinaceae	*Tsuga canadensis*	7	5
Poaceae	*Brachyelytrum erectum*	1	0
Poaceae	*Cinna latifolia*	1	1

Table B.1. Continued.

Family	Species	# plots present logged	 unlogged
Poaceae	*Danthonia compressa*	0	1
Poaceae	*Dichanthelium boscii*	0	1
Poaceae	*Dichanthelium dichotomum var. dichotomum*	1	0
Poaceae	*Panicum* spp.	1	0
Poaceae	*Poa* spp.	2	1
Primulaceae	*Lysimachia quadrifolia*	0	1
Pteridaceae	*Adiantum pedatum*	0	3
Pteridaceae	*Cheilanthes* spp.	0	1
Pyrolaceae	*Chimaphila maculata*	0	3
Ranunculaceae	*Actaea pachypoda*	3	0
Ranunculaceae	*Actaea racemosa var. racemosa*	5	7
Ranunculaceae	*Anemone quinquefolia*	2	2
Ranunculaceae	*Hepatica nobilis*	1	0
Ranunculaceae	*Ranunculus recurvatus*	0	1
Ranunculaceae	*Thalictrum clavatum*	0	2
Ranunculaceae	*Thalictrum dioicum*	0	2
Ranunculaceae	*Thalictrum pubescens*	0	1
Ranunculaceae	*Thalictrum thalictroides*	1	4
Ranunculaceae	*Trautvetteria caroliniensis*	0	1
Rosaceae	*Amelanchier arborea*	4	3
Rosaceae	*Aruncus dioicus*	0	1
Rosaceae	*Porteranthus stipulatus*	1	0
Rosaceae	*Porteranthus trifoliatus*	0	1
Rosaceae	*Potentilla simplex*	0	1
Rosaceae	*Prunus pensylvanica*	2	0
Rosaceae	*Prunus serotina*	12	4
Rosaceae	*Rubus* spp.	11	5
Rubiaceae	*Galium lanceolatum*	2	3
Rubiaceae	*Galium triflorum*	2	7
Rubiaceae	*Houstonia purpurea var. purpurea*	1	1
Rubiaceae	*Houstonia serpyllifolia*	1	1
Rubiaceae	*Mitchella repens*	6	5
Santalaceae	*Pyrularia pubera*	2	6
Saxifragaceae	*Astilbe biternata*	1	0
Saxifragaceae	*Chrysosplenium americanum*	0	1
Saxifragaceae	*Mitella diphylla*	1	0
Saxifragaceae	*Saxifraga michauxii*	0	1
Saxifragaceae	*Tiarella cordifolia*	7	10
Smilacaceae	*Smilax glauca*	1	1
Smilacaceae	*Smilax hugeri*	0	2
Smilacaceae	*Smilax rotundifolia*	10	6
Smilacaceae	*Smilax* spp.	0	1
Smilacaceae	*Smilax tamnoides*	0	2
Styracaceae	*Halesia tetraptera var. monticola*	9	11
Thelypteridaceae	*Phegopteris hexagonoptera*	7	10

Table B.1. Continued.

Family	Species	# plots present logged	unlogged
Tiliaceae	*Tilia americana*	4	4
Urticaceae	*Laportea canadensis*	7	8
Violaceae	*Viola blanda*	7	6
Violaceae	*Viola canadensis*	6	6
Violaceae	*Viola hastata*	5	10
Violaceae	*Viola macloskeyi ssp. pallens*	1	0
Violaceae	*Viola rotundifolia*	6	6
Violaceae	*Viola* spp.	3	8
Vitaceae	*Parthenocissus quinquefolia*	3	5
Vitaceae	*Vitis* spp.	6	6

Table B.2. Number of logged (n = 15) and unlogged (n = 15) plots in which each tree (≥ 10 cm dbh) species was recorded in 1978.

