

Compositional stability and diversity of vascular plant communities following logging disturbance in Appalachian forests

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Abstract. Human-caused changes in disturbance regimes and introductions of nonnative species have the potential to result in widespread, directional changes in forest community structure. The degree that plant community composition persists or changes following disturbances depends on the balance between local extirpation and colonization by new species, including nonnatives. In this study, we examined species losses and gains, and entry of native vs. exotic species to determine how oak forests in the Appalachian Mountains might shift in species composition following a gradient of pulse disturbances (timber harvesting). We asked (1) how compositional stability of the plant community (resistance and resilience) was influenced by disturbance intensity, (2) whether community responses were driven by extirpation or colonization of species, and (3) how disturbance intensity influenced total and functional group diversity, including the nonnative proportion of the flora through time. We collected data at three spatial scales and three times, including just before, one year post-disturbance, and 10 years post-disturbance. Resistance was estimated using community distance measures between pre- and one year post-disturbance, and resilience using community distance between pre- and 10-year post-disturbance conditions. The number of colonizing and extirpated species between sampling times was analyzed for all species combined and for six functional groups. Resistance and resilience decreased with increasing timber-harvesting disturbance; compositional stability was lower in the most disturbed plots, which was driven by colonization, but not extirpation, of species. Colonization of species also led to increases in diversity after disturbance that was typically maintained after 10 years following disturbance. Most of the community-level responses were driven by post-disturbance colonization of native forbs and graminoids. The nonnative proportion of plant species tended to increase following disturbance, especially at large spatial scales in the most disturbed treatments, but tended to decrease through time following disturbance due to canopy development. The results of this study are consistent with the theory that resources released by disturbance have strong influences on species colonization and community composition. The effects of management activities tested in this study, which span a gradient of timber-harvesting disturbance, shift species composition largely via an increase in species colonization and diversity.

Key words: Appalachian Mountains, USA; colonization; compositional stability; disturbance; forest management.

INTRODUCTION

Sustaining both natural resources and biological diversity requires understanding of the factors influencing responses of ecosystems to human-caused disturbances. Disturbances influence species composition and diversity through a variety of mechanisms that vary with the frequency, intensity, and spatial and temporal extent of the disturbance (Grubb 1977, Roberts 2004), and which interact with the life history and physiological traits of individual species (McGill et al. 2006). Disturbance may directly affect community composition

by increasing mortality of individuals or groups of species, or indirectly by altering environmental conditions or resource availability and heterogeneity, which in turn permit colonization of new species (Pickett and White 1985), including nonnatives (Belote et al. 2008). The study of community assembly following disturbance has been instrumental to understanding the relative importance of biotic and environmental processes determining composition and diversity of communities and their change through time (Clements 1916, Gleason 1926, Egler 1954, Simberloff and Wilson 1969).

The stability of communities in response to disturbance has intrigued ecologists for decades (Odum 1969, Chapin et al. 1996, McCann 2000). Community stability can be defined as a function of both resistance and resilience (*sensu* Halpern 1988). Ecological resistance

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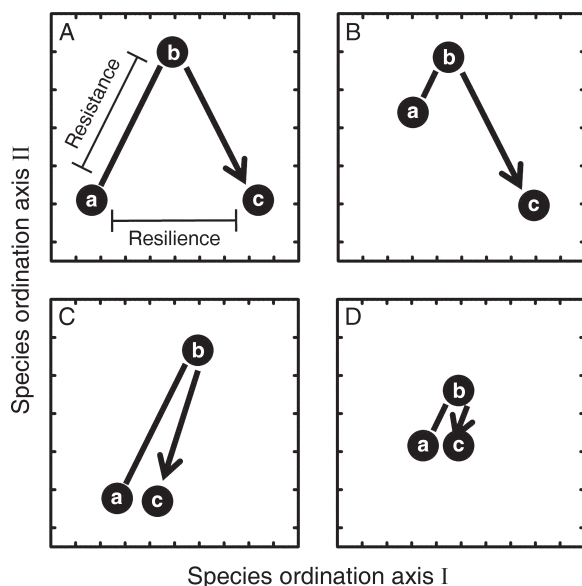


FIG. 1. Conceptual figure of resistance and resilience as changes in species composition and return to pre-disturbance conditions in plots before disturbance (a); one year post-disturbance (b); and 10 years post-disturbance (c). Panel A shows compositional differences among sampling times and conceptual resistance and resilience. Panel B illustrates a situation where community species composition is resistant to disturbance but not resilient. Panel C represents a community that is not resistant to disturbance but is relatively resilient (i.e., nearly returns to pre-disturbance composition). Panel D represents a community that is both resistant and resilient. Larger values of compositional dissimilarity represent less resistant and resilient communities.

and resilience may be conceptualized using ecosystem-level functions (i.e., productivity or water retention) or community-level structure (i.e., species composition). In this paper, we consider resistance of communities as the ability of a community to maintain compositional integrity immediately following a disturbance event (cf. Sankaran and McNaughton 1999, Foster et al. 2002), and resilience as a measure of return to pre-disturbance conditions (Fig. 1). The relative resistance and resilience of communities is likely a function of the initial species composition of communities (Halpern 1988) as well as regional species pools (Belote et al. 2009), which influence losses and gains of species.

Land managers deliberately apply a variety of disturbances to forests to direct ecological structure or function to meet a variety of management objectives (Roberts and Gilliam 1995). For example, forest managers use fire and tree harvesting to maintain wildlife habitat (McShea et al. 2007) and vegetation structure (Franklin et al. 2003), and to promote regeneration of favored tree species (Loftis 1990). If maintaining biodiversity is a goal of forest management, it is important to understand how various silvicultural practices and timber harvesting intensities affect shifts in species composition of forest vegetation (Simberloff

1999), including the introduction of nonnative species (Belote et al. 2008). This is especially true in biologically rich areas that are embedded within regions of high human population growth and development, such as hardwood forests of the Appalachian Mountains, USA.

In this study, we investigated how an experimentally applied, replicated forest canopy disturbance gradient influenced species composition and diversity of all vascular plants in Appalachian oak-dominated forests immediately after disturbance, and 10 years following disturbance during canopy development (see Plate 1). The disturbance gradient represents silvicultural treatment alternatives used in the Appalachian Mountains to facilitate oak regeneration and harvest timber resources (Fox et al. 2006). Our goal was to understand how disturbance intensity representing management alternatives influenced stability and diversity of the vascular plant community.

We formulated three overarching predictions related to how stability, turnover, and diversity of the plant community would vary with disturbance intensity and through time.

Prediction 1.—We predicted that greater disturbance intensity would lead to greater shifts in species composition that would be sustained through time via colonization and extirpation of species. In other words, we predicted that the most disturbed communities would be the least compositionally stable (resistant and resilient).

Prediction 2.—To better understand the processes that influence compositional stability, we investigated species turnover (i.e., colonization and extirpation) of all species and functional groups of species in response to disturbance and through time. We predicted that both colonization and extirpation of species would mediate compositional stability.

Prediction 3.—We further predicted that balances between colonization and extirpation in response to disturbance would alter native and nonnative plant diversity. We assessed the proportion of species that are nonnative among disturbance treatments through time to investigate whether human-applied disturbance shifts community composition toward a more nonnative-dominated community (i.e., are nonnative species persistent passengers of forest change?). We investigated these predictions at various spatial scales to determine whether patterns depended on scale of observation.

