NATURAL CANOPY DAMAGE AND THE ECOLOGICAL RESTORATION OF FIRE-INDICATIVE GROUNDCOVER VEGETATION IN AN OAK-PINE FOREST

J. Stephen Brewer

Department of Biology, University of Mississippi,
214 Shoemaker Hall, University, Mississippi 38677-1848, USA

Tel.: +001-662-915-1077; e-mail: jbrewer@olemiss.edu

ABSTRACT

An important goal of restoring fire to upland oak-dominated communities that have experienced fire exclusion is restoring groundcover plant species diversity and composition indicative of fire-maintained habitats. Several studies have shown that fire alone, however, may not be sufficient to accomplish this goal. Furthermore, treatment-driven declines in rare forest specialists could negate the benefits of ecological restoration in these ecosystems. I present the results of an experiment examining effects of tornado-generated canopy openings and biennial spring burning on groundcover vegetation at an oak-pine forest in north Mississippi, USA. Results from four years of monitoring showed that species richness and abundance of species indicative of fire-maintained open habitats were greater at sites with canopy damage than at sites with undamaged canopies, especially in years without drought. Annual ruderals increased initially following canopy damage but then decreased. Few forest indicator species changed in abundance, and the few that did increased. Canopy openings appeared to have a greater effect than fire on groundcover vegetation, although some legumes and panicgrasses appeared to benefit directly from fire.

RESUMEN

Un objetivo importante para restaurar el fuego en comunidades de altura dominadas por robles que han experimentado la exclusión de incendios, es restaurando la diversidad y composición de las especies del sotobosque indicativas de hábitats mantenidos por el fuego. Diversos estudios han mostrado que el fuego, por sí mismo, podría no ser suficiente para lograr ese objetivo. También, la conducción de tratamientos que disminuyen las especies raras podrían impedir los beneficios de la restauración en esos ecosistemas. Presento en este trabajo los resultados de un experimento que examina los efectos de un tornado, que generó la apertura del dosel, y de quemas bienales en primavera, sobre la cobertura de la vegetación del sotobosque en un bosque mixto de pino y roble en el norte de Mississippi, EEUU. Los resultados de cuatro años de monitoreo muestran que la riqueza y abundancia de especies indicadoras de sitios abiertos mantenidos por fuegos fue mayor en lugares abiertos dañados por el tornado que en aquellos no dañados, especialmente en años sin sequía. Las especies ruderales anuales se incrementaron inicialmente después del daño provocado en el dosel, y luego decrecieron. Algunas pocas especies indicadoras del sotobosque cambiaron su abundancia, incrementándola. Las aperturas en el dosel parecieran tener un mayor efecto que el fuego en la cobertura de la vegetación del sotobosque, aunque algunas especies de leguminosas y pastos del género *Panicum* L. pa-

Results suggest that fire restoration treatments must include both canopy openings and fire to effectively increase the diversity and distinctiveness of groundcover vegetation in mixed oak-pine forests. Prescribed burning after years of fire exclusion, by itself, does not constitute effective restoration of fire (at least in the short term), but it also does not appear to reduce the abundance of rare, forest-specialist groundcover species.

recen beneficiarse directamente con el fuego. Los resultados sugieren que los tratamientos de restauración deben incluir tanto las aperturas del dosel como las quemas prescriptas para incrementar efectivamente la diversidad y la diferenciación de la vegetación del sotobosque en bosques mixtos de pino y roble. Las quemas prescriptas después de muchos años de exclusión, por sí mismas, no constituyen una efectiva restauración del fuego (al menos en el corto plazo), pero tampoco parecen reducir las especies raras típicas del sotobosque.

INTRODUCTION

Throughout much of eastern North America, modern fire exclusion efforts have converted plant communities that previously were open habitats dominated by fire-tolerant tree species to more or less closed-canopy upland forests containing a mix of fire-tolerant and mesophytic tree species (Nowacki and Abrams 2008). During the periods of early European settlement and before in the eastern and southern United States, fire frequency in many oak-dominated portions of the upland landscape was greater than observed following modern fire suppression in the twentieth century (Van Lear and Waldrop 1989, Delcourt and Delcourt 1998, Guyette and Spetich 2003, Hart *et al.* 2008, Fesenmeyer and Christensen 2010, Spetich *et al.* 2011). Although direct accounts of groundcover plant species composition prior to modern fire exclusion are scarce, the more open tree canopies associated with frequently burned oak-pine forests in the past likely supported more productive groundcover plant communities. Modern fire exclusion (in addition to other land use changes) likely resulted in dramatic losses of groundcover plant production and diversity in these ecosystems (Smith 1994, Heikens and Robertson 1995, Taft 1997, Bowles and McBride 1998, Hutchinson *et al.* 2005, Phillips and Waldrop 2008, Surrette and Brewer 2008, Brewer and Menzel 2009, McCord *et al.* 2014, Brewer *et al.* 2015).

