

Do natural disturbances or the forestry practices that follow them convert forests to early-successional communities?

J. STEPHEN BREWER,¹ CHRISTINE A. BERTZ, JEFFERY B. CANNON, JASON D. CHESSER, AND ERYNN E. MAYNARD

Department of Biology, University of Mississippi, P.O. Box 1848, University, Mississippi 38677 USA

Abstract. Stand-replacing natural disturbances in mature forests are traditionally seen as events that cause forests to revert to early stages of succession and maintain species diversity. In some cases, however, such transitions could be an artifact of salvage logging and may increase biotic homogenization. We present initial (two-year) results of a study of the effects of tornado damage and the combined effects of tornado damage and salvage logging on environmental conditions and ground cover plant communities in mixed oak–pine forests in north central Mississippi. Plots were established in salvage-logged areas, adjacent to plots established before the storm in unlogged areas, spanning a gradient of storm damage intensity. Vegetation change directly attributable to tornado damage was driven primarily by a reduction in canopy cover but was not consistent with a transition to an early stage of succession. Although we observed post-storm increases of several disturbance indicators (ruderals), we also observed significant increases in the abundance of a few species indicative of upland forests. Increases in flowering were just as likely to occur in species indicative of forests as in species indicative of open woodlands. Few species declined as a result of the tornado, resulting in a net increase in species richness. Ruderals were very abundant in salvage-logged areas, which contained significantly higher amounts of bare ground and greater variance in soil penetrability than did damaged areas that were not logged. In contrast to unlogged areas severely damaged by the tornado, most upland forest indicators were not abundant in logged areas. Several of the forest and open-woodland indicators that showed increased flowering in damaged areas were absent or sparse in logged areas. Species richness was lower in salvage-logged areas than in adjacent damaged areas but similar to that in undamaged areas. These results suggest that salvage logging prevented positive responses of several forest and open-woodland species to tornado damage. Anthropogenic disturbances such as salvage logging appear to differ fundamentally from stand-level canopy-reducing disturbances in their effects on ground cover vegetation in the forests studied here and are perhaps more appropriately viewed as contributing to biotic homogenization than as events that maintain diversity.

Key words: *biotic homogenization; canopy gap; forest understory; ground cover vegetation; habitat specialist; Mississippi, USA; ruderal; salvage logging; soil disturbance; species diversity.*

INTRODUCTION

Understanding precisely how natural and anthropogenic disturbances affect forest plant communities is crucial for managing forests to maintain biodiversity and wildlife habitat quality. Stand-replacing disturbances in mature forests are traditionally seen as events that revert forests to early stages of succession (Connell and Slatyer 1977, but see Abrams and Scott 1989). Because different sets of species are affiliated within recently disturbed and long undisturbed forests, nonequilibrium maintenance of species diversity is hypothesized to be favored by intermediate frequencies of disturbance (the intermediate disturbance hypothesis [Connell 1978]). In addition, patchiness in the intensity of stand-level

disturbance (Boucher et al. 1990, Brokaw and Walker 1991, Foster and Boose 1992) and the combination of large, multiple-treefall and small, single-treefall gaps may be important for maintaining species diversity (Watt 1947, Denslow 1980, Canham and Marks 1985, Runkle 1985). Hence, the frequency, size, and intensity of disturbances potentially influence species diversity and must be considered in forest management decisions.

Although stand-level disturbances potentially maintain plant species diversity by balancing gains and losses of species, such a result may be of limited conservation value if gains result from increases in widespread ruderals and losses result from reductions of late-successional specialists (Alverson et al. 1994). Such changes are an example of increased biotic homogenization and potentially mask a loss in regional or global species diversity (McKinney and Lockwood 1999). Such threats have led some authors to suggest setting aside minimally managed forested areas that are large enough

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¹ E-mail: jbrewer@olemiss.edu

to enable disturbance-sensitive species to recover from large-scale natural disturbances (Pickett and Thompson 1978, Alverson et al. 1994). The necessity of establishing such reserves to minimize biotic homogenization, however, depends on whether large-scale disturbances substantially increase the abundance of widespread ruderal species and decrease late-successional forest specialists.

With respect to ground cover vegetation (including tree seedlings) in forests, species reductions and gains following disturbances and the resulting changes in biotic homogenization depend in part on how different species respond to reductions of the tree canopy (Canham and Marks 1985, Collins et al. 1985, Nelson and Halpern 2005, Roberts 2007). Opportunistic ruderal species that are intolerant of shade grow rapidly following a large-scale disturbance (Marks 1975, Zangerl and Bazzaz 1983). In contrast, shade-dependent, late-successional species (inflexible shade species sensu Collins et al. 1985), if they are not directly killed by the disturbance, are predicted to respond negatively to increased light levels following canopy reduction (Boardman 1977, Nelson and Halpern 2005). Likewise, seedlings of some shade-tolerant tree species either do not show dramatic increases in growth or show decreased growth above a given light intensity (Logan and Krotkov 1968, Marks 1975, Canham and Marks 1985). Patterns of species replacement following natural disturbances do not always follow the sequence predicted by shade tolerance, however (Peterson and Pickett 1995). Much of the ground cover vegetation of mature forests may be dominated by late-successional species that can tolerate shade but benefit greatly from increased light levels and thus survive, grow faster, and reproduce following disturbance (light-flexible species sensu Collins et al. 1985, Johnson et al. 2002). As a result, canopy damage can lead to accelerated succession (Abrams and Scott 1989, Abrams and Nowacki 1992, Rebertus and Meier 2001).

Successional responses to tree canopy disturbance must be considered within the context of long-term fire suppression within the forest prior to the canopy disturbance. Within upland forests that have had a history of frequent fires prior to widespread fire suppression, the ground cover vegetation may be dominated by light-flexible species that are relics of a fire-maintained open woodland that existed at the site prior to prolonged fire suppression (Hutchinson et al. 2005, Nowacki and Abrams 2008, Brewer and Menzel 2009). In addition, however, light-flexible, late-successional forest species may be abundant in the ground cover of such forests as a result of fire suppression. Hence, determining whether ground cover vegetation of a naturally disturbed forest reverts to earlier stages of succession or exhibits accelerated forest succession in part requires identifying the habitat affiliations of established perennial species present in the ground cover before the disturbance, and then measuring growth and

reproductive responses of those species to the opening of the tree canopy following a stand-level disturbance.

In addition to tree canopy disturbances, responses of ground cover plant species to a disturbance event depend on the extent of soil disruption associated with or following the disturbance event (Roberts 2007). Soil disturbances potentially cause much more mortality of established ground cover vegetation than do canopy disturbances (Cooper-Ellis et al. 1999). Hence, patterns of succession may reflect interspecific differences in colonizing ability following soil disturbance (Connell and Slatyer 1977, Roberts 2007). Traditional succession theory predicts that opportunistic ruderal species that are widely dispersed or produce a persistent seed bank will colonize first following a large-scale disturbance (Marks 1974). In contrast, poor dispersal and the absence of a persistent seed bank of some late-successional understory species often preclude their rapid recovery from such disturbances (Matlack 1994). The effects of increased soil disturbances on light-flexible ground cover species (many of which may be long-lived perennials with low seed production) may differ fundamentally from the effects of increased light availability associated with canopy reduction on these species (Roberts 2007, Surrette and Brewer 2008, Brewer and Menzel 2009). Whereas such species may respond positively to canopy gaps associated with stand-level disturbances, they may respond negatively to soil disturbances (Surrette and Brewer 2008). The net effect of natural disturbances that create both canopy gaps and soil disturbance (e.g., disturbed soil associated with uprooted trees) on ground cover vegetation therefore depends on whether the canopy or the disruption of the soil is affected more by the disturbance event.