METHODS

Study sites

The study sites are part of an experimental manipulation of canopy disturbance in Appalachian oak forests. Disturbances were applied to examine the influences of regeneration harvesting intensities on multiple system components including plant (Wender 2000, Hood 2001) and animal diversity and composition (Knapp et al. 2003, Homyack and Haas 2009), invasions by nonnative species (Belote et al. 2008), oak regener-

ation (Atwood et al. 2009), and soil ecosystem processes (Sucre and Fox 2008). Seven sites (experimental blocks) were chosen in the Ridge and Valley province and Appalachian Plateau region of southwest Virginia and northeastern West Virginia located on the Jefferson National Forest and the MeadWestvaco Corporation (501 South 5th Street, Richmond, Virginia, USA) Wildlife and Ecosystem Research Forest, respectively (Fig. 2). Sites were selected to represent similar overstory composition and age and were dominated by *Quercus* spp. (red and white oaks), *Acer rubrum* L. (red maple), yellow-poplar (*Liriodendron tulipifera* L.), and *Carya* spp. (hickories). The sites are floristically diverse with richness exceeding 700 species, including a variety of understory trees (e.g., *Sassafras albidum* (Nutt.) Nees, *Amelanchier arborea* (Michx. f.) Fernald, *Nyssa sylvatica* (Marsh.)), shrubs (e.g., *Rhododendron* spp., *Vaccinium* spp.), graminoids (e.g., *Carex* spp., *Dichanthelium* spp.), herbaceous monocots (e.g., members of Liliaceae and Orchidaceae) and dicots (e.g., species from Asteraceae and Roseaceae; hereafter forbs), vines (e.g., *Smilax* spp.), and ferns (e.g., *Osmunda* spp., *Dennstaedtia punctilobula* (Michx.) T. Moore). Sites were located on similar topographic positions with generally south-facing, moderate slopes (10–40%) and intermediate elevations (600–1200 m). Soils at all sites are rocky, well drained, acidic, and derived from sandstone and shale residuum and colluvium. Precipitation is generally evenly distributed throughout the year.

At each of the seven sites, seven 2-ha experimental units (EUs) were established with no buffer between units. The experimental design includes seven treatments (Knapp et al. 2003), but we focus on five treatments in this study (Fig. 2). Nested within each EU, three permanent 576-m² (24 × 24 m) plots were randomly arranged so that they were 23 m from the EU edge and were separated by an azimuth of 120° from EU center. Six 1-m² subplots were nested within each 576-m² plot; there were thus 18 subplots per experimental unit (Fig. 2). For additional information about the sites, disturbance treatments, and plot designs see Knapp et al. (2003), Belote et al. (2008, 2009), Homyack and Haas (2009), and Atwood et al. (2009, 2011).

Disturbance treatments

Disturbance treatments were applied to the 2-ha experimental units between 1993 and 1998, during the nongrowing season. Treatments were randomly assigned to EUs within each site, and included a gradient of overstory removal including clearcut (95% basal area removed), leave-tree harvest (74% of basal area removed leaving a few dominants), shelterwood harvest (56% of basal area removed to thin the stand), understory herbicide (removal of suppressed trees via basal application of herbicide), and uncut control (see Atwood et al. 2011 for additional details on treatments). During tree harvest, limbs and branches were removed from main stems and typically scattered and left in situ.

Control treatments were intended to represent areas that experience no disturbance related to timber harvesting. However, during treatment application of nearby EUs, some minor disturbance associated with skid trails and diffuse light from adjacent treatments occurred within some uncut control EUs. These disturbances were mostly restricted to the edges of the EUs (cf. Matlack and Litvaitis 1999). One West Virginia site did not include the understory herbicide treatment and we were not able to resample the leave-tree treatment at 10 years post-disturbance because of time constraints; thus the experimental setup is an unbalanced randomized block design consisting of 33 EUs.

Data collection

Pre-disturbance and initial post-disturbance data were collected one year prior to and one or two years following disturbance treatment application, with the exception of one site where pre-disturbance data were collected two years prior to harvesting disturbance (Hammond et al. 1998, Wender 2000, Hood 2001). Sites and permanently marked plots were revisited and sampled 9 or 11 years following disturbance, depending on the site (Atwood et al. 2009). Here, we refer to the 9- or 11-year post-disturbance sampling effort as 10-year post-disturbance. Presence of all herbaceous and woody plant species was recorded at each of the three scales (EU, plot, and subplot). At the subplot scale, species-specific canopy cover was estimated using modified Daubenmire cover classes (Daubenmire 1959). All scales were sampled twice during the growing season to account for seasonal differences in species composition and to ensure species were reliably identified; data were collected in May or June and again in late August or September. Species lists from both samples were combined and analyzed together. For subplots, the maximum cover estimated for a species during the sampling times was used in analyses. Using number of species present, we generated estimates of richness of native and nonnative species at each scale and at each sampling time. We classified all species as native or nonnative and as six functional groups based on typical growth form and life history characteristics including tree, shrub, forb, graminoid, vine, or fern based on classifications in the PLANTS database (USDA, NRCS 2008).

Statistical analysis

Using the nested sampling design within each experimental unit, we calculated frequency and importance values of all species observed in plots and subplots, respectively. Plot frequency was calculated as the number of plots a species occurred in within each EU. Subplot importance values (IV) were calculated as the sum of relative cover (cover of species/total cover) and relative frequency (frequency/total frequency) as described in Mueller-Dombois and Ellenberg (1974).

Prediction 1: community resistance and resilience.—We used a blocked multi-response permutation procedure

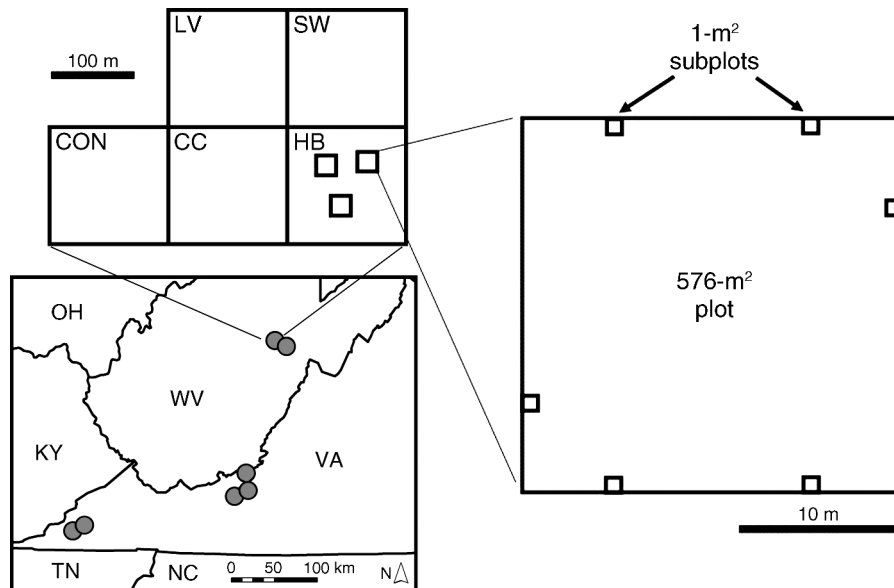


FIG. 2. Typical site and sampling layout of permanently marked experimental units, plots, and subplots in an experiment investigating effects of disturbance on diversity and stability of the plant community in oak forests of the southern Appalachian Mountains, USA. Codes within 2-ha experimental units represent examples of treatment layout: CON, control; HB, herbicide; SW, shelterwood; LV, leave-tree; CC, clearcut. Treatments were randomly applied to each experimental unit within each site.

