

Change within and among forest communities: the influence of historic disturbance, environmental gradients, and community attributes

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Understanding how ecological communities change over time is critical for biodiversity conservation, but few long-term studies directly address decadal-scale changes in both the within- and among-community components of diversity. In this study, we use a network of permanent forest vegetation plots, established in Great Smoky Mountains National Park (USA) in 1978, to examine the factors that influence change in community composition within and among communities. In 2007, we resampled 15 plots that were logged in the late 1920s and 15 plots that had no documented history of intensive human disturbance. We found that understory species richness decreased by an average of 4.3 species over the 30-yr study period in the logged plots, but remained relatively unchanged in the unlogged plots. In addition, tree density decreased by an average of 145 stems ha^{-1} in the logged plots, but was relatively stable in the unlogged plots. However, we found that historic logging had no effect on within-community understory or tree compositional turnover during this time period. Instead, sites at lower elevations and sites with lower understory biomass in 1978 had higher understory compositional turnover than did sites at higher elevations and sites with higher understory biomass. In addition, sites with lower soil cation exchange capacity (CEC) and with lower tree basal area in 1978 had higher tree compositional turnover than did sites with higher soil CEC and higher tree basal area. Among-community similarity was unchanged from 1978 to 2007 for both the logged and unlogged plots. Overall, our results indicate that human disturbance can affect plant communities for decades, but the extent of temporal change in community composition may nevertheless depend more on environmental gradients and community attributes.

Both within- and among-community attributes can change over time, and understanding these changes often requires long-term empirical data (Magnuson 1990, Wardle et al. 2008). 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 (GSMNP) in eastern Tennessee to examine changes in forest understory plant communities and tree communities across 30 yr. Specifically, we examine the factors that influence compositional change within communities and change in compositional similarity among communities.

Human-caused disturbance can lead to large and persistent differences in understory communities in disturbed forests compared with undisturbed forests (Meier et al. 1995, Flinn and Vellend 2005, Harrelson and Matlack 2006). Furthermore, disturbance may also influence the magnitude of compositional change through time in disturbed versus undisturbed communities (Collins and Smith 2006). While general models of forest development (Oliver and Larson 1996) describe forest communities as undergoing rapid changes in the short term after disturbance, the long-term influence of disturbance on within-community change is less clear.

In addition to disturbance, environmental gradients can influence variation in within-community compositional turnover. For example, the extent of compositional turnover through time in low-elevation sites may be higher than that of high elevation sites (Aplet and Vitousek 1994, Selmants and Knight 2003, Taverna et al. 2005), and a number of factors that are often associated with

elevation – precipitation, soil fertility, species richness, and primary productivity-have been shown or hypothesized to affect temporal change within communities (Peet and Christensen 1988, Chase and Leibold 2002, Verheyen et al. 2003, Yurkonis and Meiners 2004, Taverna et al. 2005, Smart et al. 2006, White et al. 2006, Anderson 2008). However, the relative influence of these factors on compositional turnover within plant communities is poorly understood and likely varies with community composition and structure.

Over time, communities within a region can become either more similar or less similar to one another depending on the extent of change within individual communities of the region. Recent studies of decadal-scale change in forest communities in the eastern U.S. indicate that declines in species richness (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. Land-use history can have large effects on forest communities (Foster et al. 1998, Vellend et al. 2007), and the legacy of human disturbance may therefore be important for understanding patterns in among-community similarity in these long-lived communities.

In this study, we investigated changes in understory plant communities as well as tree communities in forests of GSMNP that were logged in the late 1920s and forests that were not logged. Specifically, we examined plant community data collected in 1978 (50 yr after logging) and in 2007 (80 yr after logging) to test four explicit hypotheses: 1) community composition of logged plots differs from that of unlogged plots both 50 and 80 yr after the logging event. 2) Historically logged plots have greater within-community compositional turnover than unlogged plots. 3) Elevation and associated edaphic and community attributes influence within-community compositional turnover. 4) The temporal change in similarity of logged communities to one another differs from the temporal change in similarity of unlogged communities to one another.