Understanding how ground cover vegetation responds to natural disturbances is complicated by post-disturbance salvage logging (logging of damaged trees that follows a natural disturbance [Foster et al. 1997, Lindenmayer and Noss 2006, Peterson and Leach 2008a, b]). Timber recovery operations can create more soil disturbance than the natural disturbance (Foster et al. 1997). Salvage logging and natural disturbances can differ in their effects on local environmental conditions (Van Nieuwstadt et al. 2001, Peterson and Leach 2008a, b, Palik and Kastendick 2009). Given the potentially different effects of canopy reduction and soil disturbances associated with logging (Zenner and Berger 2008), post-disturbance salvage logging could counter any positive responses (e.g., increased growth or flowering) of established ground cover species to canopy reduction, slow the rate of succession, and/or reduce environmental heterogeneity associated with downed trees (Foster and Boose 1992, Lindenmayer and Ough 2006, Peterson and Leach 2008a). Therefore, to understand how stand-level disturbances affect ground cover vegetation in forests, it is important to distinguish the effects of natural disturbances from those of the

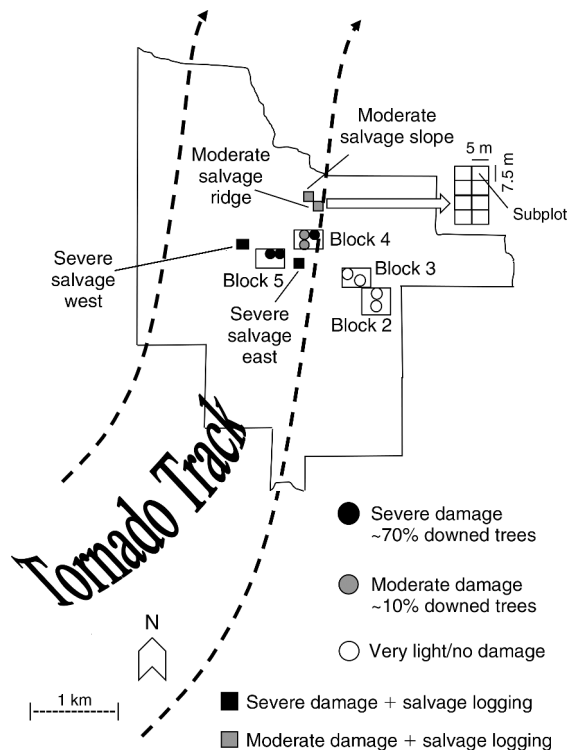


FIG. 1. Map of the Tallahatchie Experimental Forest (Mississippi, USA) showing the 2008 tornado track, blocks, plots, and subplots.

combined effects of natural disturbances and post-disturbance salvage logging.

In the current study, the occurrence of tornado damage in established long-term research plots provided a unique opportunity to investigate the combined effects of natural disturbance and post-disturbance management activities on ground cover vegetation and the future condition of fire-suppressed upland forests. We present initial results of a study of the effects of tornado damage and the combined effects of tornado damage and salvage logging on environmental conditions and ground cover plant communities in mixed oak–pine forests in north central Mississippi. All forests had a long history (~30 years) of fire suppression in the 20th century prior to recent, sporadic attempts to implement a prescribed burning program. We tested the following three hypotheses: (1) Differences in ground cover composition between damaged and undamaged stands are correlated with differences in canopy cover (and to a lesser extent soil disturbance), whereas differences between logged and unlogged stands are most strongly correlated with differences in soil disturbance and bare ground. (2) Vegetation differences between damaged and undamaged stands are the result of increases in light-demanding and light-flexible species, which include ruderals and some fire-dependent and forest indicators, but with no significant losses of forest indicators. (3) Differences between logged and unlogged tornado-

damaged stands mostly reflect the replacement of forest indicators by ruderals, a finding that suggests a reduction in diversity via increased biotic homogenization that is not necessarily reflected in species richness changes.

METHODS

Description of study sites and stand structure and composition before the tornado

The upland hardwood–pine forests studied here were located within the northern hilly coastal plains of Mississippi (Holly Springs National Forest and the Tallahatchie Experimental Forest within the Greater Yazoo River Watershed, USA; 34.5° N, 89.43° W). Soils were acidic sandy loams and silt loams on the ridges and acidic loamy sands on side slopes and in the hollows (Surrette and Brewer 2008). Readily erodible sands within the top 10–30 cm overlay silts within the soils studied here (Morris 1981). Historically (i.e., in the early 1800s, before extensive logging and fire suppression), open, self-replacing stands of fire-tolerant tree species such as *Quercus velutina* Lam., *Q. marilandica* Munchh., *Q. stellata* Wangenh., *Q. falcata* Michx., and *Pinus echinata* Mill. dominated the upland landscape of this portion of hilly coastal plains (Surrette et al. 2008). As a result of fire suppression in the 20th century, second-growth stands developed following extensive logging and currently have approximately twice the stand density of mature stands in the early 1800s (Brewer 2001). Also, tree species that for the most part were historically restricted to, or that reached tree size primarily within floodplains (e.g., *Liquidambar styraciflua* L., *Acer rubrum* L., *Quercus alba* L., and *Nyssa sylvatica* Marshall), commonly occur in these upland forests today and dominate the understory (Surrette et al. 2008). These stands are now dominated in the overstory by a mixture of some of the upland oak species (e.g., *Q. velutina*, *Q. stellata*, *Q. falcata*, but not *Q. marilandica*), pines (mostly *P. echinata*), some species historically common in floodplains (e.g., *Q. alba*, *Liquidambar styraciflua*), and some species that were common in both uplands and floodplains historically (e.g., *Carya* Nutt. spp. [Surrette et al. 2008]).

Design and layout of sampling plots

In 2003, we established two 10 × 30 m plots nested within each of four 75 × 70 m blocks for determining species composition of ground cover vegetation (Fig. 1). All blocks were chosen and positioned to meet the following criteria: (1) located on upland soils (i.e., not floodplains or floodplain terraces); (2) contained mature (90–100+ yr old) trees; (3) burned no more than three times since 1978, preceded by a prolonged period (30+ years) of active fire suppression, and (4) contained a ridge and a lower slope or hollow.

A tornado of notable size led to an unprecedented opportunity to study tornado and salvage logging effects on vegetation in this area. The tornado struck the area

on 5 February 2008 and generated moderate to severe damage in two of the four blocks. Block 5 experienced severe damage, with >70% of stems ≥ 10 cm dbh downed. Block 4 experienced moderate damage (10% of trees being snapped or uprooted) to severe damage. Neither of the two 10×30 m plots within block 4 experienced severe damage, however. Therefore, to capture severe damage within this block, we established an additional 10×30 m plot in April 2008. Damage severity was judged by the percentage of downed (but not necessarily dead) canopy trees, which we assumed were toppled by the storm, by virtue of sprouting buds or in the case of pines by the persistence of needles that were present before the storm. The remaining blocks experienced minimal damage (0–1% downed trees).

In April of 2008, we established two 10×30 m groundlayer/sapling plots adjacent to (but outside of a 30–50 m buffer belt surrounding) blocks 4 and 5 in areas marked by the staff of the Holly Springs Ranger District for salvage timber harvest. Timber harvest began in June 2008 and continued in the area until the end of 2008. The 10×30 m plots were established in these areas immediately following timber harvest (before significant colonization of vegetation). After all plots were established, we subdivided each plot within blocks 2, 3, 4, and 5, the four salvage logged plots, and the new severely damaged plot into eight 5×7.5 m subplots to obtain more detailed and precise estimates of ground cover plant species composition and associated environmental variation (Fig. 1). The new, severely damaged, unlogged plot within block 4 contained an additional (ninth) subplot to capture more of the observed tree damage.

Initial measurements of environmental variation

In June and September 2008, immediately after timber harvest had ceased adjacent to block 5, we measured soil penetrability, percentage of bare ground, and canopy cover within the following plots: the ridge plot of block 5 (severely damaged but not logged), the plot within a salvage-logged plot adjacent to block 5 to the east (severely damaged and logged), and a ridge plot in block 3 (undamaged and not logged). Initial measurements of canopy cover within the unlogged plots were compared with prestorm (2006) measurements of this variable (obtained from Surrrette and Brewer [2008]) to determine changes caused by the tornado. Follow-up measurements of soil penetrability, bare ground, and canopy cover were taken in September 2009 to assess delayed changes in these variables as a result of the storm and logging. Soil penetrability was measured at 10 cm depths during a rain-free period using a soil penetrometer. Overhead canopy cover was estimated near ground level (1 m) using a spherical densitometer. Initial differences in canopy cover and percentage of bare ground were examined using one-way ANOVA and subsequent Tukey's tests, whereas initial and delayed differences in variance in soil penetrability were examined using *F* tests and Bonferroni adjustments for multiple comparisons.

Changes in canopy and percentage of bare ground between 2008 and 2009 were analyzed using univariate repeated-measures ANOVA. ANOVAs and *F* tests were conducted using JMP, Version 5.0.1 (SAS 1989–2002).

Measurements of environmental variation among subplots in 2009

In addition to measuring time-sensitive environmental variables in a subset of plots in 2008 and 2009, we measured less time-sensitive environmental variables after all logging operations within the area had ceased. Between late April and October 2009 (after leaf flush and before significant leaf fall) the following environmental measurements were taken within all subplots of all plots (a total of 105 subplots within 13 plots): percent canopy cover, leaf litter percent cover, percent soil disturbance (which was the sum of percent uproot pits, percent uproot mounds, and percent vehicle tracks/skid trails), percent bare ground, percent cover by dead and downed crowns, and percent cover by live, downed crowns. Overhead canopy cover was estimated near ground level as described in *Initial measurements of environmental variation*. In addition, two soil cores down to 20 cm were taken at each subplot to quantify average percent sand, silt, clay, and organic matter per subplot. Percent sand and silt were measured using a traditional suspension method, and percent organic matter was estimated from dry mass loss upon combustion in a muffle furnace. Northerly aspect was estimated at each subplot using a compass and trigonometric conversion (north-facing = 1 and south-facing = -1).