(MRPP) to investigate overall compositional differences between the disturbance treatments while accounting for experimental blocking by site. MRPP uses distance measures and randomization tests to investigate whether assigned groups (e.g., disturbance treatments) are compositionally different (McCune and Grace 2002). We ran separate MRPPs for pre-disturbance, 1-year post-disturbance, and 10-year post-disturbance data to investigate if compositional differences between treatments were detected at each of the sampling periods. Separate analyses were also performed on the community data collected at the plot and subplot scales using relative frequency data and importance values, respectively, so that six total MRPPs were conducted (three sampling times \times two spatial scales). Because blocked MRPPs require balanced designs, we omitted data from the WV1 site for this analysis; WV1 is the only incomplete site without all treatments.

To quantify community resistance and resilience following disturbance, we calculated Sørensen dissimilarity measures on the sample \times species matrix using relative frequency data at the plot scale and importance values at the subplot scale as abundance measures. Sørensen dissimilarity is calculated as a percentage difference in species composition considering species presence and abundance (McCune and Grace 2002) by summing differences in abundance between two samples and dividing by the product of the sum of species abundance within samples. Resistance is defined as the inverse of the initial displacement following disturbance. (Small shifts in community composition represent greater resistance than larger shifts; Fig. 1.) Resilience

is defined as the inverse of the distance between pre-disturbance and 10-year post-disturbance. (Compositional return to near pre-conditions indicates greater resilience; Fig. 1.) Plot and subplot analyses were performed separately to investigate the effects of spatial scale on community stability.

We performed nonmetric multidimensional scaling (NMS) using Sørensen dissimilarity values to display compositional relationships. Successional vectors that connect repeatedly measured samples through time were overlaid onto the ordination to visualize compositional shifts of samples from pre-disturbance, to one year post-disturbance, and 10 years post-disturbance (Fig. 3). All multivariate distance measures were calculated using PC-ORD v. 5 (MjM Software, Gleneden Beach, Oregon, USA).

We analyzed the effects of disturbance treatment on resistance and resilience estimates with a mixed analysis of covariance (ANCOVA) using PROC MIXED (SAS 9.1; Littell et al. 2006, SAS Institute 2007) with the following model:

$$\text{Sørensen dissimilarity} = \mu + \text{treatment} + \text{diversity} + \text{treatment} \times \text{diversity} + \text{site} + \epsilon$$

where treatment is the fixed effect of disturbance treatment; diversity is pre-disturbance species richness; and site is the random block effect. Pre-disturbance species richness was included in the model as a covariate to account for effects of initial species richness on compositional responses to disturbance. Initial species richness of sites has been shown to be related to post-disturbance responses (Belote et al. 2008). After plotting

the data we observed that several relationships between pre-disturbance diversity and distances followed a quadratic form, so we tested both linear and quadratic diversity terms in the models. We also investigated species compositional shifts using Euclidean distances to investigate the potential that different multivariate distance measures would yield different results. Because of similarities in results we report only patterns using Sørensen dissimilarity here, but see Appendices A–D and Belote (2008) for resistance and resilience measures using Euclidean distances in species composition between sampling times.

To investigate whether initial compositional changes were related to compositional return to pre-disturbance conditions, we calculated Pearson correlation coefficients between values of resistance and resilience. We also used *t* tests within treatments to determine whether initial compositional resistance differed from compositional resilience. Specifically, we tested whether initial compositional differences between pre-disturbance and one year post-disturbance increased, decreased, or remained the same after 10 years. At the subplot scale, we calculated change in species evenness (Pielou's *J* [McCune and Grace 2002]) between pre-disturbance and one year post-disturbance and plotted pre-disturbance richness against initial change in evenness, and change in evenness against initial compositional change, using Sørensen dissimilarity to investigate how dominance influenced patterns of community stability.

Prediction 2: species turnover.—We determined turnover of species within each functional group between each sampling time and at each spatial scale. In other words, we calculated the number of species that were “gained” (i.e., established from soil seed bank or colonized) or “lost” (i.e., locally undetected or extirpated) within each functional group between pre-disturbance and one year post-disturbance and between one year post- and 10 years post-disturbance sampling times (i.e., ephemeral species that colonized but did not persist). For the two nested scales, we composited the species lists across the plots and subplots within each experimental unit to generate richness values from the three 576-m² plots and 18 1-m² subplots per EU. We investigated whether turnover of species (i.e., species gained and lost) within functional groups differed between disturbance treatments with mixed-model ANOVAs with site entered as a random blocking factor. We calculated Spearman rank correlation coefficients between pre-disturbance richness and total species turnover (i.e., species gained and lost) to investigate how colonization and “extirpation” were related to initial diversity. We also calculated Spearman rank correlation coefficients between species turnover of functional groups with measures of resistance and resilience to investigate whether colonization or extirpation may have been responsible for the patterns of compositional stability.

Prediction 3: richness of native and nonnative species.—Total species richness was calculated as the number of

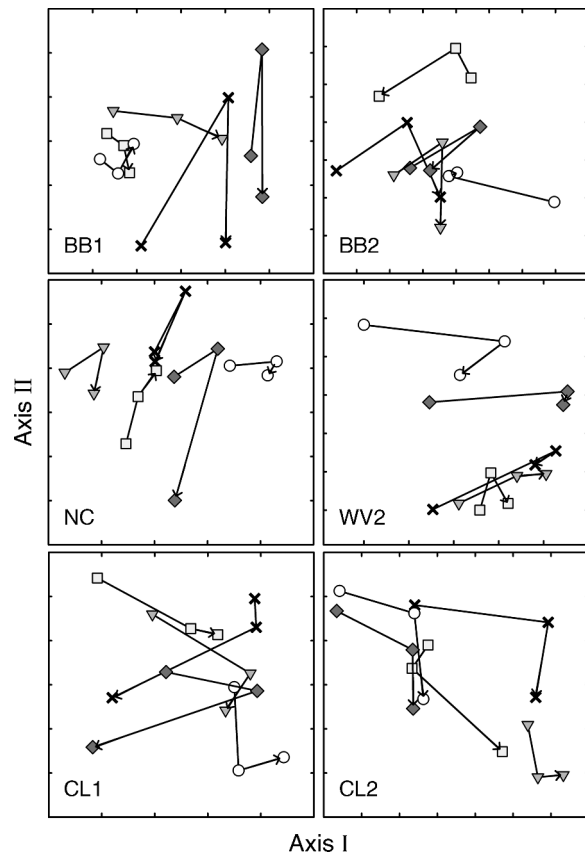


FIG. 3. DCA ordination of subplots with “successional vectors” (sensu Halpern 1988) connecting repeatedly sampled subplots receiving five disturbance treatments within six of the seven sites. Control treatments are represented as circles, herbicide treatments as hexagons, shelterwood treatments as triangles, leave-tree treatments as diamonds, and clearcuts as black crosses. The figure panels provide a depiction of compositional changes through time. (The arrowheads point to the 10-year post-disturbance samples.) Each panel is scaled for only one site. (BB1 is Blacksburg site 1; BB2 is Blacksburg site 2; CL1 is Clinch site 1; CL2 is Clinch site 2; NC is New Castle site; WV2 is West Virginia site 2; West Virginia site 1 is not shown). Visual distances should not be compared across sites.

species encountered at each spatial scale. Effects of disturbance on total species richness were analyzed separately at each spatial scale through time using a repeated-measures randomized complete block ANCOVA with the mixed model

$$\text{richness} = \mu + \text{treatment} + \text{site} + \text{time} + \text{treatment} \times \text{time} \\ + \text{pre} - \text{treatment richness} + \varepsilon$$

where μ is the overall mean; richness is the number of species observed at each scale; treatment is the effect of each disturbance treatment; site is the random block effect of site; time is the effect of time; pre-treatment richness is a covariate to account for variation in initial richness; and ε is the residual error. Residuals of all models were tested for normality using Shapiro-Wilks'