In addition to fire-maintained open habitats, significant portions of the early-settlement landscape in the eastern United States were dominated by mesophytic species with low tolerance of fires. In contrast to most fire-dependent ecosystems, most mesic and hydric forests were restricted to fire refugia such as rich floodplains and terraces, steep mesic ravines, or loess bluffs with deep fertile soils (Braun 1950, Delcourt and Delcourt 1977, Grimm 1984, Schwartz 1994, Frost 1998, Brewer 2001, Surrette *et al.* 2008). Except in areas near human settlements (Delcourt 1987, Patterson and Sassaman 1988, Guyette and Cutter 1997, Platt and Brantley 1997), conditions were likely not conducive to fires of sufficient severity or frequency to limit the establishment of fire-sensitive tree species (Beil-

mann and Brenner 1951, Grimm 1984, Frost 1998). Because of the fertile soils associated with some of these mesic and alluvial communities (i.e., floodplains and terraces), many of these sites have been converted to agriculture, resulting in losses of groundcover plant diversity (Bellemare *et al.* 2002, Flinn and Velland 2005). Hence, like fire-maintained open habitats, forests dominated by fire-sensitive, mesophytic species have been dramatically altered, but would most likely benefit from protection from frequent or intense fires (Mola *et al.* 2014). Both community types warrant serious consideration for protection and ecological restoration to maintain biodiversity.

Restoring historical fire regimes to upland oak and oak-pine forests that have experienced modern fire exclusion could be justified if it reverses declines in rare, fire-dependent species and does not have the unintended consequence of increasing widespread ruderals or invasives or decreasing regionally rare, fire-sensitive species (Brawn 2006, Brewer and Menzel 2009). Both critics and proponents of the use of fire in oak-dominated forests of eastern North America agree that maintenance of biodiversity is a worthwhile conservation goal (Nowacki and Abrams 2008; Matlack 2013, 2015; Stambaugh *et al.* 2015). Nevertheless, precisely how one manages oak-dominated ecosystems in such a way as to maintain biodiversity is not entirely clear. At a minimum, there needs to be a consensus as to how to quantify diversity. Frequently, investigators quantify diversity by measuring local species diversity, but there is currently no evidence that local plant species diversity is, on balance, decreasing worldwide, despite general agreement that global diversity is declining (Velland *et al.* 2013). Ultimately, effects of fire management on the abundance of species indicative of rare habitats or communities will have a greater effect on global biodiversity than will effects on local species diversity (Brewer and Menzel 2009; Velland *et al.* 2013).

I hypothesized that the beneficial effects of restoring historical fire regimes on the abundance of species indicative of rare habitats are likely if the following three conditions hold: 1) historical fire regimes (regardless of their cause: lightning, Native Americans, early European settlers) previously eliminated most fire-intolerant species from uplands (assuming any were present) and favored fire-tolerant species; 2) modern fire exclusion has not completely eliminated fire-dependent species from uplands and has not significantly benefited fire-sensitive species that are rare or threatened; and 3) restoration of low- to moderate-intensity fire regimes comparable to those that were prevalent prior to modern fire suppression benefits species that are indicative of habitats that are currently rare within the landscape (i.e., fire-maintained open woodlands). I hereafter refer to the positive responses of groundcover vegetation to the restoration of historical fire regimes under these conditions as the fire tolerance hypothesis. In contrast, some upland areas have been subjected to active or passive fire exclusion for so long that they have lost (or never had) many fire-tolerant species and are dominated by fire-intolerant species. If so, attempts at restoring fire in these areas may largely benefit widespread ruderals that are able to colonize disturbed sites rapidly and have a negative effect on rare or declining fire-sensitive forest species that currently occur in these areas (Matlack 2013). Prescribed burning in these areas would therefore be ill advised. I refer to this alternative hypothesis as the disturbance sensitivity hypothesis.

In this study, I tested the predictions of the fire tolerance and disturbance sensitivity hypotheses by examining the effects of natural canopy reduction from an EF4 tornado and prescribed burning on groundcover vegetation changes in upland oak-pine forests with a history of fire exclusion in north Mississippi, USA. I specifically addressed the following two questions:

1) How does herbaceous groundcover plant species richness respond to tornado damage alone, biennial prescribed fire, and the combination of the two? and

2) How do the abundances of herbaceous groundcover plants indicative of fire-maintained open habitats (hereafter, open-habitat species), closed-canopy forests (hereafter, forest species), and severe anthropogenic disturbance (hereafter, ruderals) differ in their responses to tornado damage, prescribed burning, or both?

Increases in plants indicative of fire-maintained open habitats (combined with no decreases in forest species) support the fire tolerance hypothesis, whereas decreases in plants of indicative of forests (combined with no increases in fire-maintained open habitat indicators) support the disturbance sensitivity hypothesis.

METHODS

Study Area

This study was conducted in an upland oak-pine forest within the Tallahatchie Experimental Forest (TEF; the site of long-term monitoring of oak-pine forest dynamics; Surrette *et al.* 2008, Brewer *et al.* 2012, Cannon and Brewer 2013, Brewer 2015). The Center for Bottomland Hardwood Forest Research unit of the USDA Forest Service Southern Research Station administers research activities at TEF, whereas the Holly Springs Ranger District of The National Forests of Mississippi implements fire management. The TEF is located within the northern hilly coastal plains of Mississippi (within the Greater Yazoo River Watershed, USA; 34° 30′ N, 89° 25′ 48″ W). Soils in the upland forests are acidic sandy loams and silt loams on the ridges, and acidic loamy sands on side slopes and in the hollows (Surrette and Brewer 2008).

In the early 1800s, before extensive logging and modern fire exclusion, open stands of fire-resistant tree species such as blackjack oak (*Quercus marilandica* Münchh.), post oak (*Q. stellata* Wangenh.), Southern red oak (*Q. falcata* Michx), black oak (*Q. velutina* Lam.), and shortleaf pine (*Pinus echinata* Mill.) dominated the upland landscape (Surrette *et al.* 2008). Following fire exclusion in the twentieth century, the overstory of the second-growth forests became dominated by a mixture of some of the historically dominant upland oak species (but not blackjack oak), pines (mostly shortleaf), some species historically common in floodplains (e.g., white oak [*Q. alba* L.], sweetgum [*Liquidambar styraciflua* L.]), and some species that were common in both uplands and floodplains historically (e.g., hickories [*Carya* spp. Nutt.]; Surrette *et al.* 2008].