A previous study showed that the elevation of a subplot below the closest ridge (hereafter relative elevation) was among the best predictors of local plant species richness and the relative abundance of open-woodland indicators and shady mesic forest indicators at these sites, and thus was an important covariable (Surrrette and Brewer 2008). Relative elevation was determined by measuring slope angle and distance between the nearest point on the ridge and the center of the subplot. We used a clinometer to measure the slope angle between a point on the ridge and the center of the sub-subplot. Distances were measured between these points, and elevation of each subplot below the closest associated ridge was calculated trigonometrically. Absolute elevation above sea level was estimated from these measurements of relative elevation by obtaining the elevation of benchmarks with the aid of a GPS unit (*x*-*y* coordinates) and a topographic map (*z* coordinate).

Measurements of vegetation

We quantified ground cover vegetation within all subplots in the spring of 2009 and continued through October 2009. Ground cover vegetation (including forbs, grasses, tree seedlings, small shrubs, vines) was quantified by counting stems or caespitose clumps of all herbaceous plants, as well as all woody stems <1 m tall.

Coverage by vines (e.g., *Vitis rotundifolia* Michx., *Lonicera japonica* Thunb.) was quantified by measuring ground coverage and assuming that coverage of a square decimeter of ground was equivalent to one stem. Each subplot was divided into quarters to ensure greater precision of the counts. The counts for each quarter were summed across the subplots. In addition to obtaining total counts on all species, we quantified flowering of common indicators of open woodlands, forests, or disturbed areas and calculating the proportion of stems with flowering stalks. We also quantified obvious signs of herbivory (e.g., by white-tailed deer, *Odocoileus virginianus*). Because the intensity of herbivory was apparently low and sporadic in the forests studied here, however, the results of these observations were not analyzed.

Statistical analysis of relationships between ground cover vegetation and environmental variation associated with tornado damage and logging

Because the effects of a single storm event could not be truly replicated, we used a multivariate regression approach to examining ground cover vegetation responses to the effects of tornado damage and salvage logging. We examined the relationship between ground cover species composition and environmental variation within subplots to determine if those environmental variables predicted to distinguish damaged/logged stands from undamaged/unlogged stands accounted for a significant amount of variation in ground cover species composition.

We used distance-based redundancy analysis (db-RDA), a constrained ordination technique (Legendre and Anderson 1999), to relate Bray-Curtis distances among subplots in species space in 2009 to measured environmental variation. Db-RDA differs from traditional RDA in that any species distance measure can be used. Db-RDA therefore avoids the problems associated with using Euclidean distances and the assumption of linear responses of species distributions to environmental gradients (Legendre and Anderson 1999). All abundance data were $\log + 1$ transformed prior to conducting analyses to give greater weight to the influence of rare species (Clarke and Gorley 2006). To assess compositional differences in relation to tornado damage alone, we used db-RDA to examine the relationship between post-storm species composition and environmental variation within only those blocks that were not logged (blocks 2, 3, 4, and 5). The analysis included the following environmental covariables: percent canopy cover, relative elevation, percent organic matter, sand/silt ratio, percent clay, percent soil disturbance, percent bare ground, percent cover by leaf litter, percent cover by dead crowns, and northerly aspect. Absolute elevation was not included in the analysis to avoid multicollinearity caused by its very high correlation with relative elevation ($r > 0.8$). Likewise, percent cover by live, downed crowns was

not included in the analysis to reduce multicollinearity caused by its very highly negative correlation with percent cover by leaf litter and percent bare ground ($r < -0.8$). A second db-RDA was done to examine the relationship between post-storm species composition and environmental variation within storm-damaged subplots that had either been logged or had not been logged (i.e., those within blocks 4 and 5 and in adjacent salvage-logged subplots). We eliminated blocks 2 and 3 (the undamaged blocks) from consideration. We used the same environmental variables as in the analysis of damage severity, alone, except that in the second analysis, percent cover by leaf litter was also removed from the analysis to avoid multicollinearity caused by its high negative correlation with percent bare ground ($r < -0.8$). We used the 2008 or early-2009 estimates of percent bare ground in the severely damaged and logged plots to reduce the effect of colonizing vegetation on bare ground percentage. The species-environment relationships were presented in joint-vector ordination diagrams upon which symbol-coded damage severity or logging intensity categories of the subplots were superimposed. All percentage data were converted to proportions and arcsine square-root transformed, and the sand/silt ratio was log-transformed prior to the analysis.

The relative importance of salvage-logging plus tornado damage vs. tornado damage alone in explaining post-disturbance variation in species composition was assessed using principal coordinate analysis (PCO; Gower 1966) based on Bray-Curtis distances and symbol-coding subplots according to logging and tornado damage. To explore the association between ground cover plant diversity and the type and severity of disturbance, we superimposed vectors corresponding to two different measures of diversity (richness and Simpson's index) as well as the degree of biotic homogenization. (The calculation of the last parameter is described in *Interpretation of relationships between ground cover vegetation and tornado damage and logging: implications for biotic homogenization*.)

Changes in species composition in tornado-damaged and undamaged subplots

To determine the extent to which post-storm associations between vegetation and environmental conditions were the result of changes in composition (as opposed to pre-storm relationships), we examined changes in 2006 (pre-storm) and 2009 (post-storm) abundances using permutation multivariate analysis of variance (perMANOVA; Anderson 2001), Spearman rank correlations of the increase in abundance (2009 abundance – 2006 abundance) against the decrease in canopy cover within a plot (2006 canopy cover – 2009 canopy cover), and weighted averages of change in relation to canopy reduction (ordinal change $\times$ [2006 canopy cover – 2009 canopy cover]). Because nested subplots were not

established until 2009, total abundance of each species was estimated in each of the eight plots in 2006 (as in Surrette and Brewer 2008) and pooled across all eight subplots within each of the eight plots in 2009. Total abundance was estimated in five ordinal categories (as in Surrette and Brewer 2008). Multivariate statistical analyses were run using Minkowski distances among samples. PerManova was conducted using Primer version 6 (perManova+; Anderson et al. 2008) and Spearman correlations were conducted using JMP v. 5 (SAS 1989–2002).

Interpretation of relationships between ground cover vegetation and tornado damage and logging: implications for biotic homogenization

We used an objective method for distinguishing between species that were indicative of anthropogenically disturbed habitats (e.g., ruderals: opportunistic species associated with soil disturbances created by human activities) and those indicative of more natural or premodern ecosystems, including upland forests, shady mesic forests, and fire-maintained woodlands, savannas, and grasslands [Brewer and Menzel 2009]. We calculated habitat indication for each identified species using the method described in Brewer and Menzel (2009) and Brewer (2010). We used a binary species by habitat matrix derived from a list of 251 plant species encountered in surveys of 34 10×30 m ground cover vegetation plots in mature upland, oak- and oak-pine-dominated forests and associated edges and canopy openings throughout north-central Mississippi (Surrette and Brewer 2008). Overall, these species were associated with 65 different named habitats, as defined by Jones (2005) or Radford et al. (1968). Lists of all identified habitats and species are presented in Appendices A and B.

We identified four general habitat categories of interest: anthropogenically disturbed, upland forest, open woodlands/savannas, and shady mesic forest. Using our habitat $\times$ species matrix, we calculated Sorensen's quotient of similarity between each tabulated specific habitat and each of the four general habitat categories of interest (pooled from a subset of specific habitats; Appendix A). We then inserted the resulting community similarity quotient back into the habitat $\times$ species matrix (replacing the ones) and calculated weighted averages for each species for each of the four general habitat categories. These scores represented unrefined habitat indication scores (Appendix B). To account for correlations of scores among the four habitat categories, we regressed the scores for each habitat category against the remaining three and obtained the residual scores. These residual scores represented refined habitat indication scores and thus quantified each species' indication of a given specific habitat (Appendix B).

The refined scores were used as species weights to determine the weighted mean fidelity of each subplot to

anthropogenically disturbed habitats, upland forests, open woodlands/savannas, or shady mesic forests. Interpretation of all ordination results was accomplished by superimposing simple correlation vectors associated with the weighted mean fidelity of subplots to each of the four general habitat categories.

An index of biotic homogenization was calculated for each subplot and was equivalent to the weighted mean fidelity to anthropogenically disturbed habitats minus weighted mean fidelities to the remaining three habitat categories. High biotic homogenization indices therefore indicated dominance by widespread ruderals and/or habitat generalists, whereas low values indicated dominance by habitat specialists. In north Mississippi, ruderals and habitat generalists tend to have larger geographical ranges than do habitat specialists (Brewer 2010), and thus contribute more to biotic homogenization.