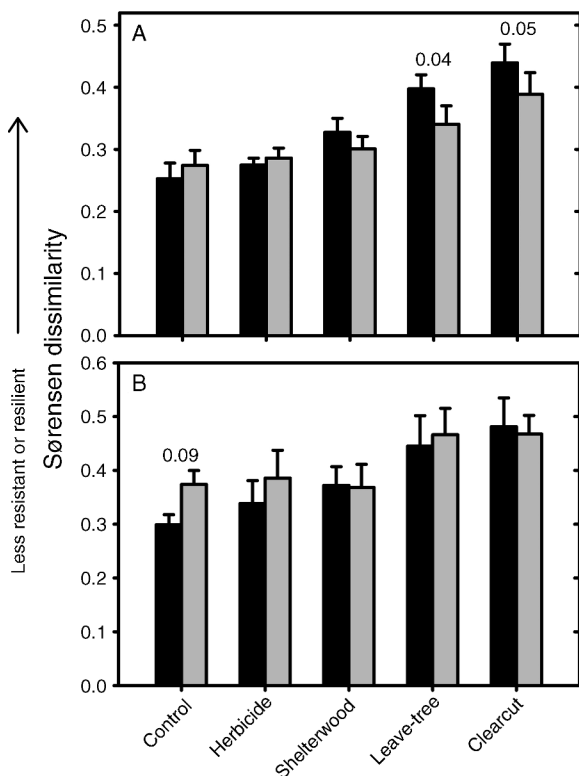


FIG. 4. Resistance and resilience of community composition within each disturbance treatment as measured by Sørensen dissimilarity index (mean \pm SE) measured at plot (panel A) and subplot (panel B) scales. Resistance (black bars) is the difference in species composition from pre-disturbance to one year post-disturbance. Resilience (gray bars) is the difference in species composition from pre-disturbance to 10 years post-disturbance. Larger values represent greater compositional differences and thus less resistant and resilient communities. Statistics for disturbance treatment effects are in Appendices A and B; P values are shown above resistance and resilience values within a treatment when they are <0.10 to highlight changes in compositional difference between 1 and 10 years post-disturbance.

W statistic (Shapiro and Wilk 1965); data not meeting this assumption were log-transformed.

We calculated the proportion of species (presented as percentage) that were nonnative (nonnative richness divided by total species richness $\times 100$) within experimental units, plots, and subplots and investigated how this proportion varied through time within disturbance treatments and among our broad life history classification. In other words, we used this analysis to ask how the proportion of nonnative species varied along the disturbance gradient and through time and whether patterns depended on scale (EUs, plots, subplots) and among trees, shrubs, forbs, graminoids, vines, and ferns.

RESULTS

Prediction 1: community resistance and resilience

Differences in species composition at the plot and subplot scales were apparent between sites and revealed

differences in physiographic provinces of the Appalachian region (patterns not shown); these compositional differences between sites were accounted for in the blocked MRPP analysis. As expected, compositional differences between treatments were not detected using MRPP before disturbances were applied for either plot ($P = 0.85$) or subplot ($P = 0.98$) scales. Following disturbance, treatments differed in species composition at the plot ($P = 0.0003$) but not the subplot scale ($P = 0.14$). After 10 years, compositional differences between treatments were still apparent at the plot ($P = 0.02$) and still not detected at the subplot scale ($P = 0.23$).

The most disturbed plots tended to be less resistant and resilient (Figs. 3 and 4). Specifically, species composition in more-disturbed treatments was more different after both 1 and 10 years than less-disturbed treatments (Fig. 4). Relationships between stability and pre-disturbance species richness were complex and were accounted for as a covariate in the ANOVA model. See Belote (2008) and Appendices A–D for additional details.

Resistance and resilience values were positively correlated ($r \geq 0.70$, $P < 0.0001$); the least resistant plots and subplots were also the least resilient. In other words, plots and subplots that experienced large shifts in species composition tended to remain different 10 years after disturbance. In fact, resistance and resilience values did not differ in most treatments (Fig. 4) at either scale, with some exceptions. At the plot scale, the leave-tree and clearcut sites tended to be more similar to pre-disturbance conditions after 10 years than after one year. At the subplot scale, we found little difference between resistance and resilience values, although the control treatment tended to be more dissimilar after 10 years than after one year following disturbance (Fig. 4). Relationships between change in evenness and initial shifts in composition were nonlinear. Subplots that experienced a decrease in evenness tended to shift composition more, whereas increases in evenness had little effect on compositional shifts (Appendix E).

Prediction 2: species turnover

Colonization of all species tended to be greater in more disturbed treatments and at all spatial scales (Table 1, Fig. 5). Colonization of all functional groups, except vines and ferns, increased at the EU and plot scale with greater disturbance intensities. At the subplot scale, only the colonization of trees and forbs increased as disturbance increased. One year after disturbance the number of species lost across all species or any functional group did not differ by treatment at any scale (Table 1, Fig. 5).

After 10 years and across all treatments, 42%, 51%, and 57% of the initial colonizers were not detected (i.e., were ephemeral) in EUs, plots, and subplots, respectively. Loss of initial colonizers was higher in more disturbed plots (Table 2, Fig. 6). We refer to these species as “ephemeral,” because they were only observed

TABLE 1. *P* values for a mixed model investigating disturbance treatment effects on the number of species colonized (1-year colonizers) and extirpated (1-year extirpated) at three spatial scales one year after experimental forest harvests treatment applications.

Colonized or extirpated	Experimental unit	Plot	Subplot
1-year colonizers			
All	<0.01	<0.01	<0.01
Tree	0.08	<0.01	<0.01
Shrub	0.02	0.02	0.54
Forb	<0.01	<0.01	0.02
Graminoid	<0.01	<0.01	0.16
Vine	0.49	0.39	0.61
Fern	0.75	0.50	0.26
1-year extirpated			
All	0.19	0.64	0.50
Tree	0.83	0.14	0.32
Shrub	0.07	0.06	0.29
Forb	0.30	0.73	0.60
Graminoid	0.56	0.24	0.32
Vine	0.68	0.38	0.33
Fern	0.29	0.88	0.06

Note: Means for each treatment and scale are in Fig. 5.

one year after disturbance, not one year before or 10 years after. Tree and forb colonizers were lost in the most disturbed sites at all scales, and colonizing graminoids at EU and plot scales after 10 years of canopy development (Table 2, Fig. 6). Total colonization of all species between one and 10 years post-disturbance did not vary between treatments. During this time, colonization of tree species tended to be greater in the herbicide treatments than in other

TABLE 2. *P* values for a mixed model investigating disturbance treatment effects.

Colonized or ephemeral species	Experimental unit	Plot	Subplot
10-year colonizers			
All	0.84	0.05	0.49
Tree	0.18	0.01	0.87
Shrub	0.27	0.85	0.05
Forb	0.73	0.17	0.27
Graminoid	0.99	0.37	<0.01
Vine	0.01	0.88	0.54
Fern	0.86	0.12	0.55
Ephemeral species			
All	<0.01	<0.01	<0.01
Tree	0.01	0.03	<0.01
Shrub	0.62	0.35	0.31
Forb	<0.01	<0.01	<0.01
Graminoid	<0.01	<0.01	0.32
Vine	0.39	0.57	0.05
Fern	0.86	0.41	0.37

Notes: The effects studied were on the number of species that colonized between 1 and 10 years post-disturbance (10-year colonizers) and species that colonized after one year but were absent 10 years following experimental forest harvests treatment (ephemeral species). Means for each treatment and scale are in Fig. 6.

treatments at the plot scale, and graminoid species colonized leave-tree and clearcut more than other treatments at the subplot scale.