Methods

Great Smoky Mountains National Park (GSMNP) is a 211 000 ha protected area that straddles the Tennessee–North Carolina stateline. Elevations in GSMNP range from 271 to 2025 m, and climate and vegetation types vary

considerably along the elevational gradient. Mean annual rainfall in low elevation sites is 1400 mm with mean temperatures >12°C, while annual rainfall is >2000 mm and temperature averages 6°C at high-elevation peaks. GSMNP contains over 70 vegetation associations, varying from low- to mid-elevation mixed hardwood forests and xeric *Pinus* and *Quercus* forests to high-elevation *Picea–Abies* forests and heath balds. Prior to its establishment, ca 80% of the area that became GSMNP was subject to anthropogenic disturbance (Pyle 1988). Despite its history of disturbance, GSMNP is considered a center for diversity in North America.

Plot selection and field methods

In 2007, we resampled thirty 20 × 50 m forest plots originally established in 1978. The plots were randomly distributed using a stratified design that divided watersheds into units based upon elevation, slope position, and aspect. Fifteen of the resampled plots were in historically logged forests and fifteen plots were in unlogged forests. Historically logged forests were defined using the “corporate logging” category of Pyle (1988) and included only those areas in which the use of railroads, mechanized skidding, non-selective cutting practices, and highly extensive cutting on slopes occurred. We defined unlogged forests using Pyle’s “high in virgin forest attributes” and “big trees with diffuse disturbance” categories.

We chose the thirty resampled plots from a pool of over 100 permanent plots. Since our primary goal was to evaluate the effects of historic disturbance and elevation on community dynamics, we used 1978 field data and 2007 pre-sampling surveys to exclude plots with high levels of recent disturbance. Toward this end, we resampled only plots dominated by hardwood species, sites without recent or frequent fires, and sites that were not (or have not been) influenced by *Dendroctonus frontalis* (southern pine beetle), *Adelges piceae* (balsam woolly adelgid) or *Adelges tsugae* (hemlock woolly adelgid). Because of this rigorous selection process, we consider the thirty resampled plots to be relatively free of disturbance in the thirty years between sampling events.

The logged and unlogged plots were topographically similar to one another: mean elevation and percent slope of logged plots did not differ from the mean elevation and percent slope of unlogged plots (Table 1). The 15 logged plots ranged in elevation from 727 to 1402 m and

Table 1. Comparison of topographic and edaphic variables in historically logged and unlogged plots, using t-tests or Wilcoxon rank-sum tests to test for mean differences.

Variable	Mean ± SE		Logged vs unlogged
	logged	unlogged	p-value
Elevation (m)	1104 ± 61.6	1034 ± 67.3	0.41
Slope (%)	19.0 ± 3.26	19.8 ± 2.42	0.95
Soil pH	4.2 ± 0.11	4.5 ± 0.12	0.02
Soil cation exchange capacity (meq 100 g ⁻¹)	9.4 ± 0.40	7.1 ± 0.16	<0.0001
Soil K (ppm)	68.5 ± 9.04	64.8 ± 4.93	0.63
Soil Ca (ppm)	326 ± 71.9	165 ± 27.1	0.12
Soil Mg (ppm)	44.9 ± 6.63	32.3 ± 3.45	0.13
Soil P (ppm)	14.3 ± 1.70	15.4 ± 2.46	0.77
Soil organic matter (%)	5.1 ± 0.28	3.1 ± 0.33	0.0002

occurred on north- ($n = 8$), east- ($n = 4$), and west- ($n = 3$) facing slopes. The 15 unlogged plots ranged in elevation from 664 to 1400 m and occurred on north- ($n = 11$), east- ($n = 1$), and west- ($n = 3$) facing slopes. Both the logged and unlogged plots are characterized by well-drained loamy soils classified as either humic or typic dystrochrepts (A. R. Khiel, NRCS, unpubl. report).