		# plots present	
Family	Species	logged	unlogged
Aceraceae	*Acer pensylvanicum*	6	3
Aceraceae	*Acer rubrum*	11	7
Aceraceae	*Acer saccharum*	6	9
Aquifoliaceae	*Ilex montana*	2	0
Aquifoliaceae	*Ilex opaca*	1	0
Betulaceae	*Betula alleghaniensis var. alleghaniensis*	10	9
Betulaceae	*Betula lenta*	11	5
Cornaceae	*Cornus florida*	1	5
Ericaceae	*Oxydendrum arboreum*	5	3
Fabaceae	*Robinia pseudoacacia*	4	3
Fagaceae	*Fagus grandifolia*	5	7
Fagaceae	*Quercus alba*	0	2
Fagaceae	*Quercus coccinea*	1	0
Fagaceae	*Quercus prinus*	2	2
Fagaceae	*Quercus rubra*	6	6
Hamamelidaceae	*Hamamelis virginiana*	2	1
Hippocastanaceae	*Aesculus flava*	3	7
Juglandaceae	*Carya* spp.	2	4
Lauraceae	*Sassafras albidum*	3	2
Magnoliaceae	*Liriodendron tulipifera*	4	7
Magnoliaceae	*Magnolia acuminata*	3	2
Magnoliaceae	*Magnolia fraseri*	7	3
Nyssaceae	*Nyssa sylvatica*	2	1
Oleaceae	*Fraxinus americana*	1	4
Pinaceae	*Pinus pungens*	1	0
Pinaceae	*Tsuga canadensis*	13	7
Rosaceae	*Prunus pensylvanica*	5	0
Rosaceae	*Prunus serotina*	10	3
Styracaceae	*Halesia tetraptera var. monticola*	12	12
Tiliaceae	*Tilia americana*	6	6

APPENDIX C

Table C.1. Number of logged (n = 15) and unlogged (n = 15) plots in which each understory species was recorded in 2007.

		# plots present	
Family	Species	logged	unlogged
Aceraceae	*Acer pensylvanicum*	8	14
Aceraceae	*Acer rubrum*	14	11
Aceraceae	*Acer saccharum*	6	10
Aceraceae	*Acer spicatum*	2	1
Apiaceae	*Osmorhiza claytonii*	1	4
Apiaceae	*Osmorhiza longistylis*	1	0
Apiaceae	*Thaspium trifoliatum*	0	1
Aquifoliaceae	*Ilex montana*	2	0
Aquifoliaceae	*Ilex opaca*	1	2
Araceae	*Arisaema triphyllum*	2	8
Araliaceae	*Panax quinquefolius*	0	2
Aristolochiaceae	*Aristolochia macrophylla*	7	4
Aristolochiaceae	*Asarum canadense*	1	0
Asteraceae	*Ageratina altissima*	6	6
Asteraceae	*Aster* spp.	1	0
Asteraceae	*Eupatorium maculatum*	0	1
Asteraceae	*Eupatorium purpureum*	1	5
Asteraceae	*Eurbyia divaricatus*	9	13
Asteraceae	*Helianthus decapetalus*	0	3
Asteraceae	*Prenanthes* spp.	7	7
Asteraceae	*Solidago curtisii*	9	12
Asteraceae	*Solidago* spp.	0	1
Asteraceae	*Symphyotrichum acuminata*	0	1
Asteraceae	*Symphyotrichum lowrieanum*	1	0
Balsaminaceae	*Impatiens pallida*	0	4
Berberidaceae	*Caulophyllum thalictroides*	5	5
Berberidaceae	*Diphylleia cymosa*	0	1
Betulaceae	*Betula alleghaniensis var. alleghaniensis*	3	0
Betulaceae	*Betula lenta*	0	6
Brassicaceae	*Cardamine diphylla*	4	2
Calycanthaceae	*Calycanthus floridus var. glaucus*	2	7
Caprifoliaceae	*Viburnum acerifolium*	2	1
Caprifoliaceae	*Viburnum lantana*	1	3
Caryophyllaceae	*Stellaria pubera*	10	11
Celastraceae	*Euonymus americana*	3	3
Celastraceae	*Euonymus obovata*	1	0
Clethraceae	*Clethra acuminata*	0	1
Cornaceae	*Cornus alternifolia*	1	1
Cuscutaceae	*Cuscuta* spp.	0	1
Cyperaceae	*Carex debilis*	1	0
Cyperaceae	*Carex digitalis*	0	1