Colonization by all species led to greater initial shifts in species composition and was related to compositional differences after 10 years. In other words, plots were less resistant and resilient where more species colonized

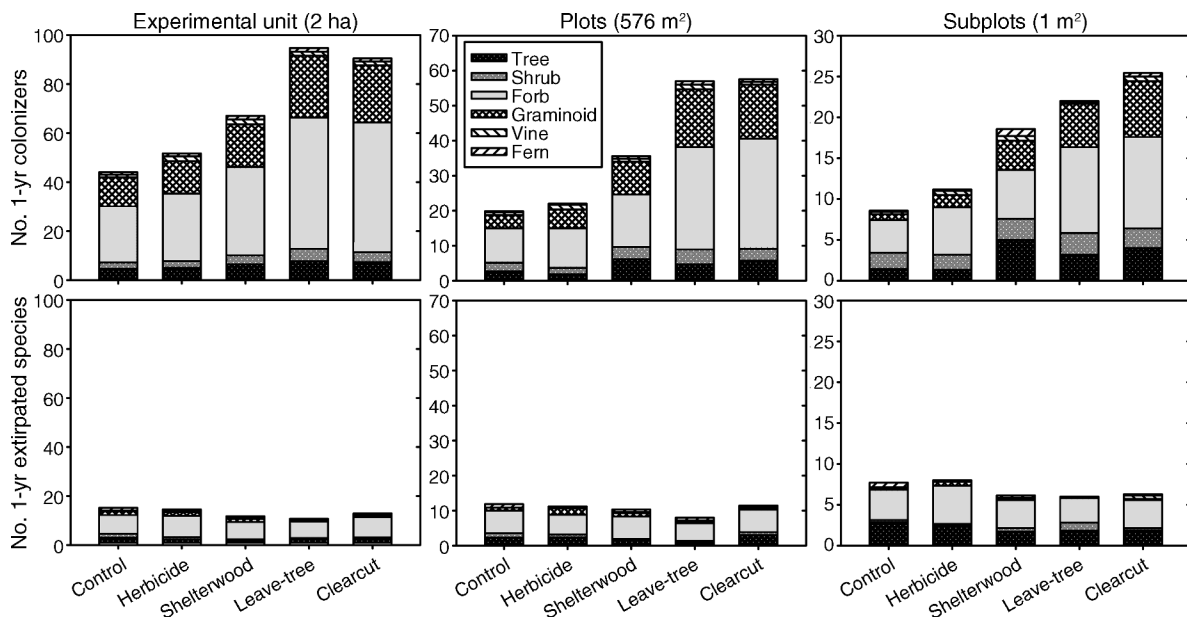


FIG. 5. Contribution of six plant functional groups to total richness of colonizers one year after disturbance (1-year colonizers; top row) and contribution of functional groups to total richness of extirpated species one year after disturbance (1-year extirpated species; bottom row) in five disturbance treatments and three spatial scales (experimental units, plots, subplots). Statistics for the total and within-functional-group tests are in Table 1.

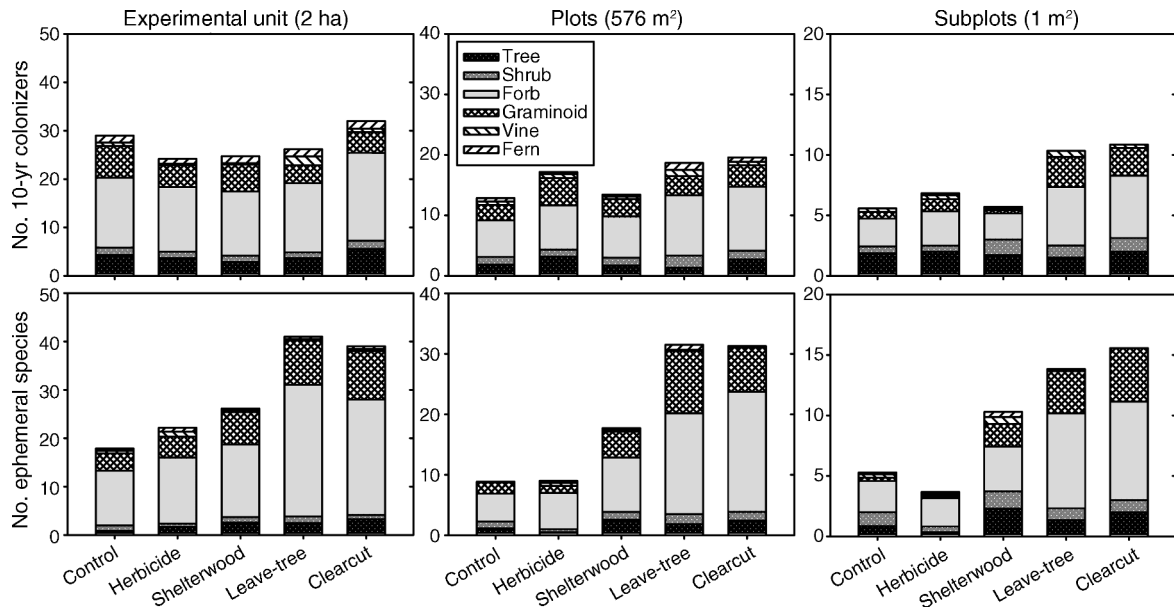


FIG. 6. The contribution of six plant functional groups to total richness of species that colonized after 10 years (10-year colonizers; top row) and richness of functional groups that colonized sites after one year but did not persist after 10 years (ephemeral species; bottom row) in five disturbance treatments and at three spatial scales (experimental units, plots, subplots). Statistics for total and within-functional-group tests are in Table 2.

(Table 3, Fig. 7). When we analyzed relationships between colonization and compositional differences by species functional groups, we found that all functional groups, except vines, were strongly positively correlated with initial species compositional shifts and differences at the plot scale (Table 3; data on individual functional groups not shown). Colonization of all functional groups except vines and ferns were related to resilience measures (difference in composition between pre-disturbance and 10 years post-disturbance). At the subplot scale, colonization of trees, forbs, and graminoids were correlated with initial compositional shifts after one year (Table 3, Fig. 8). Total initial species extirpation, or extirpation of functional groups, were uncorrelated with resistance and resilience at either scale, but loss of trees was positively correlated with resilience metrics (i.e., loss of trees led to less resilience).

Pre-disturbance richness and richness of colonizing species were not correlated at the plot ($r = 0.01$, $P = 0.96$) or subplot ($r = 0.24$, $P = 0.19$) scale. Pre-disturbance richness was not correlated with richness of species loss at the plot scale ($r = -0.15$, $P = 0.42$), but was positively correlated with richness of species loss at the subplot scale ($r = 0.68$, $P < 0.01$).

Prediction 3: richness of native and nonnative species

Richness of all native and nonnative species sampled at the EU scale increased following disturbance (Table 4, Fig. 9). Native species richness increased and was maintained through time, but nonnative species richness decreased 10 years after disturbance (Table 4, Fig. 9). Neither native nor nonnative richness at the EU scale

depended on a treatment \times time interaction. Native richness at the plot scale depended on a disturbance treatment \times time interaction (Table 4, Fig. 9). Nonnative richness was greater in more disturbed plots but did

TABLE 3. Spearman correlation coefficients relating the number of initial extirpated and colonized species.