Tree cores collected and analyzed by the GSMNP Vegetation Monitoring Program were available for a subset of the plots (Jenkins unpubl.). Dominant trees in unlogged plots were 150–228 yr old (complete cores) or a minimum 132–147 yr old (cores without pith) in 2007. As expected from logging history records, dominant trees in logged plots were 75–80 yr old in 2007.

In 1978, the 20×50 m forest plots were permanently marked with rebar and witness tree tags, which allowed us to reestablish the plots in 2007. In the 2007, we used the same sampling design used in 1978. Within each 20×50 m plot, we recorded understory shrub and tree seedling species < 1 m tall in 25 4-m^2 subplots and understory herbaceous species in 25 1-m^2 subplots nested within the shrub and seedling subplots. We defined the understory community as the shrub, seedling, and herbaceous species recorded in all 25 subplots within the 20×50 m plot. We also recorded all individual trees (≥ 10 cm dbh) by species in the 20×50 m plot and used these data to characterize 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 19 June and 26 August in 1978 and between 9 July and 26 August 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.

To characterize the sampling plots, we estimated a suite of topographic and edaphic parameters (Table 1). We estimated elevation using topographic maps and calculated percent slope by averaging three slope measurements taken at the two 20-m end lines and at the center of each plot facing downslope. 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 h, 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).

Analysis of the influence of historic logging on community composition

We used nonparametric, permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) based on Bray-Curtis similarity values of species abundances to compare understory and tree community composition between logged and unlogged plots in both 1978 and 2007. PERMANOVA compares the variability in species similarity between plots within a treatment to the

variability in species similarity between plots from different treatments and is performed using the FORTRAN program PERMANOVA (Anderson 2005). 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 randomly shuffles the sample labels within and among treatment groups 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 as the percentage of the 25 subplots in which the species occurred. For the tree communities, we used the number of individual trees of a species as the abundance value. We chose to use understory frequency and tree density as the abundance measures rather than understory cover and tree basal area because these measures are more repeatable between observers and across years. The choice to use these frequency-based abundance measures did not change the results. 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). To confirm that compositional differences between logged and unlogged communities were due to location differences rather than to dispersion differences, we used permutational analysis of multivariate dispersions (PERMDISP; Anderson et al. 2006) performed in the FORTRAN program PERMDISP (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. 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.

We tested whether particular species accounted for the observed differences in community composition between logged and unlogged communities with indicator species analysis (Duf rene and Legendre 1997) using PC-ORD 5.0

(MjM Software Design, Glendon Beach, OR). The indicator analysis uses the relative abundance of each species (for example, percent cover of the species in the logged plots divided by percent cover of the species in all plots) and the relative frequency of the species within each group (for example, the number of logged plots in which the species occurs out of the 15 total logged plots) 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. In other words, a species with an indicator value of 100 for logged plots occurs in every logged plot and no unlogged plots, and is thus, a good indicator of plots that have been logged. A Monte Carlo test based on Bray-Curtis distance was used to test the significance of the indicator value (Dufrêne and Legendre 1997).

Analysis of change within communities

We analyzed within-plot change in species richness and tree density with paired t-tests, where the species richness and density values for a plot in 1978 were compared with the species richness and density values for the same plot in 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, ver. 6, PRIMER-E, 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 and Colwell 2001).

To estimate compositional turnover within communities (i.e. change within a plot over the 30-yr period), we calculated the similarity of each plot in 1978 to itself in 2007 using the Chao-Sørensen incidence-based index and the Bray-Curtis index in EstimateS (Colwell 2005). 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 plant community. 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 and Bray-Curtis indices produced qualitatively similar results for the understory community, so we chose to focus on only the Chao-Sørensen index in the results and discussion. Since we did not expect “unseen shared species” in the tree community, we used the Bray-Curtis index to assess tree compositional turnover.