After decades of fire exclusion in the mid to late 1900s, but prior to damage by a tornado in 2008, the sapling layer in all stands at TEF was dominated by blackgum (*Nyssa sylvatica* Marshall), hickories, black cherry (*Prunus serotina* Ehrh.), red maple (*Acer rubrum* L.), and sweetgum. After damage by the 2008 tornado, damaged stands with open canopies at TEF contained these non-oak species and saplings of various oak species, including the aforementioned and scarlet oak (*Quercus coccinea* Münchh.; Cannon and Brewer 2013).

Tornado Damage and Prescribed Burning

On 5 February 2008, an EF4-intensity tornado struck a portion of TEF, damaging some already-established vegetation study plots, while leaving others undamaged. The study contained four ~1 ha study plots in which tree, sapling, and groundcover vegetation composition had been monitored since 2006 and before (back to 1998 for two plots). The tornado reduced canopy cover to about an average of 40 % initially within one plot (hereafter, the severely damaged plot; Brewer *et al.* 2012, Brewer 2015), which then recovered to 55 % by 2012. A second plot (hereafter, the variably

damaged plot) experienced variable canopy damage, ranging from about 35 % post-storm canopy to about 80 %, increasing by about 10 % in the more severely damaged areas by 2012. Two other plots (hereafter, undamaged plot 1 and undamaged plot 2) experienced little or no damage from the tornado and exhibited canopy coverage of about 85 % to 95 %. A discriminant function analysis involving 11 variables, including percent canopy cover; leaf litter percent cover; percent soil disturbance from tip-ups; percent bare ground; percent cover by dead and downed crowns; percent cover by live, downed crowns; sand to silt ratio; percent clay; percent organic matter; and elevation revealed that percent canopy cover was the most important distinguishing environmental variable between damaged and undamaged portions of the plots in 2009 (Brewer *et al.* 2012).

Beginning in 2010, the Holly Springs Ranger District applied a biennial prescribed-burning treatment to two of the four plots. Prescribed fires in the severely damaged plot and undamaged plot 2 followed prescription guidelines from the National Forests of Mississippi and from the Mississippi Department of Environmental Quality. Due to time constraints, the Ranger District staff burned the severely damaged plot on 25 March 2010, and undamaged plot 2 was burned on 1 April 2010. (See Cannon and Brewer [2013] for fire temperature data for the 2010 fires.) The Ranger District staff burned both plots again on 29 March 2012. For the prescribed fire on 25 March 2010, ambient air temperatures ranged from 22 °C to 24 °C; relative humidity ranged from 30 % to 34 %. Patchy fuels resulted in a patchy burn (~50 % coverage). In burned areas, topkilled oaks regrew more rapidly than did topkilled non-oaks (Cannon and Brewer 2013). The second prescribed fire was conducted on 29 March 2012. Ambient air temperatures ranged from 26 °C to 27 °C; relative humidity ranged from 58 % to 68 %. The fire in 2012 was less patchy than the 2010 fire due to an increase in grass-based fuels (~70 %

coverage). Flame lengths ranged from 0.3 m in hardwood litter fuels and 1 m to 1.25 m in grass-based fuels. In general, fires were less patchy in undamaged plot 2 than in the severely damaged plot due to reduced fuel connectivity and high moisture of long-duration fuels in the latter. Despite these differences, fire visited and consumed all groundcover vegetation sampled and caused significant sapling topkill (Cannon and Brewer 2013, Brewer 2015).

Groundcover Vegetation Surveys

The herbaceous groundcover vegetation plots that were established in 2006 or earlier were revisited and censused in 2009, 2010, 2012, and 2013. The censuses for each of these years consisted of a fall census, which captured most identifiable species, and a subsequent early-April census of the following year (to capture spring ephemerals and winter annuals). Initial censuses involved approximate counts of all groundcover plant species within two 10 m × 30 m subplots located on the upper slope or the lower slope, nested within each plot. Beginning in 2009, I conducted more precise counts of groundcover plant abundance within each 10 m × 30 m subplot by subdividing the subplots into eight 5 m × 7.5 m sub-subplots. I quantified extremely abundant or difficult-to-count species by subsampling a 1.5 m × 1.5 m quadrat and extrapolating the resulting counts to the corresponding 5 m × 7.5 m sub-subplot. I converted counts of stems or clumps per species per sub-subplots to seven abundance classes: 1 (1 to 15), 2 (16 to 31), 3 (32 to 79), 4 (80 to 159), 5 (160 to 319), 6 (320 to 543), and 7 (>543). I assigned a value of 0 to species absent from a sub-subplot.

I quantified groundcover species composition within sub-subplots (or subplots in 2006) by calculating species richness and fidelity of the sub-subplot assemblage to open habitats, forests, and disturbed habitats. I derived habitat fidelity calculations from weighted sums of

abundances of all species with habitat indicator values of greater than 0 for a given habitat category, wherein the weights were species-specific habitat indication scores. For details of the calculation, see Brewer and Menzel (2009), Brewer *et al.* (2012, 2015), and Appendix 1. In short, I obtained each species' habitat indication score from the proportional similarity in species composition between those specific habitats in the region in which the species occurred (as determined from regional flora manuals) and species composition of the general habitat category of interest (e.g., open or forest or disturbed), again as determined by regional flora manuals (see Appendix 1). I further refined each species' habitat indication score by subtracting from the score the average of the indication scores of the other two habitats of interest. If the resulting difference was positive, then I considered the species to be a positive indicator of that habitat (see Appendix 2 for species list and associated refined indicator scores).