Extirpated or colonized	Resistance		Resilience	
	Plot	Subplot	Plot	Subplot
Extirpated				
All	-0.13	0.00	-0.13	0.08
Trees	0.06	-0.14	0.20	-0.08
Shrubs	-0.35	0.16	-0.23	0.10
Forbs	-0.16	-0.01	-0.22	0.08
Graminoids	-0.17	0.13	-0.11	0.26
Vines	0.20	0.13	0.13	0.04
Ferns	-0.10	-0.17	-0.27	0.03
Colonized				
All	0.83	0.63	0.71	0.39
Trees	0.60	0.45	0.61	0.17
Shrubs	0.52	-0.02	0.44	0.02
Forbs	0.75	0.52	0.74	0.34
Graminoids	0.86	0.56	0.45	0.33
Vines	0.09	-0.03	0.13	-0.12
Ferns	0.38	0.28	0.19	0.24

Notes: Coefficients related the number of initial extirpated and colonized species (total and functional groups) one year after disturbance to resistance and resilience of community composition (Sørensen dissimilarity index) at two spatial scales. Values in boldface type indicate significant correlations ($P < 0.05$). Plots showing relationships between all colonizers and extirpated species and resistance and resilience are in Fig. 7; subplot data are in Fig. 8. Positive correlations suggest that more colonizing species caused a greater shift in species composition (i.e., community composition was less resistant).

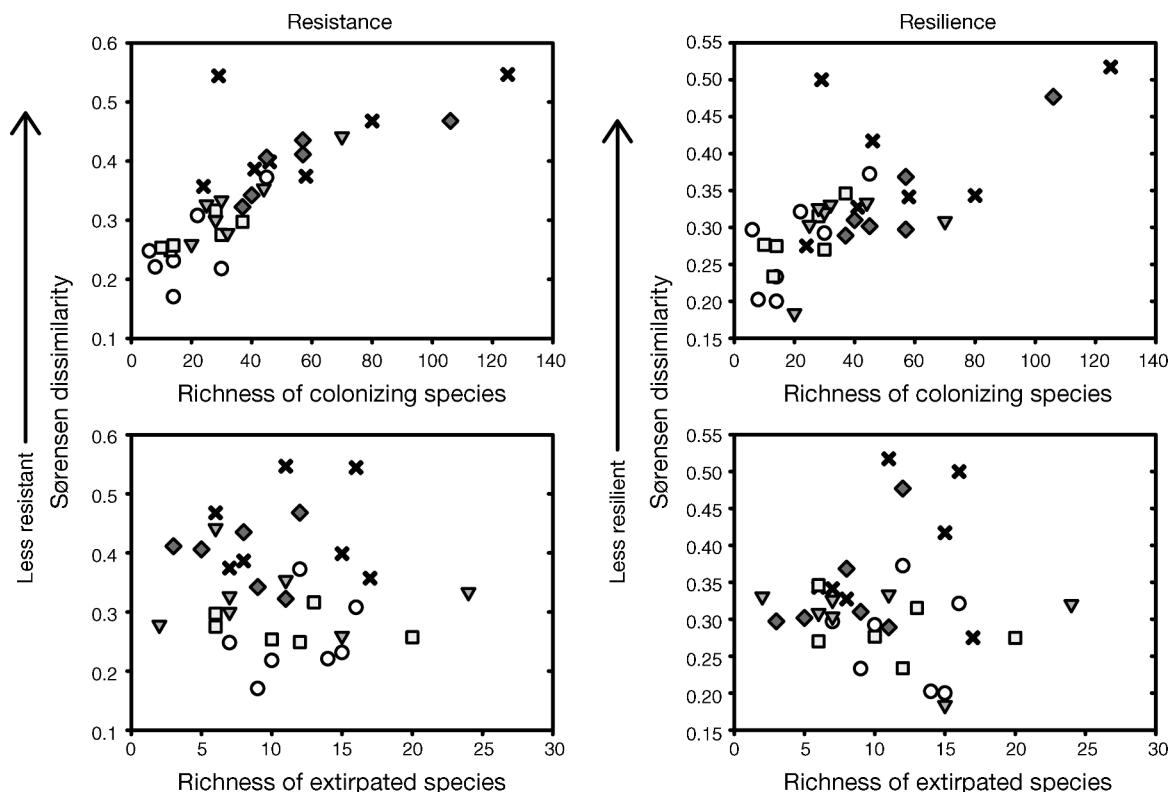


FIG. 7. The relationship between initial (i.e., 1-year) colonizing and extirpated species richness, and resistance or resilience based on the Sørensen dissimilarity index at the plot scale. Correlation statistics are shown in Table 3.

not depend on time. At the subplot scale, native richness depended on disturbance treatment and time, but not on their interaction (Table 4, Fig. 9). Nonnative richness in the subplots only marginally depended on disturbance treatment.

The percentage of nonnative plant species to total richness varied by disturbance treatment, through time, and by spatial scale and plant functional group. The proportion of nonnative to native species increased following disturbance, especially in the more intensively harvested units, but declined following 10 years of forest canopy development (Appendix F). Nonnative proportion also increased with spatial scale: as the size of sampling scale increased, nonnative species made up proportionally more of the total species composition, especially of graminoids and forbs.

DISCUSSION

As observed elsewhere throughout the Appalachian Mountains (Elliott and Knoepp 2005) and other forested regions (Reiners 1992, Thomas et al. 1999, Halpern et al. 2005, McDonald et al. 2008), timber harvesting tended to shift species composition, which lasted at least 10 years, and increased overall plant diversity. Resistance and resilience of community composition following disturbance were mediated by several factors including intensity of timber-harvesting

disturbance, increases in light availability (Atwood et al. 2011), and regional species pools (Belote et al. 2009), which allowed colonization of new species into the sites.

Our first prediction that community resistance and resilience would depend on disturbance intensity was supported. As in other forested systems (Halpern 1988, Rydgren et al. 2004), species composition tended to shift more dramatically and remained more dissimilar in the most disturbed treatments, even after 10 years, when stump sprouting and seed regeneration formed a dense stand of small-diameter trees with a closed canopy (Atwood et al. 2009). Compositional differences caused by the initial colonization of species immediately following disturbance prevented many sites from returning to pre-disturbance compositions, even though nearly half of the colonizers were ephemeral and not observed during canopy closure 10 years after disturbance.

The number of colonizing species was not correlated with the number of species present before disturbance (i.e., species occurring before disturbance did not exclude colonizers after disturbance). However, colonizing species did influence composition and diversity after disturbance. Despite differences across our sites, we found that treatments of increasing disturbance tended to increase colonization and diversity, supporting our second prediction. Colonization was greatest in the most