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 turnover as the degree of compositional dissimilarity between 1978 and 2007 within an individual plot. Therefore, we calculated turnover as $1-L_{inc}$ for the understory community and $1-C_N$ for the tree community. To evaluate whether historic logging influenced compositional turnover, we performed t-tests to compare mean logged and unlogged community turnover values. We then used mixed stepwise multiple regression (a combination of forward and backward steps; $\alpha=0.1$) to determine whether elevation, edaphic, or community attributes influenced variation in compositional turnover. We used JMP 6.0 (SAS Inst., Cary, NC, USA) for all analyses of within-plot compositional turnover.

Analysis of change among communities

To examine whether similarity among communities (i.e. how similar plots were to one another within a sampling period) 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. Among-community similarity is the average distance among plots within a group to the group centroid in multivariate space (i.e. multivariate dispersion as in Anderson et al. 2006) and is statistically tested for differences in among-community similarity between years with a permutational ANOVA (described above) in the PERMDISP program. 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 was highly correlated with average distance to the group centroid in 1978 ($r=0.99$, $p<0.001$) and in 2007 ($r=0.99$, $p<0.0001$). 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

In 1978 (50 yr 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. In 2007 (80 yr 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. 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 (Supplementary material Table S1). 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 (Supplementary material Table S2).

Influence of historic logging on community composition

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: $F_{1,28} = 1.80$, $p = 0.05$). These differences 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: $F = 0.54$, $p = 0.52$; 2007 PERMDISP: $F = 0.40$, $p = 0.59$). Seven understory species had significantly higher indicator values (a combination of relative abundance and relative frequency) in unlogged plots than in logged plots in 1978 and eight understory species were significant indicators of unlogged plots in 2007 (Table 2). Five understory species had significantly higher indicator values in logged plots in 1978, but only one understory species was still an indicator of logged plots in 2007 (Table 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 *Eurybia divaricata*. 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: $F_{1,28} = 2.37$, $p = 0.02$). These differences 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: $p = 0.36$, $P = 0.59$). *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* Marsh. was the only tree species with a significantly higher indicator value in unlogged plots than in logged plots and was an indicator of unlogged plots in only 2007 (Table 2).

Change within communities

Understory species richness in individual logged plots was, on average, 13% lower in 2007 than in 1978 ($t = 2.35$, $DF = 14$, $p = 0.03$). However, richness did not change in the unlogged plots over the 30-yr study period ($t = 1.06$, $DF = 14$, $p = 0.31$). The decrease in overall understory species richness in the logged plots resulted from decreased richness of herbaceous species (Supplementary material Fig. S1). Shrub, seedling, and tree species richness did not change over time in either logged or unlogged plots ($p > 0.08$ in all cases; Supplementary material Fig. S1). Stem density of trees decreased by an average of 21% in the historically logged plots ($t = 6.14$, $DF = 14$, $p < 0.0001$)

Table 2. Indicator species analysis for compositional differences between 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. Understory includes herbs, shrubs, and seedlings <1 m tall and tree includes trees ≥ 10 cm dbh. Species with significant IV in at least one year are listed alphabetically.