Table C.1. Continued.

		# plots present	
Family	Species	logged	unlogged
Cyperaceae	*Carex pensylvanica*	0	1
Cyperaceae	*Carex plantaginea*	2	1
Cyperaceae	*Carex* spp.	3	2
Dennstaedtiaceae	*Dennstaedtia punctilobula*	0	1
Diapensiaceae	*Galax urceolata*	2	2
Dioscoreaceae	*Dioscorea villosa*	0	3
Dryopteridaceae	*Athyrium filix-femina ssp. asplenioides*	2	7
Dryopteridaceae	*Deparia acrostichoides*	5	6
Dryopteridaceae	*Dryopteris intermedia*	12	10
Dryopteridaceae	*Polystichum acrostichoides*	8	10
Ericaceae	*Gaylussacia ursina*	2	2
Ericaceae	*Kalmia latifolia*	2	1
Ericaceae	*Leucothoe fontanesiana*	3	0
Ericaceae	*Oxydendrum arboreum*	2	3
Ericaceae	*Rhododendron calendulaceum*	0	1
Ericaceae	*Rhododendron maximum*	8	2
Ericaceae	*Vaccinium erythrocarpum*	2	0
Ericaceae	*Vaccinium pallidum*	0	4
Fabaceae	*Amphicarpaea bracteata*	2	4
Fabaceae	*Robinia pseudoacacia*	3	2
Fagaceae	*Castanea dentata*	0	2
Fagaceae	*Fagus grandifolia*	5	6
Fagaceae	*Quercus alba*	1	2
Fagaceae	*Quercus prinus*	3	3
Fagaceae	*Quercus rubra*	7	11
Hamamelidaceae	*Hamamelis virginiana*	1	3
Hippocastanaceae	*Aesculus flava*	7	7
Hydrangeaceae	*Hydrangea arborescens*	2	5
Hydrophyllaceae	*Hydrophyllum canadense*	1	0
Iridaceae	*Iris cristata*	0	1
Juglandaceae	*Carya cordiformis*	4	5
Juglandaceae	*Carya glabra*	2	1
Juncaceae	*Luzula* spp.	1	0
Lamiaceae	*Collinsonia canadensis*	0	1
Lamiaceae	*Monarda clinopodia*	0	1
Lamiaceae	*Monarda didyma*	2	1
Lamiaceae	*Pycnanthemum montanum*	1	0
Lamiaceae	*Stachys clingmanii*	0	2
Lauraceae	*Lindera benzoin*	1	2
Lauraceae	*Sassafras albidum*	4	3
Liliaceae	*Allium tricoccum*	1	1
Liliaceae	*Clintonia umbellulata*	1	0
Liliaceae	*Lilium superbum*	0	1
Liliaceae	*Maianthemum canadense*	1	1
Liliaceae	*Maianthemum racemosum ssp. racemosum*	9	3

Table C.1. Continued.