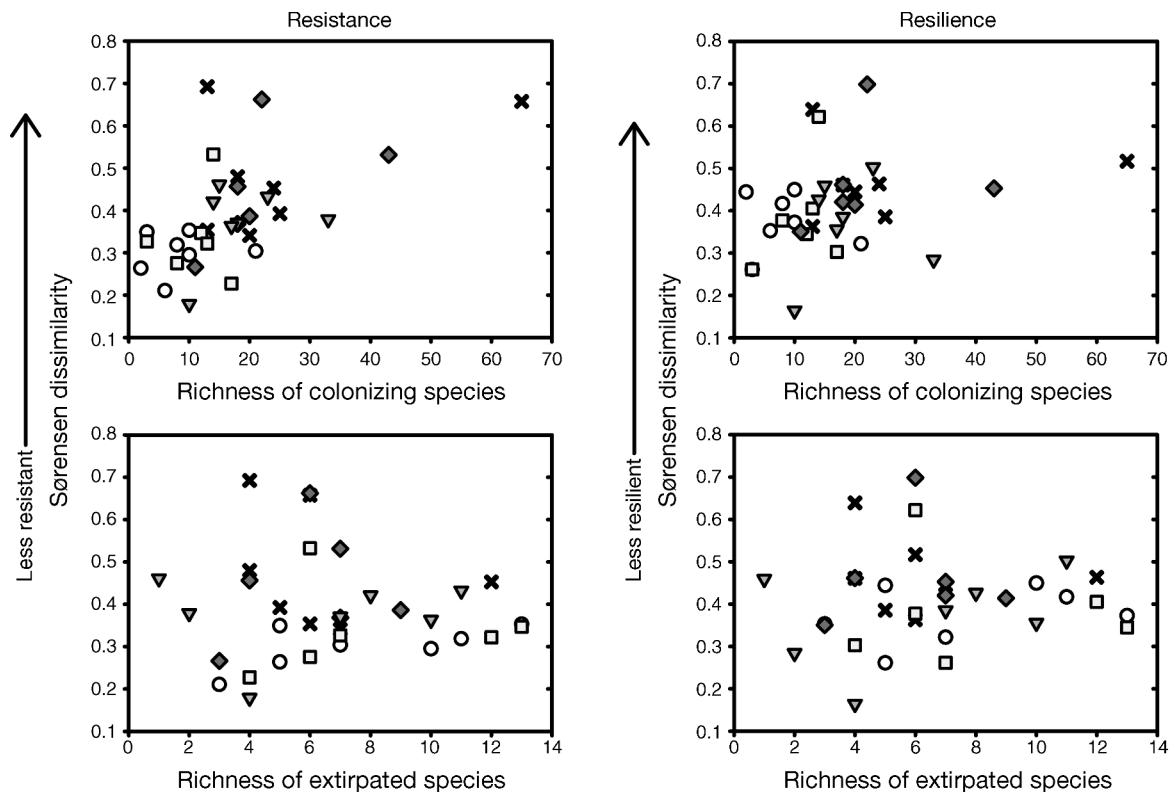


FIG. 8. The relationship between initial (i.e., 1-year) colonizing and extirpated species richness, and resistance or resilience based on Sørensen dissimilarity at the subplot scale. Correlation statistics are shown in Table 3.

disturbed treatments, and most colonizing species were forbs and graminoids. Graminoids and forbs are also the most diverse functional groups across all of the sites and typically possess traits that make them good dispersers into new habitats (Gilliam and Roberts 2003). Many of these colonizing species did not persist through canopy closure, probably because of their intolerance to shade cast by tree regeneration. After 10 years, extirpation of colonizers (i.e., ephemeral species) led to a decrease in diversity at smaller spatial scales. However, at the largest spatial scale, diversity of native species did not tend to decrease after 10 years, but nonnative species richness decreased.

In subplots, pre-disturbance richness and richness of species extirpation were correlated, suggesting that species-rich sites may be more prone to local extirpation events than species-poor sites at small scales. Sankaran and McNaughton (1999) found similar patterns in savanna-grassland communities of India, which they attribute to the presence of greater numbers of infrequent species in the most diverse sites before disturbance. Infrequent species had a greater tendency to be locally extirpated after disturbance, which is likely true in our system. While species loss was greater in more diverse sites, richness of lost species was not related to resistance or resilience and did not vary by treatment.

Other studies have documented potential long-term effects of extirpation of species in the Appalachian region following timber harvesting (Duffy and Meier 1992), but these initial results were met with considerable criticism (Elliot and Loftis 1993, Johnson et al. 1993). Duffy and Meier (1992) compared old-growth forests with second-growth forests and found old-growth forests to be more diverse than second-growth forests. Additionally, they found that the oldest second-

TABLE 4. *P* values for effects of disturbance treatment and time, and their interaction, on richness of native and nonnative species at three spatial scales.

Spatial scale and factor	Native	Nonnative
Experimental unit		
Treatment	<0.01	0.05
Time	0.56	<0.01
Treatment \times time	0.38	0.29
Plot		
Treatment	<0.01	<0.01
Time	0.01	0.13
Treatment \times time	<0.01	0.28
Subplot		
Treatment	<0.01	0.08
Time	<0.01	<0.01
Treatment \times time	0.16	0.78

Note: Means and standard errors are shown in Fig. 9.

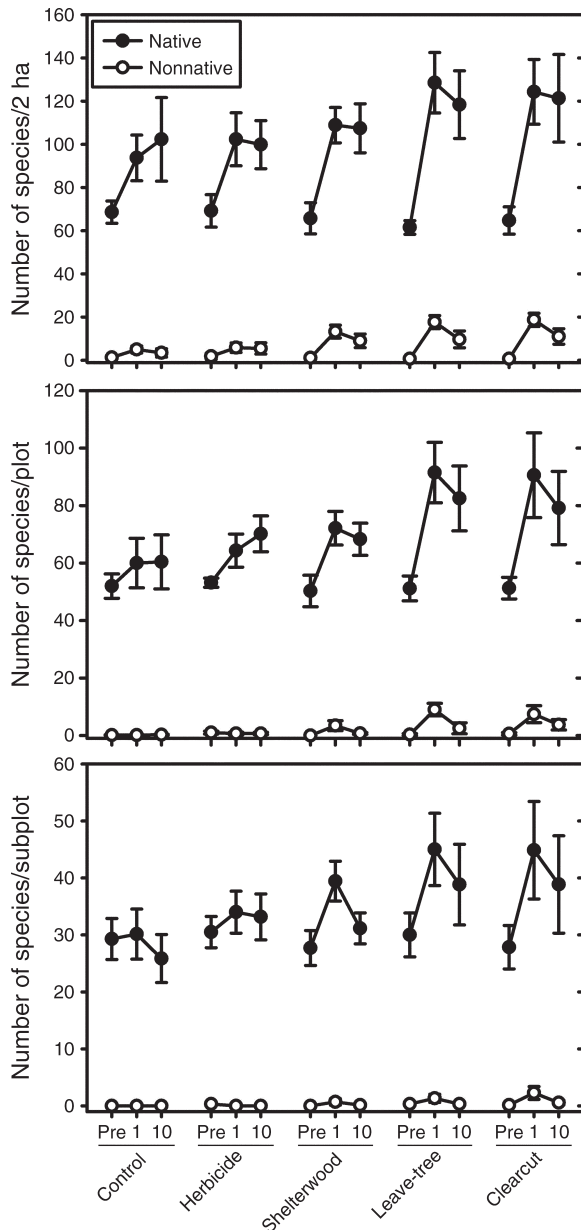


FIG. 9. Changes in richness (mean \pm SE) of all native and nonnative species through time within five disturbance treatments and at three spatial scales. Data for pre-treatment, one year post-treatment, and 10 years post-treatment are shown. Statistics for treatment and time effects are in Table 4. The nonnative proportion of total richness by plant functional groups is in Appendix F.

growth forests had as few species as the younger second-growth forests, suggesting lasting suppression of species diversity after timber harvesting. Our sites differed in composition of dominant tree species compared with those studied by Duffy and Meier (1992), but our results, in conjunction with other studies conducted in the central Appalachians (Gilliam 2002), suggest that timber harvesting may not have the suppressive effect on

plant species diversity reported by Duffy and Meier (1992). However, at the time of our 10-year post-disturbance sample, our uncut control sites were only slightly older (60–100 years old) than the second-growth forests Duffy and Meier (1992) sampled (45–87 years old). Therefore, it is possible that species may have been lost during the historic timber harvests that occurred across our sites during the early to mid-1900s. In other words, the pre-disturbance richness of our undisturbed forests may have been influenced by historic timber harvests (cf. Wyatt and Silman 2010), although we have no way of testing this hypothesis.