Species name	1978			2007		
	Group	IV	p	Group	IV	p
Understory						
<i>Acer saccharum</i>	unlogged	44.6	0.16	unlogged	55.0	0.03
<i>Amphicarpaea bracteata</i>	unlogged	31.7	0.04	unlogged	18.7	0.45
<i>Arisaema triphyllum</i>	unlogged	63.6	0.001	unlogged	45.1	0.02
<i>Athyrium filix-femina</i>	unlogged	12.6	0.91	unlogged	44.6	0.02
<i>Betula alleghaniensis</i>	logged	44.9	0.03	logged	20.0	0.25
<i>Betula lenta</i>	unlogged	10.0	0.87	unlogged	40.0	0.02
<i>Calycanthus floridus</i>	unlogged	53.3	0.002	unlogged	37.0	0.06
<i>Collinsonia canadensis</i>	unlogged	60.0	0.002	unlogged	6.7	1
<i>Dioscorea villosa</i>	unlogged	48.0	0.01	unlogged	20.0	0.25
<i>Eurybia divaricata</i>	unlogged	51.2	0.16	unlogged	59.3	0.04
<i>Liriodendron tulipifera</i>	unlogged	51.2	0.02	unlogged	37.2	0.29
<i>Osmunda claytoniana</i>	logged	40.0	0.02	–	–	–
<i>Prunus serotina</i>	logged	72.5	0.001	logged	51.4	0.15
<i>Quercus rubra</i>	unlogged	58.9	0.01	unlogged	31.7	0.63
<i>Rhododendron maximum</i>	logged	42.9	0.02	logged	49.9	0.01
<i>Rubus</i> spp.	logged	55.7	0.02	unlogged	33.7	0.97
<i>Thalictrum thalictroides</i>	unlogged	22.2	0.23	unlogged	36.7	0.05
<i>Trillium</i> spp.	unlogged	29.2	0.15	unlogged	72.3	0.002
<i>Viola hastata</i>	unlogged	49.6	0.07	unlogged	58.4	0.003
Tree						
<i>Acer saccharum</i>	unlogged	39.2	0.24	unlogged	62.2	0.03
<i>Betula lenta</i>	logged	68.3	0.005	logged	60.4	0.02
<i>Magnolia fraseri</i>	logged	40.0	0.05	logged	43.9	0.05
<i>Prunus pensylvanica</i>	logged	33.3	0.03	–	–	–
<i>Prunus serotina</i>	logged	56.9	0.02	logged	50.0	0.02

but did not change in unlogged plots ($t = 0.30$, $DF = 14$, $p = 0.77$) (Supplementary material Fig. S2). Tree basal area did not change over 30 yr in either the historically logged plots ($t = 2.0$, $DF = 14$, $p = 0.07$) or the unlogged plots ($t = 1.07$, $DF = 14$, $p = 0.30$).

Historic logging had no effect on within-plot understory compositional turnover ($t = 0.08$, $DF = 28$, $p = 0.94$) or on within-plot tree compositional turnover ($t = 1.4$, $DF = 27$, $p = 0.17$). A model containing elevation and 1978 understory biomass (estimated using percent cover values) accounted for 36% of the variation in within-plot understory compositional turnover (i.e. how similar a plot was to itself over the 30-yr period; $p = 0.003$; Table 3). Overall, plots at higher elevations had lower understory compositional turnover over the 30-yr period than did plots at lower elevations (Fig. 1a). With the exception of one statistical outlier (determined using Cook's D and hat matrix analyses) that contained ca 55% cover of two fern species (*Phegopteris hexagonoptera* and *Dennstaedtia punctilobula*), plots with high understory biomass in 1978 had lower understory turnover than did plots with low understory biomass in 1978 (Fig. 1b).

Change in understory community composition was not related to tree compositional turnover ($r = 0.19$, $p = 0.32$). Variation in tree compositional turnover was best explained by a model containing soil cation exchange capacity (CEC) and 1978 tree biomass ($R^2 = 0.43$, $p = 0.0005$; Table 3). Plots with high CEC had lower compositional turnover in the tree community than did plots with low CEC (Fig. 2a). In addition, plots with high tree biomass (estimated using stand basal area) in 1978 had lower tree turnover than did plots with low tree biomass in 1978 (Fig. 2b).

Change among communities

Among-community similarity was unchanged from 1978 to 2007 in both the logged and unlogged plots (Table 4). We found no differences in the multivariate dispersion of understory communities in 2007 compared with 1978 in either the logged (PERMDISP: $F = 0.18$, $p = 0.74$) or unlogged (PERMDISP: $F = 0.19$, $p = 0.69$) 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

Logging history affected 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 elevation, soil properties, and community biomass explained 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.

Table 3. Results of stepwise multiple regressions for change in species richness and community composition over 30 yr. Understory includes herbs, shrubs, and seedlings <1 m tall and trees includes trees ≥ 10 cm dbh.