Family	Species	# plots present logged	unlogged
Liliaceae	*Medeola virginiana*	3	5
Liliaceae	*Melanthium parviflorum*	0	1
Liliaceae	*Polygonatum biflorum*	7	10
Liliaceae	*Prosartes lanuginosa*	7	9
Liliaceae	*Streptopus roseus*	0	1
Liliaceae	*Trillium* spp.	4	13
Liliaceae	*Veratrum viride*	0	1
Lycopodiaceae	*Huperzia lucidula*	4	1
Magnoliaceae	*Liriodendron tulipifera*	6	8
Magnoliaceae	*Magnolia acuminata*	2	2
Magnoliaceae	*Magnolia fraseri*	7	3
Monotropaceae	*Monotropa uniflora*	0	1
Nyssaceae	*Nyssa sylvatica*	0	2
Oleaceae	*Fraxinus americana*	3	8
Onagraceae	*Circaea alpina*	0	2
Ophioglossaceae	*Botrychium virginianum*	2	1
Orchidaceae	*Galearis spectabilis*	0	1
Orchidaceae	*Goodyera pubescens*	2	5
Orchidaceae	*Platanthera* spp.	1	0
Osmundaceae	*Osmunda cinnamomea*	0	2
Oxalidaceae	*Oxalis montana*	3	4
Papaveraceae	*Sanguinaria canadensis*	2	3
Phytolaccaceae	*Phytolacca americana*	0	1
Pinaceae	*Tsuga canadensis*	7	5
Poaceae	*Cinna latifolia*	0	1
Poaceae	*Danthonia compressa*	1	0
Poaceae	*Dichanthelium boscii*	0	1
Poaceae	*Dichanthelium dichotomum var. dichotomum*	1	0
Primulaceae	*Lysimachia quadrifolia*	1	1
Pteridaceae	*Adiantum pedatum*	0	3
Ranunculaceae	*Actaea pachypoda*	1	0
Ranunculaceae	*Actaea racemosa var. racemosa*	3	7
Ranunculaceae	*Anemone quinquefolia*	0	1
Ranunculaceae	*Hepatica nobilis*	1	0
Ranunculaceae	*Thalictrum clavatum*	0	3
Ranunculaceae	*Thalictrum dioicum*	0	2
Ranunculaceae	*Thalictrum thalictroides*	1	6
Ranunculaceae	*Trautvetteria caroliniensis*	0	1
Rosaceae	*Amelanchier arborea*	5	3
Rosaceae	*Aruncus dioicus*	0	1
Rosaceae	*Potentilla simplex*	0	1
Rosaceae	*Prunus pensylvanica*	1	0
Rosaceae	*Prunus serotina*	11	10
Rosaceae	*Rubus* spp.	10	10
Rubiaceae	*Galium lanceolatum*	0	3

Table C.1. Continued.

		# plots present	
Family	Species	logged	unlogged
Rubiaceae	*Galium triflorum*	1	4
Rubiaceae	*Houstonia purpurea var. purpurea*	0	4
Rubiaceae	*Mitchella repens*	7	5
Santalaceae	*Pyrularia pubera*	3	6
Saxifragaceae	*Chrysosplenium americanum*	0	2
Saxifragaceae	*Saxifraga michauxii*	2	0
Saxifragaceae	*Tiarella cordifolia*	7	10
Smilacaceae	*Smilax glauca*	4	8
Smilacaceae	*Smilax hugeri*	1	0
Smilacaceae	*Smilax rotundifolia*	9	10
Smilacaceae	*Smilax* spp.	1	1
Smilacaceae	*Smilax tamnoides*	0	1
Styracaceae	*Halesia tetraptera var. monticola*	12	12
Thelypteridaceae	*Phegopteris hexagonoptera*	1	6
Thelypteridaceae	*Thelypteris noveboracensis*	2	5
Tiliaceae	*Tilia americana*	3	5
Urticaceae	*Laportea canadensis*	8	10
Violaceae	*Viola blanda*	2	4
Violaceae	*Viola canadensis*	8	8
Violaceae	*Viola hastata*	1	9
Violaceae	*Viola pedata*	0	1
Violaceae	*Viola rotundifolia*	5	5
Violaceae	*Viola* spp.	6	10
Vitaceae	*Parthenocissus quinquefolia*	2	4
Vitaceae	*Vitis* spp.	6	4

Table C.2. Number of logged (n = 15) and unlogged (n = 15) plots in which each tree (≥ 10 cm dbh) species was recorded in 2007.