Many understory species in Appalachian oak forests are perennial and maintain belowground roots and stems that contribute to their individual resilience to disturbance (i.e., the ability to persist following intense harvesting disturbance). Appalachian oak forests have historically experienced various disturbances or perturbations other than timber harvesting, including windthrow (Everham and Brokaw 1996), fire (Delcourt and Delcourt 1997, Reilly et al. 2006), and ice damage (Hooper et al. 2001), among others (Roberts and Gilliam 1995). While many species can persist following disturbance events (cf. Dietze and Clark 2008), more research is needed to understand species-specific and site-specific responses to timber harvesting (Gilliam and Roberts 2003).

Native diversity was maintained at the largest spatial scales even during the stem exclusion stage of forest succession, which was likely the result of spatial heterogeneity, wherein native shade-intolerant forbs persisted or new species colonized patches where canopy closure did not occur due to skid trail networks. Skid trails that were established during timber harvesting were in some cases maintained after 10 years. Grass species were sown into trails immediately after timber harvesting to prevent soil erosion, which may competitively exclude tree seedling establishment. Alternatively, increased soil compaction of the trails may have prevented tree regeneration. Soil compaction may have been maintained even after the initial establishment via deer and researchers who frequently used the trails. These hypotheses were not tested in the current study, but other studies suggest that soil compaction (Zenner et al. 2007) or other complex interactions (Rudgers et al. 2007) can limit tree establishment in grass-dominated sites and contribute to differences in species composition (Zenner and Berger 2008). Whatever the mechanisms, skid trail patches remained sites for shade-intolerant forbs and graminoids to persist. Other recent studies have documented dramatic shifts in species composition in skid trails (Zenner and Berger 2008), which may provide refugia for ruderal species including nonnative species to persist during canopy closure. These refugia for nonnative ruderal species (mostly graminoids and forbs, but also tree *Ailanthus altissima* (Mill.) Swingle) likely explain why the nonnative proportion of the species composition was much higher at large scales



PLATE 1. Examples of the time series included in this study of compositional stability of vascular plant communities in Appalachian forests. (Upper left) Mature Appalachian oak forest before timber harvest disturbance (southwestern Virginia, USA). (Upper right) An example of the most intense timber harvesting disturbance, clearcut, approximately one year following treatment. (Lower left) Timber harvesting that leaves some mature trees representative of the leave-tree or shelterwood treatments (photo was taken approximately one year following treatment application). (Lower right) An example of forest development and recovery about 10 years after disturbance where high densities of small-diameter trees reduce light availability to the understory community. Photo credits: B. T. Belote.

where sampling included these patches. Additional research is needed to understand how skid trails contribute to larger-scale diversity following timber harvesting (Belote et al. 2009), and serve as potential sources of soil erosion (Hood et al. 2002) and nonnative species seed pools, even as forests recover from disturbance (Call and Nilsen 2003, Zenner and Berger 2008).

Variability in site responses to disturbance limits our ability to predict how timber harvesting affects species diversity and compositional responses (Roberts and Gilliam 1995). While all sites in this study were dominated by oak species (Atwood et al. 2009), there are considerable site and regional compositional differences of species, which made investigating individual species responses to treatments difficult. There were several generalist forb species that colonized disturbed treatments at multiple sites including *Erechtites hieraciifolia* (L.) Raf. ex DC., *Potentilla* spp., *Hieracium*

spp., *Lobelia inflata* L., *Conyza canadensis* L. Cronquist, *Solidago* spp., *Pseudognaphalium obtusifolium* (L.) Hilliard and B. L. Burt, *Symphyotrichum* spp. Nees, and *Phytolacca americana* L. Graminoids that colonized multiple sites after disturbance included *Agrostis* spp., *Dactylis glomerata* L., *Danthonia* spp., *Andropogon virginicus* L., and *Dichanthelium* spp. (Hitchc. and Chase) Gould. Woody species that colonized multiple sites included the tree *Robinia pseudoacacia* L. and species of shrubs from the genus *Rubus*.

Compositional dynamics in uncut controls

Compositional shifts within the uncut control treatments were significant, which may be an indication of several factors. First, observer bias in species identification could explain some colonization and extirpation events. Dubious shifts in composition might be detected if a species was identified differently or missed between years. This explanation appears unlikely in our study.

We examined compositional and diversity patterns at the generic level, where misidentification would be less likely, and found very similar patterns in all analyses of stability and diversity. Second, disturbance associated with edges of experimental units and skid trail roads may have impacted the uncut control treatments. Control treatments were typically located next to treatments receiving significant canopy disturbance, and in some cases skid trails used by logging machinery bisected small portions of the control experimental units. This undoubtedly led to increases in diversity at the experimental unit scale and may have led to changes in composition and diversity at the nested scales. However, within the nested plots and subplots, no direct disturbance was observed in control treatment units. The third explanation for changes in composition and diversity of control plots is natural variation caused by various biotic and abiotic mechanisms such as precipitation, herbivory, competition, seed production, and gap formation. Control treatments, while not experiencing timber harvesting, did occasionally experience natural disturbances throughout the duration of the study, including windthrow and ice damage. Lastly, all sites were harvested within the past 60 to 100 years prior to experiment initiation. Bunn et al. (2010) recently found that diversity of understory plant communities decreased between 1978 and 2007 in plots that were logged in the 1920s, whereas plant diversity did not change in historically unlogged plots. While different from patterns observed in our system over 10 years, dynamics in our control plots may be the result of long-term changes during forest aggradation (Bormann and Likens 1979). Clearly, compositional shifts occur in forest understories through time, which complicates our ability to quantify compositional resilience as a return to some "stable" pre-disturbance condition.

Conclusions

Results from our study suggest that stability of plant communities following logging depends on complex factors including disturbance intensity, initial diversity of habitats, and spatial scale. In general, compositional stability decreased with disturbance intensity (i.e., species composition shifted more dramatically in the most disturbed areas, and tended to be dissimilar even after 10 years of forest aggradation) and was strongly driven by colonizing species. The relationship between diversity and stability was more complex following disturbance. Intermediate levels of diversity were more stable in some instances, whereas areas with fewer species were more stable in other instances. While compositional shifts were significant, our initial results suggest that few species are lost due to disturbance. The most intense forest management disturbance alternatives tested in this experiment may actually represent an intermediate level of possible human disturbances to these systems, where species diversity is predicted to be highest based on intermediate disturbance hypotheses

(Huston 1994). Future monitoring of these sites will help determine the long-term persistent changes in species composition in response to disturbance, and whether long-term directional shifts occur because of climate change and nonnative species.

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SUPPLEMENTAL MATERIAL

Appendix A

P values for ANCOVA terms investigating measures of resistance and resilience of vascular plant community composition to five disturbance treatments and pre-disturbance richness based on abundance data (*Ecological Archives* A022-032-A1).

Appendix B

P values for ANCOVA terms investigating measures of resistance and resilience of vascular plant community composition to five disturbance treatments and pre-disturbance richness based on presence-absence data (*Ecological Archives* A022-032-A2).

Appendix C

Plot-scale relationships between pre-disturbance richness and measures of resistance and resilience based on species frequency (*Ecological Archives* A022-032-A3).

Appendix D

Subplot-scale relationships between pre-disturbance richness and measures of resistance and resilience based on species importance values (*Ecological Archives* A022-032-A4).

Appendix E

Relationship between change in evenness of subplots following disturbance treatment application and Sørensen dissimilarity index (*Ecological Archives* A022-032-A5).

Appendix F

Mean percentage of nonnative species at three scales, at three times, and among five disturbance treatments (*Ecological Archives* A022-032-A6).