Dependent variable	Predictor(s)	Parameter estimate	Standardized estimate	p	Partial R ²	Model		
						R ²	DF	p
Understory compositional turnover	Intercept	0.32	0	<0.0001	0.36	2, 26	7.22	0.003
	Elevation	-0.0001	-0.40	0.02				
	1978 understory cover	-0.001	-0.36	0.03				
Tree compositional turnover	Intercept	0.65	0	<0.0001	0.43	2, 27	10.06	0.0005
	CEC	-0.03	-0.57	0.001				
	1978 tree basal area	-0.003	-0.33	0.03				

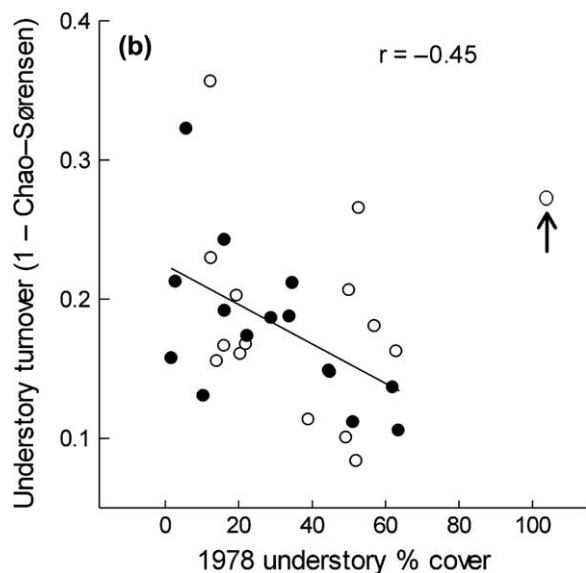
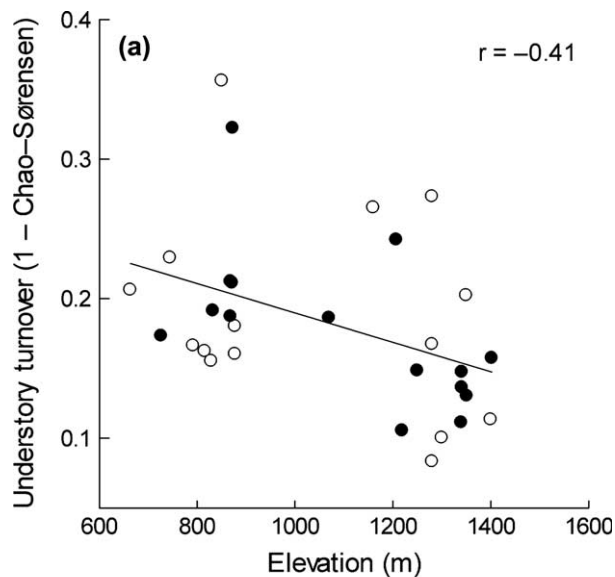


Figure 1. Correlation between understory compositional turnover across 30 yr and elevation (a) and 1978 understory percent cover (b). Filled circles represent logged plots and unfilled circles represent unlogged plots. Arrow in panel b points to an outlying data point that was excluded from the correlation.

Influence of historic logging on community composition

In 1978 (50 yr 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 yr after logging). These results are similar to some chronosequence studies comparing understory communities in recently logged forests with understory communities of older 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