		# plots present	
Family	Species	logged	unlogged
Aceraceae	*Acer pensylvanicum*	6	5
Aceraceae	*Acer rubrum*	13	8
Aceraceae	*Acer saccharum*	9	13
Aquifoliaceae	*Ilex montana*	1	0
Aquifoliaceae	*Ilex opaca*	1	0
Betulaceae	*Betula alleghaniensis var. alleghaniensis*	7	7
Betulaceae	*Betula lenta*	10	5
Cornaceae	*Cornus florida*	0	2
Ericaceae	*Oxydendrum arboreum*	3	2
Fabaceae	*Robinia pseudoacacia*	3	1
Fagaceae	*Castanea dentata*	0	1
Fagaceae	*Fagus grandifolia*	5	7
Fagaceae	*Quercus alba*	0	2
Fagaceae	*Quercus coccinea*	1	0
Fagaceae	*Quercus prinus*	2	2
Fagaceae	*Quercus rubra*	4	5
Hippocastanaceae	*Aesculus flava*	3	9
Juglandaceae	*Carya* spp.	2	4
Lauraceae	*Sassafras albidum*	1	1
Magnoliaceae	*Liriodendron tulipifera*	4	7
Magnoliaceae	*Magnolia acuminata*	5	2
Magnoliaceae	*Magnolia fraseri*	8	3
Nyssaceae	*Nyssa sylvatica*	2	0
Oleaceae	*Fraxinus americana*	1	2
Pinaceae	*Pinus pungens*	1	0
Pinaceae	*Tsuga canadensis*	14	8
Rosaceae	*Prunus serotina*	10	3
Styracaceae	*Halesia tetraptera var. monticola*	12	12
Tiliaceae	*Tilia americana*	6	5

APPENDIX D

Table D.1. Understory species recorded in only logged or only unlogged plots. The # plots present columns indicate the number of plots in which the species was recorded in the 1978 and 2007 survey periods combined.

		# plots present	
Family	Species	logged	unlogged
Apiaceae	*Osmorhiza longistylis*	2	0
Apiaceae	*Thaspium trifoliatum*	0	1
Aristolochiaceae	*Asarum canadense*	1	0
Aspleniaceae	*Asplenium platyneuron*	2	0
Asteraceae	*Achillea millefolium var. occidentalis*	0	1
Asteraceae	*Symphyotrichum acuminata*	0	1
Asteraceae	*Symphyotrichum lateriflorum var. lateriflorum*	0	1
Asteraceae	*Symphyotrichum lowrieanum*	3	0
Asteraceae	*Symphyotrichum undulatum*	0	1
Brassicaceae	*Cardamine concatenata*	0	1
Campanulaceae	*Campanula divaricata*	1	0
Clethraceae	*Clethra acuminata*	0	2
Cyperaceae	*Carex digitalis*	0	1
Dennstaedtiaceae	*Dennstaedtia punctilobula*	0	2
Dryopteridaceae	*Cystopteris protrusa*	0	2
Dryopteridaceae	*Dryopteris marginalis*	3	0
Ericaceae	*Leucothoe fontanesiana*	3	0
Ericaceae	*Vaccinium corymbosum*	1	0
Ericaceae	*Vaccinium erythrocarpum*	4	0
Ericaceae	*Vaccinium pallidum*	0	4
Ericaceae	*Vaccinium stamineum*	0	1
Fabaceae	*Cercis canadensis*	0	1
Fabaceae	*Desmodium* spp.	1	0
Gentianaceae	*Gentiana decora*	0	1
Hydrophyllaceae	*Hydrophyllum canadense*	1	0
Hydrophyllaceae	*Hydrophyllum virginianum var. atranthum*	0	1
Iridaceae	*Iris cristata*	0	1
Lamiaceae	*Collinsonia canadensis*	0	9
Lamiaceae	*Monarda clinopodia*	0	1
Lamiaceae	*Stachys clingmanii*	0	2
Liliaceae	*Lilium superbum*	0	1
Liliaceae	*Melanthium parviflorum*	0	2
Liliaceae	*Polygonatum pubescens*	0	2
Liliaceae	*Stenanthium gramineum*	1	0
Liliaceae	*Streptopus roseus*	0	1
Liliaceae	*Uvularia grandiflora*	0	4