Statistical Analysis

To examine pre-storm differences on groundcover vegetation, I used one-way analysis of variance (ANOVA) of plot-level differences in plant species richness in 2006, before the tornado, using the subplot error term. All statistical analyses of abundance were based on abundance classes (hereafter, abundance = abundance class). To examine initial differences in groundcover vegetation between subplots that were severely damaged versus those that were not, I contrasted subplot differences in species richness and weighted summed abundances of positive habitat indicator species after the tornado but before the 2010 prescribed fires (2009) using one-way ANOVA. Because slope position was partially confounded with damage severity, I did not examine the effect of slope position on species composition. Assuming there was a significant effect of subplot, I used planned orthogonal contrasts to examine differences between severely damaged subplots and undamaged subplots. Analyses focused on subplots rather than plots, because the variably damaged plot contained a severely damaged subplot and a relatively undamaged subplot. To reduce heteroscedasticity, I square-root transformed weighted summed abundances prior to analysis. To examine the effects of tornado damage and fire on changes in vegetation over time, I analyzed differences among the four different damage and fire combinations using repeated measures analysis of variance. I averaged sub-subplot values for each subplot, and used the subplot error term to test for differences among damage and fire combinations. I presented only within-subjects statistical analyses. I used two-way ANOVA to examine the change in abundance between 2009 and 2013 in some of the more common species in response to fire, damage, and the fire × damage interaction. I used the subplot error term to test effects of fire, damage, and the interaction. Where presented in Results, SE is calculated from the whole model mean square error:

$$SE = \frac{\text{square root } (\text{mean square root})}{\text{square root } (n \text{ subplots})}$$

I examined the effect of the 2012 fires on the incidence of flowering in one forest species, feathery false lily of the valley (*Maianthemum racemosum* [L.] Link) using a chi-square test of independence. I performed all statistical analyses using JMP v. 5.0.1 (SAS Corporation, Cary, North Carolina, USA).

RESULTS

Initial Responses to Tornado Damage

Plant species richness did not differ significantly among the plots in 2006, before the 2008 tornado ($F_{3,4} = 1.62$; $P = 0.32$). Particularly noteworthy was the fact that the severely damaged plot did not contain more species

than the other plots and in fact contained among the fewest species (Figure 1).
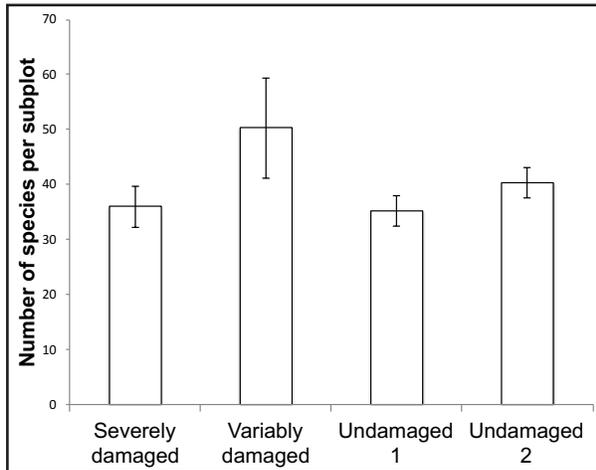
Figure 1. Pre-tornado differences in the number of herbaceous plant species per 10 m × 30 m sub-plot ($n = 2$) in 2006 among plots that differed in damage severity in 2008. Values are means ± 1 SE, which are directly calculated from two subplot values per plot.

In contrast to what was observed before the tornado in 2006, after the tornado in 2009 but before the 2010 fires, groundcover plant species richness in severely disturbed subplots was significantly greater than in subplots that were not severely disturbed ($F_{1,6} = 8.14$; $P = 0.014$; Figure 2).