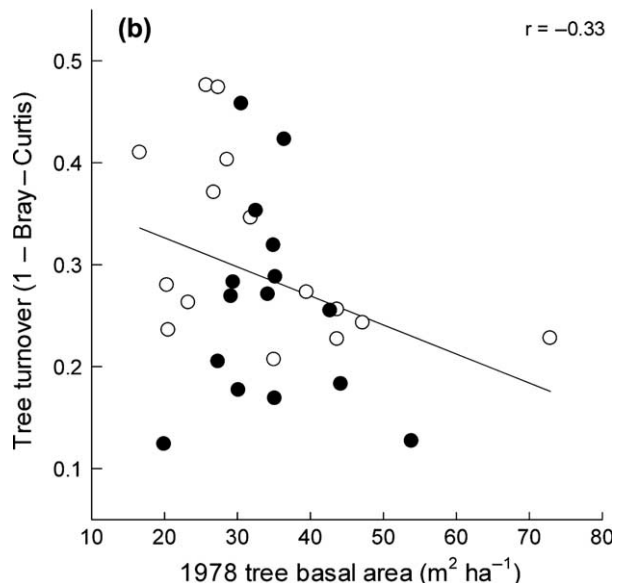
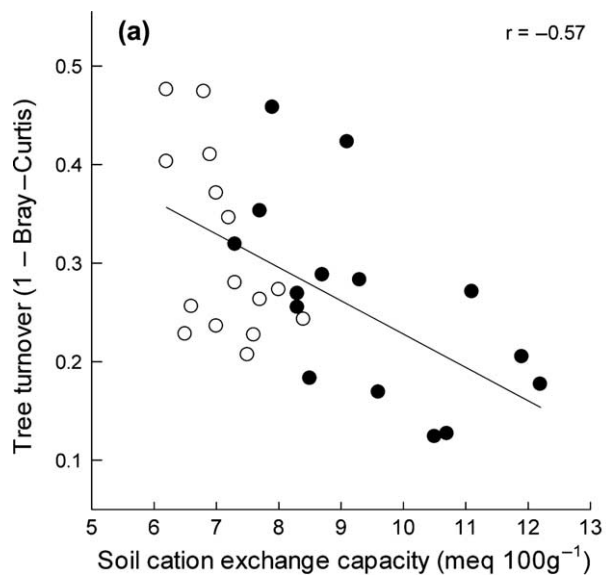


Figure 2. Correlation between tree compositional turnover and soil cation exchange capacity (a) and 1978 tree basal area (b). Filled circles represent logged plots and unfilled circles represent unlogged plots.

and undisturbed forests (Meier et al. 1995, Flinn and Vellend 2005, Harrelson and Matlack 2006).

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 and 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 primarily late-season understory species, which may be more resistant to logging effects than vernal species.

Table 4. Among-community similarity 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.

Abundance variable	Group	Mean \pm SE distance to centroid		F	p-value
		1978	2007		
Understory frequency ¹	logged	53.05 \pm 2.14	51.68 \pm 2.39	0.18	0.74
	unlogged	50.92 \pm 2.09	49.59 \pm 2.21	0.19	0.69
Tree density ²	logged	51.70 \pm 2.22	50.87 \pm 2.41	0.06	0.82
	unlogged	51.16 \pm 2.58	47.72 \pm 1.87	1.17	0.35

¹ Understory frequency is an abundance measure based on the percentage of the 25 subplots within a 20 \times 50 m forest plot in which each species occurred.

² Tree density is an abundance measure based on the number of individual trees of a species within a 20 \times 50 m forest plot.

Overall, six understory species that were indicators of unlogged plots in 1978 were no longer indicators in 2007 as these species began to recolonize logged plots. Likewise, four understory species that were indicators of logged plots in 1978 were no longer indicators in 2007 as early-colonizing species became less abundant in the logged plots. Seven understory species became indicators of unlogged plots between 1978 and 2007. Three of the seven species are spring ephemerals that generally increase in abundance as forests mature and their inclusion as indicator species of unlogged plots in 2007 but not in 1978 could be a result of variation in phenology between sample years. The remaining species that became indicators of unlogged plots in 2007 either became newly established in unlogged plots or remained unchanged in unlogged plots while occurring in fewer logged plots over time. This indicates that after 150 to 200 yr, the unlogged plots are still undergoing measureable changes in community composition. In addition, it suggests that some species associated with older forests may become established and subsequently lost then regained as disturbed forests mature.

We note that although spatial autocorrelation may have contributed to differences between logged and unlogged plots, the stratified random sampling design, wide spatial distribution of plots within disturbance types, and physical similarity of logged and unlogged sample areas likely reduced its effects.