RESULTS

Environmental conditions immediately following tornado damage and logging

In June 2008 (the first growing season following the tornado and associated logging), average percent canopy cover was significantly lower in the damaged-only and logged plots than in the undamaged plot, but did not differ between the damaged-only and logged plots (Fig. 2a; one-way ANOVA, $F_{2,21} = 95.3$; $P \ll 0.01$; Tukey's test $P < 0.05$; $n = 8$ subplots per plot; 24 total). In addition, percent canopy cover in the damaged-only plot was much lower in 2008 (24.7%) than before the tornado in 2006 (76%). No such reduction occurred in the undamaged plot ($84\% \pm 3\%$ vs. $83\% \pm 4\%$ [mean $\pm$ SE] in 2008 and 2009, respectively). There was a significant plot $\times$ year interaction after the storm (repeated-measures ANOVA, $F_{2,21} = 17.8$; $P \ll 0.01$). Canopy cover increased in the damaged-only plot but decreased in the logged plot between 2008 and 2009, while remaining about the same in the undamaged plot (Fig. 2b; contrast $F_{1,21} = 35.6$; $P \ll 0.01$).

In 2008, percent bare ground was significantly higher in the logged plot than in the damaged-only plot or the undamaged plot in 2008, whereas the amount of bare ground did not differ significantly between damaged-only and the undamaged plot (Fig. 2a; one-way ANOVA $F_{2,21} = 106.2$; $P \ll 0.01$; Tukey's test, $P < 0.05$). There was also a significant plot $\times$ year interaction (repeated-measures ANOVA $F_{2,21} = 125.5$; $P \ll 0.01$). Percent bare ground decreased significantly between 2008 and 2009 in the logged plot, while remaining relatively constant in the damaged-only and undamaged plots (Fig. 2b; contrast $F_{1,21} = 251.1$; $P \ll 0.01$).

The variance in soil penetrability was significantly greater in the logged plot than in the other two plots in 2008 (variance in the force required for surface soil penetration (in kilograms per square centimeter) = 32.5 vs. 4.7 kg/cm² for the logged plot and unlogged plots,

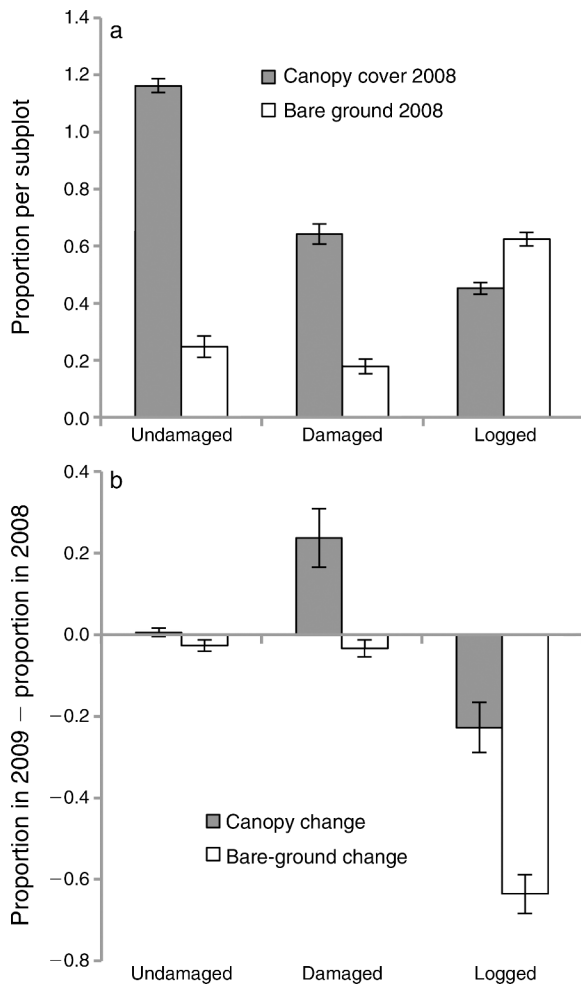


FIG. 2. (a) Proportions of canopy cover and bare ground in 2008 and (b) subsequent changes between 2008 and 2009 in an undamaged plot, a plot that was damaged but not logged, and a plot that was severely damaged and logged. Proportions were arcsine square-root transformed.

respectively; $F_{7,15} = 6.9$, Bonferroni-adjusted $P = 0.0034$). In 2009, the variance in soil penetrability was not greater in the logged plot than in the other two plots [101.9 vs. 54.7 kg/cm², respectively; $F_{7,15} = 1.9$, $P = 0.15$]. The greater variance in the logged plot in 2008 resulted from more extreme values of soil penetrability. Both the lowest and highest values of soil penetrability occurred in the logged plot (ranging from 7 to 29.5 kg/cm² force required for penetration). The most consistent values of penetrability occurred in the damaged-only plot (ranging from 15.5 to 25.3 kg/cm²).

Relationships between ground cover vegetation and environmental variation associated with tornado damage

With respect to subplots that were not logged but that varied in the severity of tornado damage, post-storm species composition was significantly and most strongly

correlated with percent canopy cover, supporting the hypothesis that tornado damage affected species composition by reducing canopy cover. Percent canopy cover by far had the strongest partial correlation with db-RDA axis 1 (partial $r = -0.77$; $P \ll 0.01$; $n = 72$ subplots), which sorted subplots according to damage severity (axis 1 scores increased with increasing severity of tornado damage; Fig. 3a). Axis 1 explained 13.7% of the total and 38.3% of the fitted variation in species composition. Percent cover by leaf litter was also significantly negatively correlated with axis 1 (partial $r = -0.39$), as were percent bare ground (partial $r = -0.33$) and sand/silt ratio (partial $r = -0.23$). Axis 2 (which explained 9.8% of the total variation and 27.2% of the fitted variation) largely indicated an elevation, soil texture, and aspect gradient (Fig. 3a). Relative elevation and sand/silt ratio were positively correlated with axis 2 (partial $r = 0.70$ and 0.57 , respectively), whereas subplots on more north-facing slopes tended to have lower axis 2 scores (partial r for aspect = -0.30).

Native disturbance indicators showed a positive association with damaged areas with open canopies and low surface leaf litter (Fig. 3b). Weighted mean fidelity of subplots to disturbed habitats was positively correlated with db-RDA axis 1 ($r = 0.35$; $P < 0.01$). A good example of a disturbance indicator that was positively associated with open canopies in damaged areas was *Erechtites hieraciifolia* (L.) Raf. (Appendix C). The abundance of mesic forest indicators as a group showed a weak negative relationship with tornado damage and canopy openness ($r_{\text{axis1}} = -0.24$; $P = 0.06$; Fig. 3b). Most of this negative relationship could be attributed to low abundance of the mesophytic herb *Maianthemum racemosum* L. (Link.), in damaged areas; Appendix C). Mesic forest indicators represented a much smaller fraction of the undisturbed forest than did upland forest indicators (-0.09 weighted mean fidelity [for mesic forests] ± 0.009 vs. 0.189 weighted mean fidelity [for upland forests] ± 0.011 [mean $\pm$ SE]) and comprised no greater fraction of the undisturbed forest than did disturbance indicators (-0.101 ± 0.006) or open-woodland indicators (-0.106 ± 0.009).

In contrast to disturbance indicators and mesic forest indicators, open-woodland indicators and upland forest indicators were more strongly associated with site variation in elevation, soil texture, and aspect than with tornado-caused canopy openings (i.e., axis 2 variation; Fig. 3b). Open-woodland indicators were more abundant on more exposed slopes at higher elevations and sandier soils, whereas upland forest indicators were more abundant on less exposed slopes at lower elevations and silty soils (Fig. 3b). Open-woodland indicators and upland forest indicators showed mixed associations with tornado-caused canopy openings. Examples of open-woodland/savanna indicators that were abundant within damaged areas with open canopies included *Galactia volubilis* (L.) Britton, *Verbesina helianthoides* Michx., and *Helianthus*