The weighted summed abundance of open habitat indicators and ruderals was also greater in severely damaged subplots than in undamaged subplots ($F_{1,6} = 6.02$, $P = 0.049$, and $F_{1,6} = 12.59$, $P = 0.012$, respectively; Figure 3). Examples of important open habitat indicators, as determined from strong positive correlations between their abundance and the weighted summed abundances of open habitat indicators as a group included Bosc's panicgrass (*Dichanthelium boscii* [Poir.] Gould & C.A. Clark; also an indicator of forests), creeping lespedeza (*Lespedeza repens* [L.] W.P.C. Barton), hairy lespedeza (*L. hirta* [L.] Hornem.), small woodland sunflower (*Helianthus microcephalus* Torr. & A. Gray; a central US oak woodland endemic), smooth ticktrefoil (*Des-*
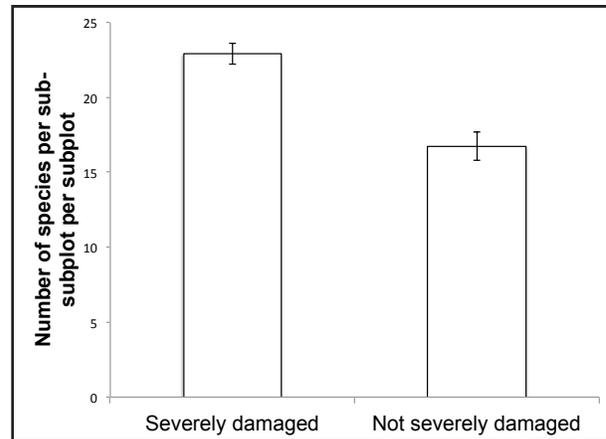
Figure 2. Post-tornado differences in the number of herbaceous plant species per 5 m × 7.5 m sub-subplot per 300 m² in 2009 among plots that differed in damage severity in 2008 ($n = 3$ severely damaged subplots and $n = 5$ undamaged subplots). Values are means ± 1 SE, which are directly calculated from subplot values for each damage severity category.
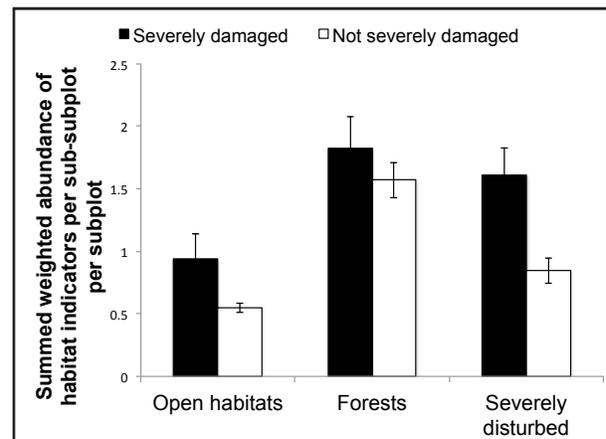
Figure 3. Post-tornado differences in the summed weighted abundance of habitat indicator species per 5 m × 7.5 m sub-subplot per 300 m² in 2009 among plots that differed in damage severity in 2008 ($n = 3$ severely damaged subplots and $n = 5$ undamaged subplots). Values are means of square-root transformed weighted summed abundances ± 1 SE, which are directly calculated from subplot values for each damage severity category.

modium laevigatum [Nutt.] DC), and Atlantic pigeonwings (*Clitoria mariana* L.). Examples of important native ruderals included the fol-

lowing annuals: Canadian horseweed (*Conyza canadensis* [L.] Cronquist), American burnweed (*Erechtites hieraciifolius* [L.] Raf. ex DC), spoonleaf purple everlasting (*Gamochaeta purpurea* [L.] Cabrera), and slender three-seed mercury (*Acalypha gracilens* A. Gray). There was no significant difference in weighted summed abundance of forest indicators between severely disturbed subplots and subplots that were not severely disturbed ($F_{1,6} = 0.83$, $P = 0.399$; Figure 3) before the two prescribed fires. Nevertheless, a couple of forest indicators increased in abundance in the severely damaged plot, including Bosc's panicgrass (also an open habitat indicator) and longleaf woodoats (*Chasmanthium sessiliflorum* [Poir.] Yates), endemic to the southern US. I found no evidence of a significant decline for any forest indicator species after the tornado but

before the two prescribed fires that was common enough to statistically analyze.

Changes in Response to Damage and Repeated Fires

Species richness appeared to change somewhat over the course of the study, between 2009 and 2013, as indicated by an effect of year that approached statistical significance depending on the type of degree of freedom adjustment used to account for the lack of sphericity (Greenhouse-Geisser $F_{1.4,5.6} = 5.27$, $P = 0.122$; Huynh-Feldt $F_{3,12} = 3.23$, $P = 0.061$). Most of the change was due to a reduction in species richness in 2010, a drought year (Figure 4). The way in which species richness changed over the course of the study differed between damaged and undamaged plots, as in-
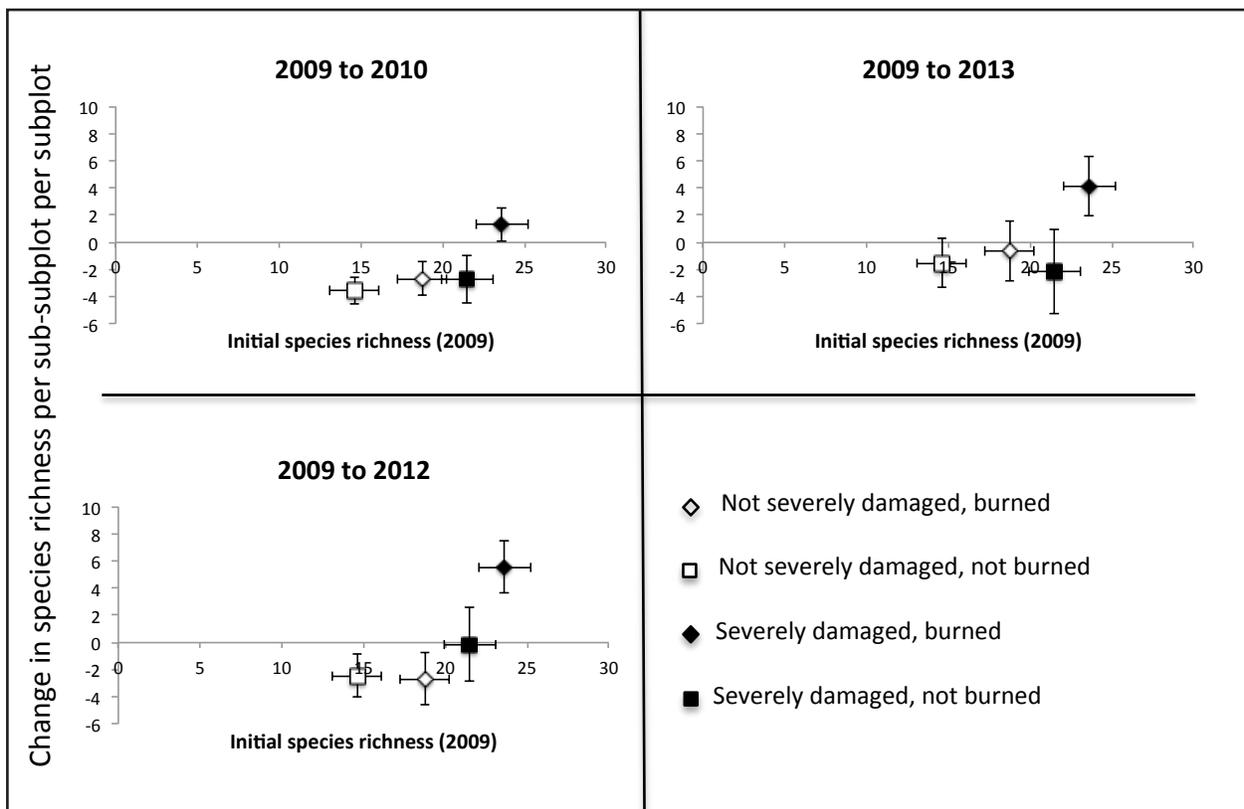
Figure 4. Changes in the number of herbaceous plant species per 5 m × 7.5 m sub-subplot per 300 m² between 2009 and 2013 among plots that differed in damage severity and prescribed burning in 2008 (*n* = 2 severely damaged and burned subplots, 1 severely damaged and unburned subplot, 2 undamaged and burned subplots, and 3 undamaged and unburned subplots). Values are means ± 1 SE.