Table D.1. Continued.

		# plots present	
Family	Species	logged	unlogged
Liliaceae	*Uvularia perfoliata*	0	2
Liliaceae	*Veratrum viride*	0	1
Lycopodiaceae	*Lycopodium obscurum*	1	0
Monotropaceae	*Monotropa uniflora*	0	2
Nyssaceae	*Nyssa sylvatica*	0	4
Onagraceae	*Circaea alpina*	0	2
Onagraceae	*Circaea lutetiana ssp. canadensis*	0	1
Orchidaceae	*Galearis spectabilis*	0	2
Orchidaceae	*Platanthera* spp.	1	0
Osmundaceae	*Osmunda cinnamomea*	0	2
Osmundaceae	*Osmunda claytoniana*	6	0
Phytolaccaceae	*Phytolacca americana*	0	1
Poaceae	*Brachyelytrum erectum*	1	0
Poaceae	*Dichanthelium boscii*	0	1
Poaceae	*Dichanthelium dichotomum var. dichotomum*	1	0
Poaceae	*Panicum* spp.	1	0
Pteridaceae	*Adiantum pedatum*	0	4
Pteridaceae	*Cheilanthes* spp.	0	1
Pyrolaceae	*Chimaphila maculata*	0	3
Ranunculaceae	*Actaea pachypoda*	3	0
Ranunculaceae	*Hepatica nobilis*	1	0
Ranunculaceae	*Ranunculus recurvatus*	0	1
Ranunculaceae	*Thalictrum clavatum*	0	3
Ranunculaceae	*Thalictrum dioicum*	0	2
Ranunculaceae	*Thalictrum pubescens*	0	1
Ranunculaceae	*Trautvetteria caroliniensis*	0	1
Rosaceae	*Aruncus dioicus*	0	2
Rosaceae	*Porteranthus stipulatus*	1	0
Rosaceae	*Porteranthus trifoliatus*	0	1
Rosaceae	*Potentilla simplex*	0	1
Rosaceae	*Prunus pensylvanica*	2	0
Saxifragaceae	*Astilbe biternata*	1	0
Saxifragaceae	*Chrysosplenium americanum*	0	2
Saxifragaceae	*Mitella diphylla*	1	0
Smilacaceae	*Smilax tamnoides*	0	2
Violaceae	*Viola macloskeyi ssp. pallens*	1	0
Violaceae	*Viola pedata*	0	1

Table D.2. Tree (≥ 10 cm) species recorded in only logged or only unlogged plots. The # plots present columns indicate the number of plots in which the species was recorded in the 1978 and 2007 survey periods combined.

		# plots present	
Family	Species	logged	unlogged
Aquifoliaceae	*Ilex montana*	2	0
Aquifoliaceae	*Ilex opaca*	1	0
Fagaceae	*Castanea dentata*	0	1
Fagaceae	*Quercus alba*	0	2
Fagaceae	*Quercus coccinea*	1	0
Pinaceae	*Pinus pungens*	1	0
Rosaceae	*Prunus pensylvanica*	5	0

Table D.3. Species recorded in only 1978 (n = 30) or only 2007 (n = 30). The # plots present columns indicate the number of plots in which the species was recorded in the logged and unlogged areas combined.