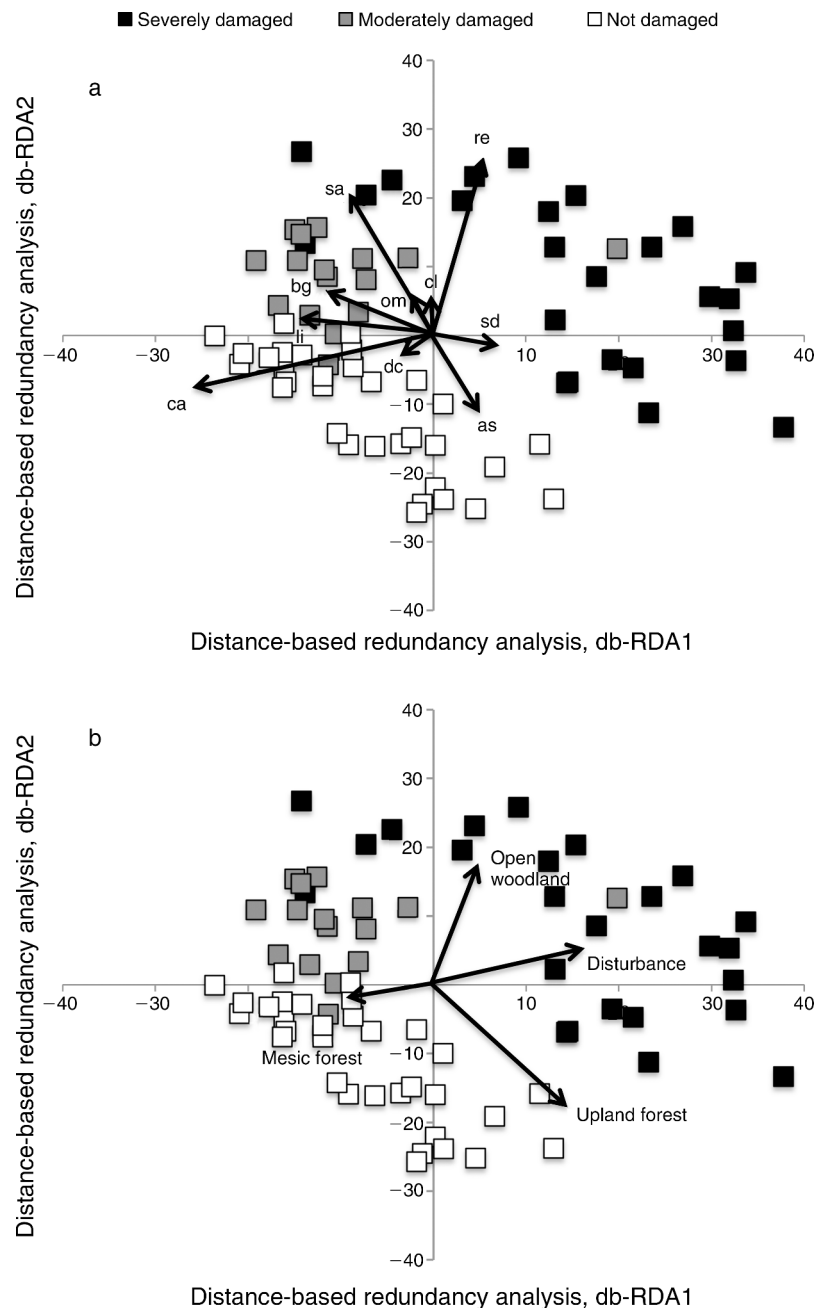


FIG. 3. Distance-based redundancy analysis of the relationship between 2009 species composition and environmental conditions in unlogged damaged and undamaged plots showing (a) partial correlation vectors of environmental variables and (b) correlation vectors of weighted mean fidelity to four general habitat categories. Abbreviations for predictor variables: as, northerly slope aspect; bg, % percent bare ground; ca, % canopy cover; cl, % clay; dc, % cover by dead crowns; li, % cover by surface litter; om, % soil organic matter; re, relative elevation; sa, sand to silt ratio; sd, % soil disturbance. Definitions of damage levels: severe damage, 70% of stems ≥ 10 cm dbh (i.e., tree-sized) downed; moderate damage, $\sim 10\%$ of tree-sized stems downed; no damage, $< 1\%$ tree-sized stems downed. Axis 1 explained 38.3% of the fitted and 13.7% of the total variation in species composition; axis 2 explained 27.2% of the fitted and 9.8% of the total variation in species composition.

microcephalus Torr. and A. Gray (Appendix C). Several species that were good indicators of upland forests (e.g., *Dichanthelium boscii* (Poir.) Gould and C. A. Clark, *Chasmanthium sessiliflorum* (Poir.) L. G. Clark, and *Callicarpa americana* L.) were more

abundant in tornado-damaged areas with open canopies than in undamaged areas (Appendix C). Other species that were good indicators of upland forests (e.g., *Monotropa hypopithys* L., *Aristolochia serpentaria* L., and *Desmodium nudiflorum* (L.) DC) were negative-

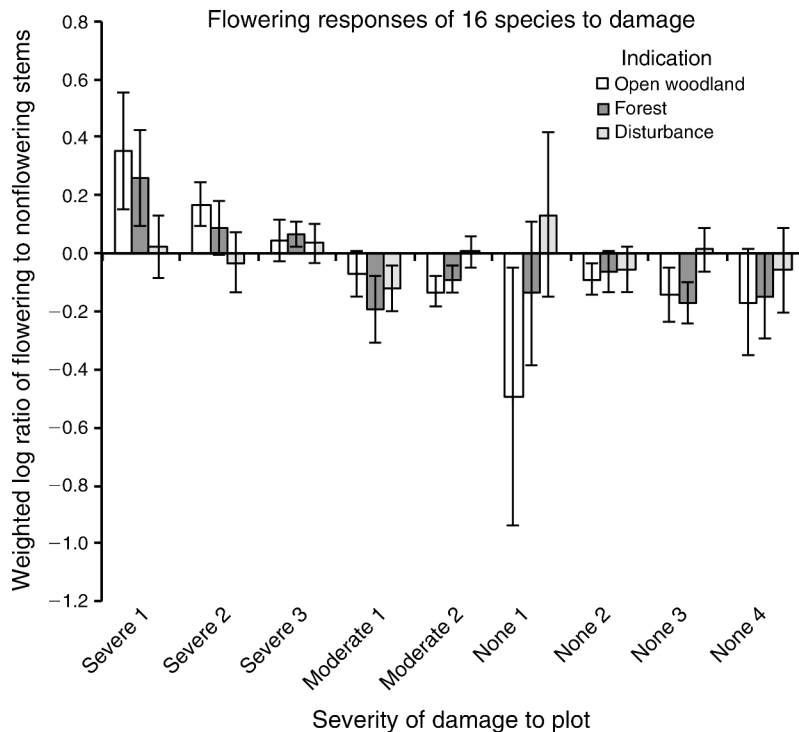


FIG. 4. Log ratio of flowering to nonflowering stalks pooled across 16 species, each weighted by its habitat indication score. (The species included were those that showed variation in flowering percentages among plots; i.e., *Andropogon virginicus* L., *Chasmanthium sessiliflorum*, *Clitoria mariana*, *Desmodium laevigatum*, *Desmodium nudiflorum*, *Desmodium viridiflorum*, *Elephantopus tomentosus*, *Helianthus microcephalus*, *Lespedeza repens* L. (Barton), *Monarda fistulosa* L., *Pityopsis graminifolia* (Michx.) Nutt., *Schizachyrium scoparium* (Michx.) Nash, *Solidago odora*, *Solidago ulmifolia*, *Symphyotrichum shortii* (Lindl.) G.L. Nesom, and *Symphyotrichum patens* (Aiton) G.L. Nesom.)

ly associated with open canopies in damaged areas (Appendix C).

Changes in species composition in relation to canopy cover/tornado damage were more consistent with an addition of species indicative of disturbed habitats rather than with a replacement of forest indicators by these species. Permutation MANOVA of the plots established prior to the tornado revealed a significant effect of year (pseudo- $F_{1,5} = 6.3$; permutation $P < 0.01$; total sample size of eight plots), as well as a significant damage severity-by-year interaction (pseudo- $F_{2,5} = 6.1$; permutation $P < 0.01$). The between-plots effect of damage severity was not statistically significant (pseudo- $F_{2,5} = 1.9$; Monte Carlo-adjusted permutation $P = 0.07$). Most of the disturbance indicators that were abundant in the damaged areas after the tornado (e.g., *Erechtites hieraciifolia*, *Conyza canadensis* (L.) Cronquist, and *Microstegium vimineum* (Trin.) A. Camus) were either absent or sparse in these areas before the tornado, which contributed greatly to the damage severity-by-year interaction (Appendix C). Likewise, some upland forest indicators (e.g., *Dichantherium boscii*, *Chasmanthium sessiliflorum*, and *Callicarpa americana*) increased in response to the damage (Appendix C). In contrast, some of the open-woodland indicators that were abundant in damaged areas after

the tornado (e.g., *Galactia volubilis*, *Verbesina helianthoides*) were not substantially less abundant in these areas before the storm (Appendix C), whereas at least one open-woodland indicator (*Helianthus microcephalus*) appeared to increase in response to damage (Appendix C). As for the upland forest indicators that were less abundant in damaged areas, only one species (*Monotropa hypopithys*) showed evidence of being negatively affected by the tornado. This species was not observed in any plot in 2006 and was observed only in undamaged or moderately damaged plots in 2009. Finally, although *Maianthemum racemosum*, a shady mesic forest indicator, was not as abundant in damaged areas as in undamaged areas after the tornado, evidence for a tornado-caused decrease in this species was weak (Appendix C). Hence, there was little evidence of a general decline in shady mesic forest indicators as a result of the tornado.

Although relatively few open-woodland indicators increased significantly in response to tornado damage, flowering of many of these species as well as that of some forest indicators was greater in tornado-damaged areas than in undamaged areas (Fig. 4). In contrast, there was no evidence of a positive effect of tornado damage on the flowering of perennial disturbance indicators (e.g.,

Elephantopus tomentosus L.) present in both damaged and undamaged forests (Fig. 4).