dicated by a damage × year interaction that was statistically significant depending on how the error degrees of freedom were adjusted (Greenhouse-Geisser $F_{1.4,5.6}$ = 3.99, P = 0.091; Huynh-Feldt $F_{3,12}$ = 3.99, P = 0.035). The recovery in species richness in 2012 from the drought in 2010 appeared to be greater in the damaged subplots than in the undamaged subplots (Figure 4). The manner in which species richness changed over time did not vary between burned and unburned subplots (Greenhouse-Geisser $F_{1.4,5.6}$ = 1.83, P = 0.238; Huynh-Feldt $F_{3,12}$ = 1.83, P = 0.193). Increases in species richness between 2009 and 2013 were only apparent in the subplots that were both damaged and burned, both of which occurred in the same plot (Figure 4). Nevertheless, the damage × fire × year interaction was not statistically significant (Greenhouse-Geisser $F_{1.4,5.6}$ = 1.62, P = 0.267; Huynh-Feldt $F_{3,12}$ = 1.62, P = 0.236). A pseudoreplicated analysis using the pooled subplot and sub-subplot error terms revealed a highly significant three-way interaction in which species richness increased in the damaged and burned subplots in 2010 and remained higher than richness in the remaining subplots throughout the study (Greenhouse-Geisser $F_{1.9,117.9}$ = 4.64, P = 0.012; Huynh-Feldt $F_{2.2,128.3}$ = 4.64, P = 0.009). Hence, low statistical power could explain the lack of a significant three-way interaction when using the subplot error term, but true replication is necessary to validate this explanation.

The abundance of open habitat indicators changed significantly over the course of the study, between 2009 and 2013, as indicated by a significant effect of year (Greenhouse-Geisser $F_{1.6,6.3}$ = 8.31, P = 0.020; Huynh-Feldt $F_{3,12}$ = 8.31, P = 0.003). Most of the change was due to an increase in the abundance of open habitat indicators after 2010 (Figure 5). None of the interactions among within-subjects factors was statistically significant (P > 0.10). However, open habitat indicators as a group appeared to be greater in burned plots than in unburned plots in 2013 compared to 2009, suggesting a

trend towards these species becoming increasingly favored by fire ($F_{1,6}$ = 6.41, P = 0.060). Two open habitat species, in particular, that appeared to increase in response to fire, irrespective of tornado damage, were Bosc's panicgrass ($F_{1, 4}$ = 22.12, P = 0.009; least square means of increase, 1.25 versus 0) and creeping lespedeza ($F_{1, 4}$ = 12.45, P = 0.024; least square means of increase, 0.44 versus −0.23).