		# plots present	
Family	Species	1978	2007
Apiaceae	*Sanicula* spp.	6	0
Aspleniaceae	*Asplenium platyneuron*	2	0
Asteraceae	*Achillea millefolium var. occidentalis*	1	0
Asteraceae	*Symphyotrichum acuminata*	0	1
Asteraceae	*Symphyotrichum lateriflorum var. lateriflorum*	1	0
Asteraceae	*Symphyotrichum undulatum*	1	0
Brassicaceae	*Cardamine concatenata*	1	0
Campanulaceae	*Campanula divaricata*	1	0
Caryophyllaceae	*Silene stellata*	3	0
Cornaceae	*Cornus florida*	9	0
Cyperaceae	*Carex digitalis*	0	1
Dryopteridaceae	*Cystopteris protrusa*	2	0
Dryopteridaceae	*Dryopteris marginalis*	3	0
Ericaceae	*Vaccinium corymbosum*	1	0
Ericaceae	*Vaccinium stamineum*	1	0
Fabaceae	*Cercis canadensis*	1	0
Fabaceae	*Desmodium* spp.	1	0
Gentianaceae	*Gentiana decora*	1	0
Hydrophyllaceae	*Hydrophyllum virginianum var. atranthum*	1	0
Lamiaceae	*Monarda clinopodia*	0	1
Liliaceae	*Maianthemum canadense*	0	2
Liliaceae	*Polygonatum pubescens*	2	0
Liliaceae	*Stenanthium gramineum*	1	0
Liliaceae	*Streptopus roseus*	0	1
Liliaceae	*Uvularia grandiflora*	4	0
Liliaceae	*Uvularia perfoliata*	2	0
Liliaceae	*Uvularia sessilifolia*	3	0
Lycopodiaceae	*Lycopodium obscurum*	1	0
Onagraceae	*Circaea lutetiana ssp. canadensis*	1	0
Ophioglossaceae	*Botrychium dissectum*	2	0
Orchidaceae	*Platanthera* spp.	0	1
Osmundaceae	*Osmunda claytoniana*	6	0
Phytolaccaceae	*Phytolacca americana*	0	1
Poaceae	*Brachyelytrum erectum*	1	0
Poaceae	*Panicum* spp.	1	0
Poaceae	*Poa* spp.	3	0
Pteridaceae	*Cheilanthes* spp.	1	0
Pyrolaceae	*Chimaphila maculata*	3	0
Ranunculaceae	*Ranunculus recurvatus*	1	0
Ranunculaceae	*Thalictrum pubescens*	1	0

Table D.3. Continued.

Family	Species	# plots present 1978	 2007
Rosaceae	*Porteranthus stipulatus*	1	0
Rosaceae	*Porteranthus trifoliatus*	1	0
Rubiaceae	*Houstonia serpyllifolia*	2	0
Saxifragaceae	*Astilbe biternata*	1	0
Saxifragaceae	*Mitella diphylla*	1	0
Thelypteridaceae	*Thelypteris noveboracensis*	0	7
Violaceae	*Viola macloskeyi ssp. pallens*	1	0
Violaceae	*Viola pedata*	0	1

VITA

Windy A. Bunn was born on March 29, 1978 in Memphis, TN. She moved to Searcy, AR at age five and graduated from Searcy High School in 1996. In 2000, she received a B. A. in Environmental Studies with a minor in Environmental Engineering from Washington University in St. Louis. From there, Windy volunteered for the Student Conservation Association for 10 months at Avon Park Air Force Range in Avon Park, FL before accepting her first job with the National Park Service. From 2001 to 2006, Windy worked for the National Park Service at Theodore Roosevelt National Park (ND), Natchez Trace Parkway (MS), and Whiskeytown National Recreation Area (CA). Windy returned to Tennessee in 2006 to work on her M. S. degree in Ecology with Dr. Nathan Sanders at the University of Tennessee and completed her M. S. degree in 2008.