Relationships between ground cover vegetation and environmental variation associated with damage combined with salvage logging

Post-storm/logging plant species composition varied in relation to percent bare ground, a variable that was apparently influenced by the intensity of salvage logging (Fig. 5a). The db-RDA diagram in Fig. 5 shows species composition responding to a gradient in percent bare ground along a diagonal from the upper left to lower right corner of the ordination (Fig. 5a). Percent bare ground was significantly positively correlated with axis 1 (partial $r = 0.36$; $P < 0.01$; $n = 72$ subplots) and significantly negatively correlated with axis 2 (partial $r = -0.33$; $P < 0.01$). Axis 1 accounted for 15.1% of the total variation in species composition, whereas axis 2 accounted for 6.2% of the total variation in species composition (Fig. 5a). This gradient in percent bare ground sorted subplots with respect to the intensity of logging. Hence, species that were most abundant in subplots with high percent bare ground tended to occur in severely damaged areas that were logged, whereas species that were most abundant in subplots with little bare ground tended to be associated with unlogged areas, irrespective of the level of tornado damage. Moderately damaged areas that were logged had intermediate species composition and amounts of bare ground (Fig. 5a). Several other variables were highly correlated with either axis 1 or axis 2. Of these, however, only sand/silt ratio and aspect sorted subplots along a gradient of logging intensity (Fig. 5a).

In general, disturbance indicators as a group were positively associated with logged areas, whereas upland forest indicators were negatively associated with logged areas (Fig. 5b). Weighted mean fidelity of subplots to disturbed habitats was strongly positively correlated with db-RDA axis 1 ($r = 0.71$; $P \ll 0.01$), whereas weighted mean fidelity to upland forests was strongly negatively correlated with db-RDA axis 1 ($r = -0.66$; $P \ll 0.01$) and significantly positively correlated with db-RDA axis 2 ($r = 0.25$; $P = 0.04$). Disturbance indicators such as the nonnative *Digitaria sanguinalis* (L.) Scop. were abundant in logged areas but absent or rare in unlogged areas (Table 1). In contrast, upland forest indicators (e.g., *Quercus alba* and *Q. velutina* seedlings) were much more abundant in unlogged areas than in logged areas (Table 1). Two of the upland forest indicators that responded positively to tornado damage (e.g., *Chasmanthium sessiliflorum* and *Dichanthelium boscii*) were not positively associated with logged stands (Table 1). *Callicarpa americana*, however, was abundant within logged stands (Table 1).

The differences in composition between logged and unlogged tornado-damaged plots were large compared to differences between damaged plots and undamaged plots (Fig. 6). This was because ruderal species were

more abundant in damaged plots that were logged than in damaged plots that were not logged, and because upland forest indicators were more abundant in damaged and undamaged plots that were not logged than in damaged plots that were logged (Fig. 6). As a result, biotic homogenization was greatest in the damaged plots that were also logged and lowest in the undamaged plots. Species richness was highest in the severely damaged plots that were not logged due primarily to an increase in ruderals (Fig. 6). Species diversity, however, was highest in the undamaged plots, and those damaged plots that did not experience dramatic increases of (and thus dominance by) *Chasmanthium sessiliflorum* (Fig. 6).

DISCUSSION

Environmental changes associated with tornado damage and salvage logging

Tornado damage and salvage logging of tornado-damaged areas differed dramatically in terms of their effects on environmental conditions during the first two years after the storm. The tornado on 5 February 2008 altered the environment of the forests studied here primarily by opening the canopy. Despite a significant reduction in canopy cover caused by the tornado in 2008, partial recovery of the canopy was evident by 2009. Because many of the damaged trees were not killed by the storm, canopy cover increased significantly during the second growing season after the storm (2009), relative to what was observed in undamaged areas. Such a “re-leafing” response was observed in a previous study of experimental, simulated hurricane damage in central Massachusetts (Cooper-Ellis et al. 1999). Although there was soil disturbance associated with uprooted trees in our study, the effect of the tornado on soils was small compared to the effect on overhead canopy. Tornado damage was not associated with a substantial increase in the percentage of bare ground during the first growing season following the storm. Hence, the most significant environmental change caused by the tornado to which ground cover vegetation was likely to respond was an increase in light levels, although we cannot discount the possibility of changes in soil temperature, moisture, or rates of mineralization of limiting nutrients.

In contrast to tornado damage, the environmental variable that most strongly distinguished logged plots from unlogged plots that were moderately or severely damaged was percent bare ground during the first growing season after logging. Percent bare ground in a logged plot diminished by the second growing season after logging, as colonization by ruderal species increased. In contrast to the effects of tornado damage, canopy cover decreased between the first and second years after logging. This reduction in canopy cover likely resulted from delayed mortality of live, standing trees in the logged plots. We saw evidence of damage to these

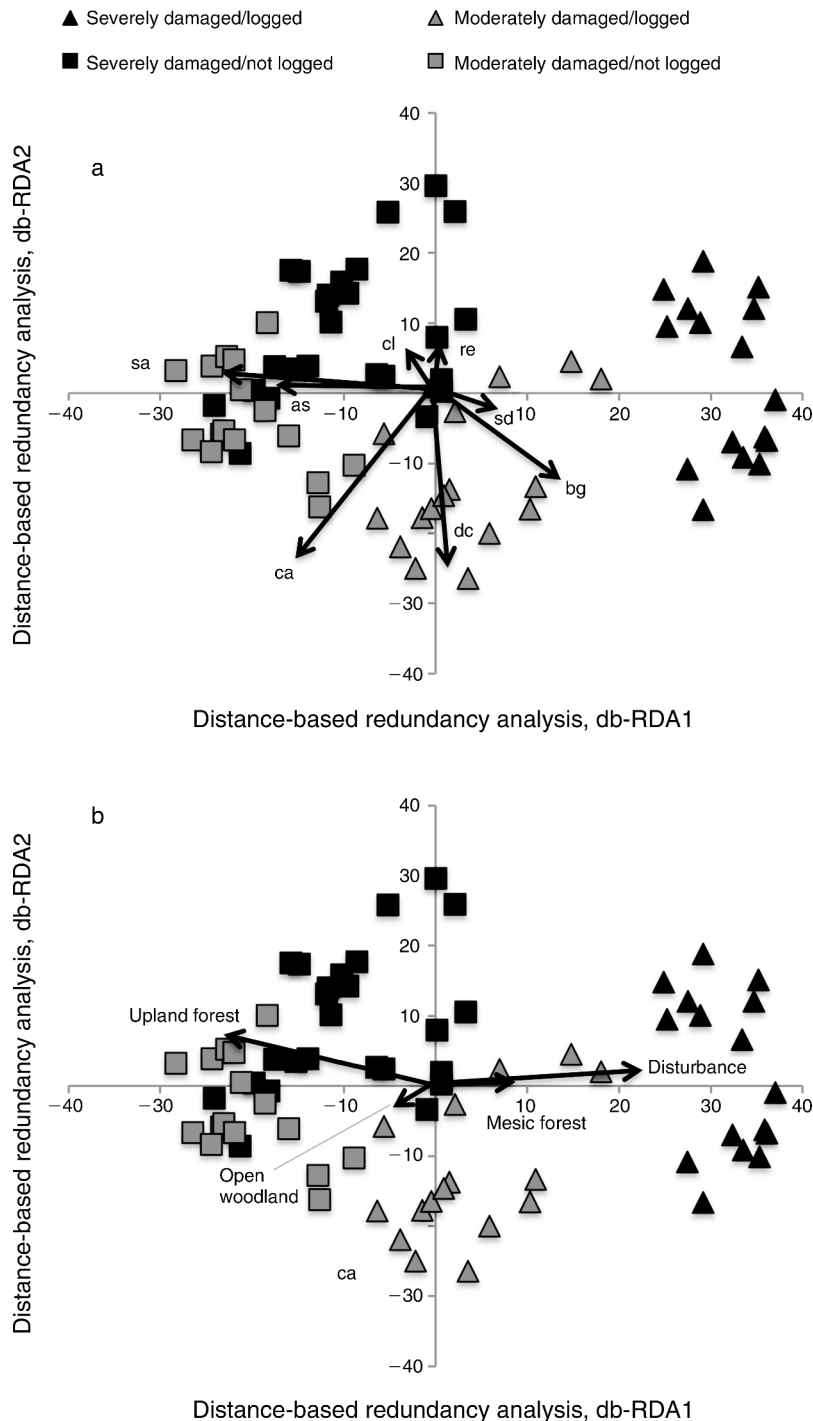


FIG. 5. Distance-based redundancy analysis of the relationship between 2009 species composition and environmental conditions in damaged plots that were either logged or not logged showing (a) partial correlation vectors of environmental variables and (b) correlation vectors of weighted mean fidelity to four general habitat categories. Abbreviations for predictor variables: as, northerly slope aspect; bg, % bare ground; ca, % canopy cover; cl, % clay; dc, % cover by dead crowns; om, % soil organic matter; re, relative elevation; sa, sand to silt ratio; sd, % soil disturbance. Definitions of damage levels: severe damage, 70% of stems ≥ 10 cm dbh (i.e., tree-sized) downed; moderate damage, $\sim 10\%$ of tree-sized stems downed; no damage $< 1\%$ tree-sized stems downed. Axis 1 explained 38.3% of the fitted and 13.7% of the total variation in species composition; axis 2 explained 27.2% of the fitted and 9.8% of the total variation in species composition.