The abundance of forest indicators changed significantly over the course of the study, between 2009 and 2013, as indicated by a significant effect of year (Greenhouse-Geisser $F_{1.8,7.3}$ = 11.30, P = 0.006; Huynh-Feldt $F_{3,12}$ = 11.30, P ≤ 0.001). Most of the change was due to a reduction in the abundance of forest indicators in 2010 (Figure 6). None of the other within-subjects factors was statistically significant (P > 0.10). Surprisingly, the reduction in forest indicators as a group in 2010 appeared to be greater in undamaged plots than in the damaged plots, suggesting that drought had a greater negative effect on these species under a closed canopy than under an open canopy ($F_{1,6}$ = 6.55, P = 0.062). Noteworthy is the fact that forest indicators as a group did not respond negatively to two repeated fires over the course of the study in either the damaged or the undamaged subplots (Greenhouse-Geisser $F_{1.8,7.3}$ = 1.76, P = 0.237; Huynh-Feldt $F_{3,12}$ = 1.76, P = 0.208). Some forest indicator species responded positively to fire between 2009 and 2013 (e.g., openflower rosette grass, *Dichanthelium laxiflorum* [Lam.] Gould; $F_{1, 4}$ = 9.97, P = 0.034; least square means of increase, 1.56 versus 0.021). Common forest species showed mixed responses to damage between 2009 and 2013. Some species increased, including Western bracken fern (*Pteridium aquilinum* [L.] Kuhn; also a ruderal; $F_{1, 4}$ = 41.79, P = 0.003; least square means of increase, 0.688 versus 0.021), anisescented goldenrod (*Solidago odora* Aiton; $F_{1, 4}$ = 8.00, P = 0.047; least square means of increase, 0.563 versus −0.021), and openflower rosette grass ($F_{1, 4}$ = 6.99, P = 0.057; least square
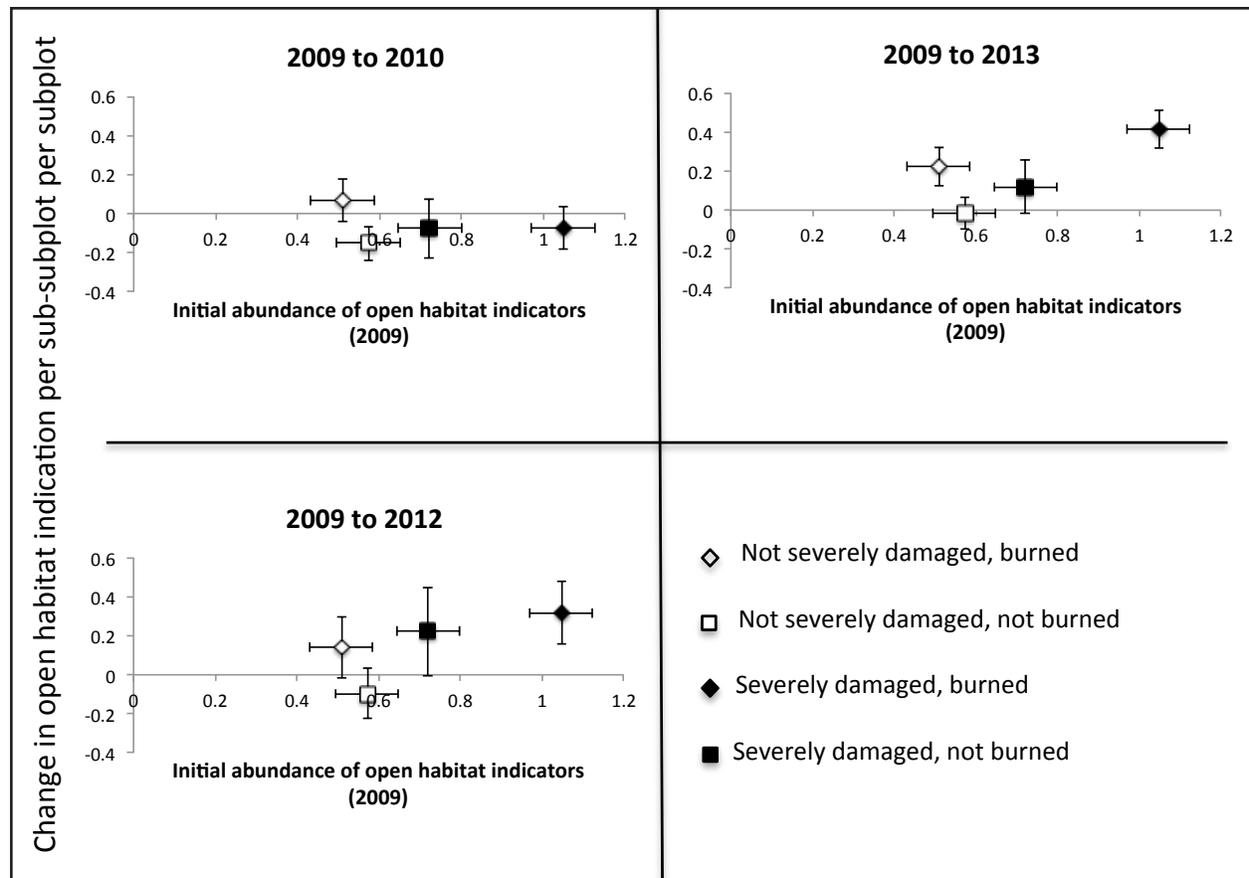
Figure 5. Changes in the weighted summed abundance of fire-maintained open habitat indicator species per 5 m × 7.5 m sub-subplot (square-root transformed) per 300 m² between 2009 and 2013 among plots that differed in damage severity and prescribed burning (*n* = 2 severely damaged and burned subplots, 1 severely damaged and unburned subplot, 2 undamaged and burned subplots, and 3 undamaged and unburned subplots). Values are means ± 1 SE.

means of increase, 1.44 versus 0.147). Other forest species such as Venus' pride (*Houstonia purpurea* L.; also a ruderal) decreased in damaged plots between 2009 and 2013 ($F_{1, 4}$ = 21.59, *P* = 0.009; least square means of increase, −0.219 versus 0.021). One forest species, feathery false lily of the valley, although not changing in abundance in response to fire, flowered only in burned subplots in 2012 (χ_1^2 = 22, df = 1, *P* ≤ 0.001).