Factors influencing change within communities

Even though change in understory species richness and tree density differed between logged and unlogged plots, the occurrence of historic logging did not affect the extent of within-community compositional turnover in the understory community or the extent of within-community tree compositional turnover during our 30-yr study period. We had 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 and Larson 1996) and tree density decreased. 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 >50 yr ago no longer affect understory dynamics in these forests. Also contrary to our expectations, the extent of tree compositional turnover in

unlogged plots was similar to tree turnover in logged plots. Since 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, which could explain the similar extent of compositional turnover we observed in logged and unlogged plots.

Elevation and community biomass best explained compositional turnover within forest understory communities. Consistent with other studies (Aplet and Vitousek 1994, Selmants and Knight 2003), we found that the extent of turnover in the understory community decreased along the elevational gradient. Mean annual temperature decreases ca 4°C and soils become more acidic over the 740 m elevational gradient in our study site (Garten and Hanson 2006). The lower temperatures at higher elevations could slow decomposition, decrease nutrient availability, and reduce overall plant growth (Vitousek et al. 1992, Aplet and Vitousek 1994), which might result in lower compositional 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 in our study plots; therefore, it is unclear whether slower ecosystem processes at high elevations are responsible for the smaller changes in understory composition over time that we observed.

In addition to temperature, soil pH also varies with elevation in our study sites, with more acidic soils at higher elevation sites. In the acidic soils of southeastern U.S. forests, higher soil pH can indicate greater nutrient availability to plants. In the understory, greater nutrient availability could lead to increased compositional turnover either by increasing the likelihood that newly arriving species will establish in a community (Peet and Christensen 1988) or by increasing the growth of dominant species that could out-compete other species in the community. In addition, the large regional pool of species that favor 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. A larger pool of potential colonizers could increase understory compositional change in high pH communities compared to low pH communities.

Unlike understory compositional turnover, tree compositional turnover was not related to elevation, but was related to soil CEC. Because turnover of individual tree

stems can be a function of elevation, latitude, and productivity in some forest systems (Phillips et al. 2004, Stephenson and van Mantgem 2005), we expected higher compositional turnover in the tree community in low elevation plots than in high elevation plots. However, elevation was not correlated with within-site 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 and cannot say whether the rate of stem recruitment or mortality changed with elevation. For trees, it may be that fertile sites allow faster tree growth regardless of elevation. Faster tree growth 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.

Understory biomass in 1978 was correlated with understory compositional turnover, and tree biomass in 1978 was correlated to tree compositional turnover. Plots with high understory percent cover (an estimate of understory biomass; Gilliam and Turrill 1993) in 1978 had lower compositional turnover than did plots with low understory cover in 1978. Similarly, plots with high tree basal area (a surrogate for tree biomass; Wardle et al. 2008) in 1978 had lower tree compositional turnover than did plots with low tree basal area in 1978. Understory percent cover and tree basal area in 1978 were not correlated with any measured topographic or edaphic factors (Supplementary material Table S3). Sites with higher biomass may have low within-site turnover because in higher biomass sites, a larger proportion of the plot is occupied by established species. The proportion of a plot initially occupied 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.

Influence of historic logging on change among communities

We documented a wide range of changes in species composition within communities, but these within-community changes did not translate into a 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 and Peet 1984, Vellend et al. 2007) suggests that younger forests may become more similar to one another over time. However, we found no change in among-community similarity in either understory or tree communities of the logged plots. We also found no change in among-community similarity in plant communities of unlogged plots over this same 30-yr time period.

The theoretical expectation for temporal change in among-community similarity in undisturbed forests is unclear. It may be that the 30-yr study period here was a relatively stable period within larger cycles of among-community heterogeneity in forest development. Additionally, among-community heterogeneity may have reached a

static point where it will remain unchanged in the absence of further disturbance (Rejmánek and Rosén 1992).

Conclusions

The extent of change in community composition was not related to historic disturbance, and among-community similarity did not change over time in either historically disturbed or undisturbed plots. Our results indicate that the extent of change in community composition over time may depend more on environmental gradients and community attributes than on the legacy of large-scale, but short-lived historic disturbances such as logging. In addition, variation in 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 and space.

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