TABLE 1. Log abundance of six selected species in damaged areas that were either logged or not logged.

Species	Log abundance for subplots			
	Severely damaged, logged	Moderately damaged, logged	Severely damaged, not logged	Moderately damaged, not logged
<i>Callicarpa americana</i>	1.32 (0.39)	0.09 (0.06)	0.26 (0.1)	0.04 (0.04)
<i>Chasmanthium sessiliflorum</i>	0	0.04 (0.04)	2.45 (0.6)	0.3 (0.19)
<i>Dichanthelium boscii</i>	0.32 (0.17)	1.42 (0.23)	2.56 (0.38)	0.82 (0.2)
<i>Digitaria sanguinalis</i>	2.21 (0.57)	0	0	0
<i>Quercus alba</i>	0.37 (0.12)	0.75 (0.15)	2 (0.21)	1.46 (0.25)
<i>Quercus velutina</i>	0.09 (0.06)	0.94 (0.15)	1.2 (0.14)	1.35 (0.16)

Note: Abundance values are subplot means with standard errors in parentheses.

trees caused by logging machinery. In turn, some of the delayed mortality might have been related to mechanical injury.

A salvage-logged plot exhibited the greatest variance in soil penetrability. One possible explanation for the greater variance in the logged plot is that log removal resulted in a “tilling” of the soil in some areas and soil compaction on skid trails (Zenner and Berger 2008). Zenner and Berger (2008) found that soil penetrability varied dramatically within logged areas of a forest in Minnesota, depending on whether or not measurements were taken directly on skid trails. Such a pattern could also have applied in our study, thus contributing to the high variance in soil compaction.

Ground cover vegetation responses to tornado damage

The applicability of traditional succession/gap theory to understanding compositional change following natural disturbances in forests depends on the assumption that disturbance-dependent species respond positively to disturbance, whereas most forest interior species respond negatively to disturbance. We found little support for this assumption in the current study of the initial effects of tornado damage on upland forests in north Mississippi, as few species were lost or declined as a result of tornado damage in this study.

Instead of tornado damage leading to the replacement of forest species by ruderals and open-habitat species, we found that damage resulted in the addition of

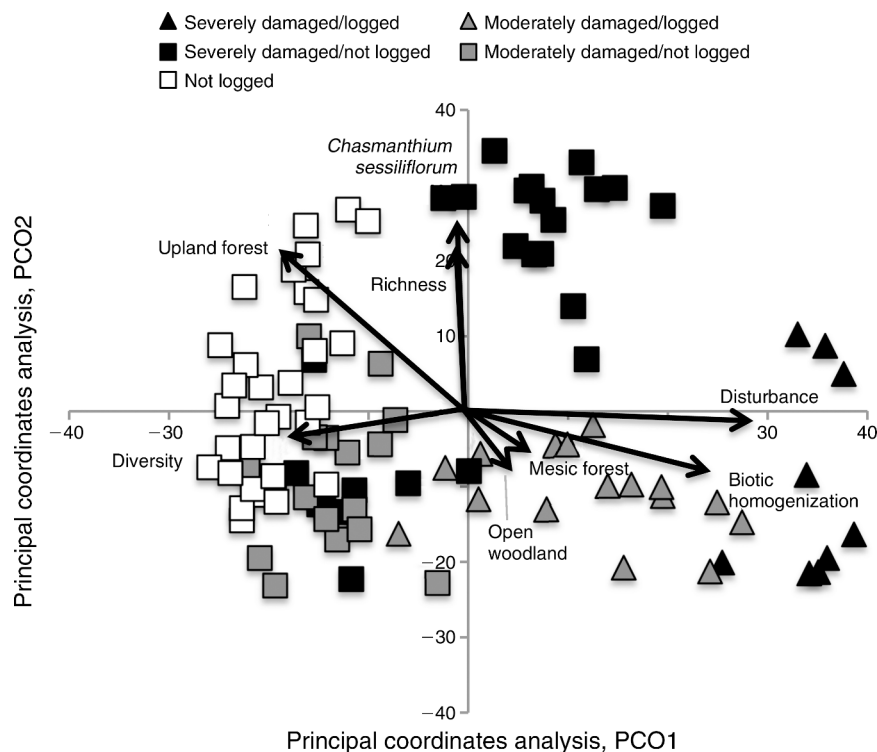


FIG. 6. Principal coordinates analysis of all subplots in species space (2009), superimposing correlation vectors of weighted mean fidelity to four general habitat categories, an index of biotic homogenization, species richness, Simpson's diversity, and the abundance of a common forest grass, *Chasmanthium sessiliflorum*. Axis 1 explained 18.7% of the total variation in species composition; axis 2 explained 10.7% of the total variation in species composition.

ruderals (e.g., the annual, *Erechtites hieracifolia*) and increases in the abundance of a few upland forest and open-woodland indicators. Such ground cover vegetation responses were similar to those found following tornado damage to an old-growth forest in western Pennsylvania (Peterson and Pickett 1995). It is possible that such increases were in part facilitated by soil disturbance (e.g., pits and mounds) caused by uprooted trees. However, our data do not definitively support this hypothesis. Pits and mounds were invariably associated with more open canopies, and canopy cover was the best predictor of ruderal abundance in unlogged stands. In addition to ruderals, *Dichanthelium boscii*, *Chasmanthium sessiliflorum*, and *Callicarpa americana*, all forest indicators, responded positively to tornado damage. The positive responses of these light-flexible species to canopy openings could be interpreted as evidence that these species are well suited to open woodlands and upland forests. The failure of regional flora manuals to discern this may be an artifact of the rarity of open oak and oak-pine woodlands in the region as a result of fire suppression. Alternatively, positive responses could indicate phenotypic plasticity in responses to light availability associated with canopy disturbances (Pascarella 1998).

Shady mesic forest indicators represented a very small fraction of the ground cover vegetation at the sites studied here, which could partially explain the fact that we observed no losses of such species following tornado damage. Among the few shady mesic forest species we encountered (e.g., *Maianthemum racemosum*), we found no definitive evidence of a decline.

Tornado damage appeared to have a greater positive effect on the flowering of open-woodland indicators than on densities of these species. Despite the lack of density increases in most open-woodland indicators (the rhizomatous *Helianthus microcephalus* was an exception), many long-lived perennials (e.g., *Desmodium viridiflorum* (L.) DC, *D. laevigatum* (Nutt.) DC, *Clitoria mariana* L., and *Solidago odora* Aiton) responded positively to tornado damage through increased flowering, possibly as a result of increased light. Nevertheless, increased flowering was no more likely to occur in open-woodland indicators than in forest indicators. Flowering of *Desmodium nudiflorum*, *Solidago ulmifolia* Muhl. and *Chasmanthium sessiliflorum*, all forest indicators, was greater in tornado-damaged areas than in undamaged areas. Hence, greater benefits of the tornado damage to open-woodland and forest species may be realized in the near future as a result of increased production of new recruits by flowering individuals.

In our system, tornado damage increased species richness by promoting the addition of some ruderal species without causing significant losses of species already established at the site. Such increases in richness and the abundance of shade-intolerant ruderals were also observed in a previous study of forest vegetation responses to tornado damage (Peterson and Pickett

1995). Given the widespread distributions of most ruderal species, their addition could diminish the biotic distinctiveness of these forests, at least in the short term. On the other hand, increases in the abundances and/or flowering of several forest and open-woodland indicators could eventually counter the effects of ruderal increases on biotic homogenization, especially if increases in ruderals (many of which are annuals) following tornado damage are short lived and an artifact of fire suppression in the past. The magnitude of canopy reduction following this tornado (and thus the beneficial effects of tornado damage on shade-intolerant ruderals) might have been greater in the upland forests examined here than what would have been observed historically before fire suppression. Many mature upland forests in North America were historically fire-dependent open woodlands (Frost 1998), and the closed-canopy conditions seen today are a product of artificially high stand densities following many years of fire suppression (Nowacki and Abrams 2008). Furthermore, dramatic increases in the dominance of large perennial grasses such as *Chasmanthium sessiliflorum* in response to the opening of the canopy by the tornado could result in a more competitive ground cover vegetation environment, which in turn might be more resistant to continued invasion by annual ruderal species that must re-establish from seed. Continued monitoring of compositional changes over the next few years should enable us to test this hypothesis.

An important caveat to our conclusions about the effects of tornado damage on upland ground cover vegetation is that our results are based on observations before and only two years after the disturbance. Neither 2008 nor 2009 experienced a severe drought. Drought-sensitive forest indicators could eventually succumb to drought in damaged areas receiving increased solar radiation on the forest floor (Nelson and Halpern 2005). A late-summer drought occurred in 2010, and further analysis of species composition could provide a test of this hypothesis. This limitation notwithstanding, having before-and-after data on composition in neighboring damaged and undamaged sites is rare and instructive in regard to predictions of classic succession theory. Our results show that attributing post-disturbance distributions entirely to storm-related changes overestimated increases in open-woodland indicators and decreases in shady mesic forest indicators.

Another important caveat to our conclusions about the effects of tornado damage on biotic homogenization of ground cover vegetation relates to our, as yet, untested hypothesis that the increases in ruderals following natural disturbances are temporary and thus will not contribute to biotic homogenization in the long term. Although some ruderal species are short lived and likely are not able to compete effectively with open-woodland or forest perennials over the long term (Peterson and Pickett 1995), other ruderal species such as the highly invasive and competitive grass *Micro-*

stegium vimineum responded favorably to tornado damage in this system and could persist and limit diversity. Natural disturbances therefore have the potential to reduce species diversity by increasing the competitive impact of highly competitive ruderal species (Brewer 2011a). Such responses could impede efforts to restore fire-maintained woodlands. *Microstegium vimineum* has been previously shown to respond positively to canopy openings (Cole and Weltzin 2005, Flory et al. 2007, Glasgow and Matlack 2007, Brewer 2010), and to have negative competitive effects on forest obligate species (e.g., *Dichanthelium* spp., *Chasmanthium laxum*, *Quercus* spp. [Flory et al. 2007, Marshall et al. 2009, Brewer 2011b]).

Ground cover vegetation responses to damage and salvage logging

In contrast to tornado damage alone, areas that were both damaged and salvage-logged were associated with a low abundance of species indicative of upland forests, suggesting a reduction of these species. In particular, seedlings of oaks (namely, *Quercus alba* and *Q. velutina*) were much less abundant in salvage-logged areas than in areas that were damaged by the tornado but not logged. This result agrees with the findings of Peterson and Leach (2008a), who also found greater seedling densities of these two species in unlogged areas than in logged areas. Oak seedling/sprout densities accumulate over many years in many forests as a result of multiple mast acorn crops, high seedling survival, and sprouting (Johnson et al. 2002). In addition, herbaceous upland forest indicators that responded positively to tornado damage (e.g., *Chasmanthium sessiliflorum*, *Dichanthelium bosci*) were not abundant in logged plots. Although we cannot be sure of changes in abundance without pre-logging data, the results strongly suggest that the low abundance of upland forest indicators in logged plots resulted from losses directly attributable to logging. Indeed, our study showed that logging might have reduced the abundance of some forest-indicative perennials that would have otherwise increased in abundance in response to the increased tree crown damage caused by the tornado. It is possible that logging machinery and skidding of logs killed a significant fraction of oak seedlings and perennial herbs and created bare patches that promoted the establishment of herbaceous ruderals. Herbaceous ruderals represented a much larger fraction of the community in the logged plots than in the plots that were damaged but not logged. However, we did not find greater abundance of seedlings of tree species known to benefit from exposed mineral soil (e.g., *Pinus* spp.), a finding consistent with another study of windthrow and salvage logging (Palik and Kastendick 2009). Continued monitoring over the next few years will be necessary to see if increased pine recruitment occurs in the logged plots. The species associations in logged vs. unlogged plots were consistent with a replacement of forest indicators by herbaceous

ruderal species. The net effects of this replacement were (1) no significant reduction in species richness in logged stands compared to undamaged and unlogged stands, and (2) an increase in biotic homogenization in damaged stands that were logged compared to damaged stands that were not logged and undamaged stands. Although the increase in biotic homogenization in logged and damaged areas due to increases in ruderals might be short lived, the loss of poorly dispersed upland forest indicators from logged plots might have much longer-lasting effects on biotic homogenization (Duffy and Meier 1992, Matlack 1994) and slow recovery (Lindenmayer and Ough 2006). We argue that local species richness and diversity provide potentially misleading indicators of floristic quality and thus diversity at a regional scale.

The apparent conversion of forest ground cover communities to early-succession communities by salvage logging of tornado-damaged areas (but not by tornado damage alone) is consistent with the findings of a previous study comparing the effects of simulated natural disturbance with the effects of salvage logging (Foster et al. 1997). These authors concluded that the replacement of late-successional tree species by early-successional tree species following damage to central Massachusetts forests by the hurricane of 1938 was more likely to have been caused by the salvage logging than by damage directly attributable to the hurricane. Compared to wind damage, the greater disturbance of the soil associated with logging operations provided greater opportunities for establishment by pioneer tree species (Foster et al. 1997).

An important caveat to our conclusions about the negative effects of salvage logging on upland forest species present before the storm is that the effects of salvage logging undoubtedly depend on the intensity and scale of logging (Peterson and Leach 2008a, b). In our study, logged stands that were severely damaged and thus experienced greater logging activity contained more ruderals and fewer upland forest indicators than did logged stands that were moderately damaged. The fact that logged stands contained more ruderals and fewer upland indicators than did stands that were damaged but not logged (irrespective of damage severity) supports the hypothesis of multiplicative effects of tornado damage and salvage logging on ground cover species composition. The greater the intensity of damage by the storm, the more downed trees are removed by loggers, and thus the greater the extent of soil disturbance, which in turn favors ruderal species.

Implications for forest management

The results of the current study, when considered in conjunction with previous studies of logging of undamaged stands, provide a clearer picture of the effects of logging on ground cover vegetation in both intact stands and damaged stands. Previous research on logged stands has provided strongly suggestive evidence that the

disturbance of the soil associated with logging has much greater and longer-lasting impacts on ground cover vegetation than canopy reduction (Foster et al. 1997, Cooper-Ellis et al. 1999, Zenner and Berger 2008). Our results suggest that natural disturbances that open the canopy potentially have beneficial effects on ground cover vegetation diversity. The same cannot necessarily be said for the combined effects of windthrow and salvage logging because of the apparent loss of forest indicators attributable to logging of severely damaged areas. On the other hand, planned logging of undamaged stands, especially when care is taken to minimize soil disturbance, like natural canopy-reducing disturbances, could have beneficial effects on ground cover plant diversity (see also Zenner and Berger 2008). If the preservation of ground cover plant diversity is a high management priority, then we suggest that planned logging of undamaged stands and salvage logging of stands moderately damaged by wind are preferable to salvage logging in stands severely damaged by wind. We base our argument on our observations that loggers had much greater difficulty restricting soil disturbance to a few skid trails in severely damaged stands than in moderately damaged stands. This might not be as great a problem, however, after disturbances that do not produce as many downed trees as tornadoes (e.g., crown fires, severe droughts, insect defoliation). On the other hand, there are other potential problems associated with salvage logging following those disturbances (McIver and Starr 2000, Donato et al. 2006). The ability to avoid soil disturbance during salvage logging will therefore depend on the type of natural disturbance.

Our results also suggest that diversity maintenance concepts based on disturbance-mediated losses of species (intermediate disturbance hypothesis and patch dynamics concepts) are not appropriate for managing ground cover plant diversity in upland forests similar to those studied here. Following tornado damage plus salvage logging, the apparent loss of forest specialists was apparently balanced by increases in ruderals, thereby maintaining local species richness (a finding consistent with the intermediate disturbance hypothesis). Nevertheless, such changes may diminish species diversity at larger scales through increased biotic homogenization. We suggest that concepts based on resilience and stability of alternative community states (e.g., fire-suppressed condition vs. fire-restored condition [Holling 1973, Cooper-Ellis et al. 1999, Hinman and Brewer 2007, Nowacki and Abrams 2008]), biotic homogenization (McKinney and Lockwood 1999), and phenotypically plastic responses of understory species to canopy disturbance (Pascarella 1998, Roberts 2007) may be more applicable to the management of disturbance regimes in upland forests similar to those studied here. If so, then restoring historic fire regimes and associated open canopies, minimizing artificial soil disturbances, and controlling competitive invasive species could be key to maintaining local and regional plant diversity.

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SUPPLEMENTAL MATERIAL

Appendix A

Quotient of similarity between each of 65 specific habitats and each of four general habitat categories based on a binary matrix with 251 species (*Ecological Archives* A022-028-A1).

Appendix B

Habitat indication scores for 251 identified species encountered in upland forests and adjacent edges throughout north central Mississippi (*Ecological Archives* A022-028-A2).

Appendix C

Responses of selected ground cover plants to tornado damage (*Ecological Archives* A022-028-A3).