The abundance of ruderals changed significantly over the course of the study, between 2009 and 2013, as indicated by a significant effect of year (Greenhouse-Geisser $F_{1.4,5.6}$ = 7.34, *P* = 0.032; Huynh-Feldt $F_{3,12}$ = 7.34, *P* = 0.005). Most of the change was due to a re-

duction in the abundance of ruderals in 2010 (Figure 7). None of the other within-subjects factors was statistically significant (*P* > 0.19). Although ruderals neither increased nor decreased as a group in response to damage (after their initial increase) or fire, some species decreased in abundance over time, whereas others increased in a manner indicative of succession. In particular, some annual and short-lived perennial ruderals, initially abundant in 2009 in damaged plots, declined to nearly 0 by 2013. Examples included American burnweed ($F_{1, 4}$ = 198.87, *P* < 0.001; least square means of increase, −1.16 versus 0.041), dogfennel (*Eupatorium capillifolium* [Lam.] Small; $F_{1, 4}$ = 42.0, *P* = 0.007; least square means of in-
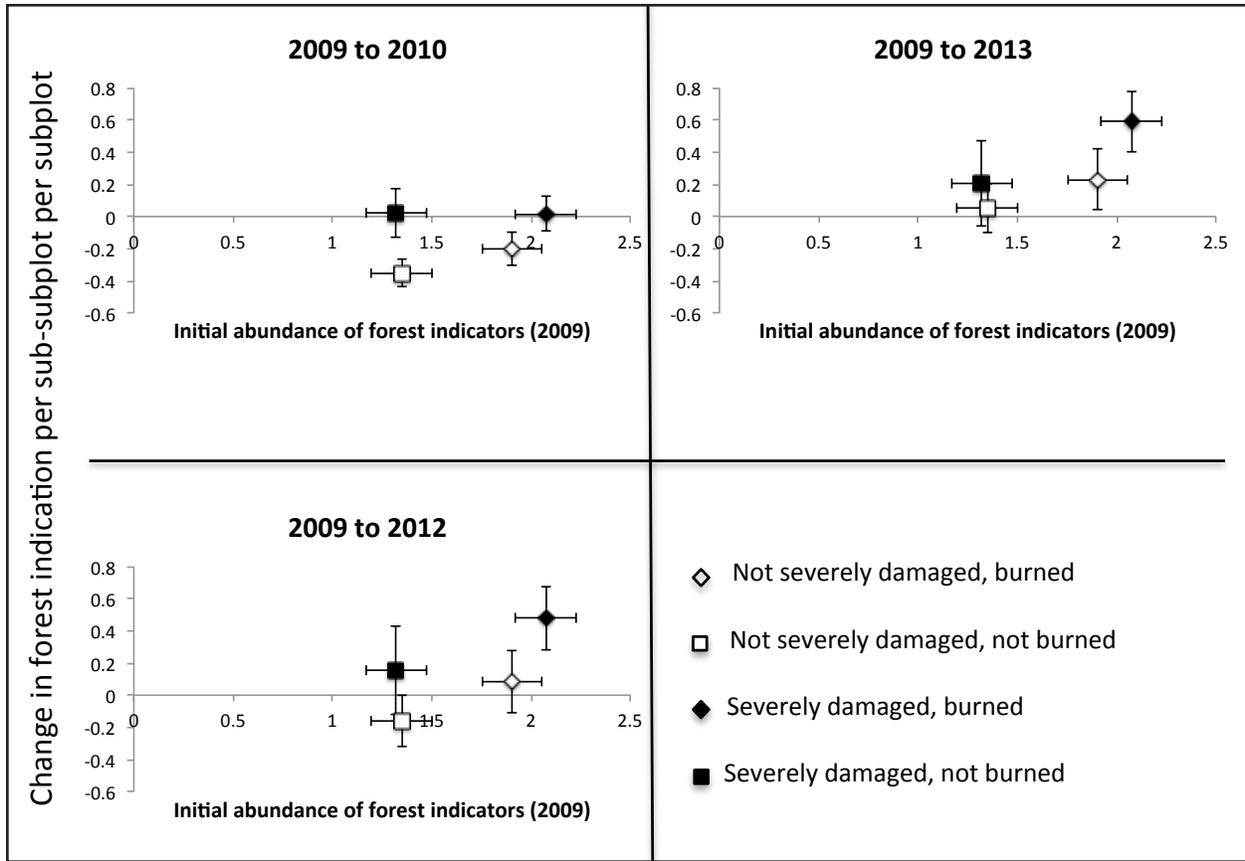
Figure 6. Changes in the weighted summed abundance of closed-canopy forest indicator species per 5 m × 7.5 m sub-subplot (square-root transformed) per 300 m^2 between 2009 and 2013 among plots that differed in damage severity and prescribed burning (n = 2 severely damaged and burned subplots, 1 severely damaged and unburned subplot, 2 undamaged and burned subplots, and 3 undamaged and unburned subplots). Values are means ± 1 SE.

crease, −0.219 versus 0), and Venus' pride. In contrast, perennial ruderal species such as sawtoothed blackberry (*Rubus argutus* Link) increased between 2009 and 2013 in damaged plots ($F_{1,4}$ = 9.49, P = 0.037; least square means of increase, 0.594 versus 0.021), as did flowering spurge (*Euphorbia corollata* L.; $F_{1,4}$ = 14.73, P = 0.019; least square means of increase, 0.188 versus −0.010).

DISCUSSION

In general, the results of these groundcover vegetation surveys indicate that >50 % canopy reduction from an EF4-intensity tornado increased the species richness and abundance of groundcover plant species indicative of fire-maintained open habitats and severe anthropogenic disturbance. The increase in species richness resulted in large part from increased occurrence of annual ruderals and short-lived perennials (e.g., Canadian horseweed, American burnweed, dogfennel, spoonleaf purple everlasting), which is not a desirable response in the context of maintaining the biotic distinctiveness of upland oak-pine ecosystems. On the other hand, tornado damage also increased the abundance of species indicative of rare, fire-maintained open habitats (e.g., Bosc's panicgrass, creeping lespedeza, hairy lespedeza, small woodland sunflower, smooth ticktrefoil, and Atlantic pigeonwings;
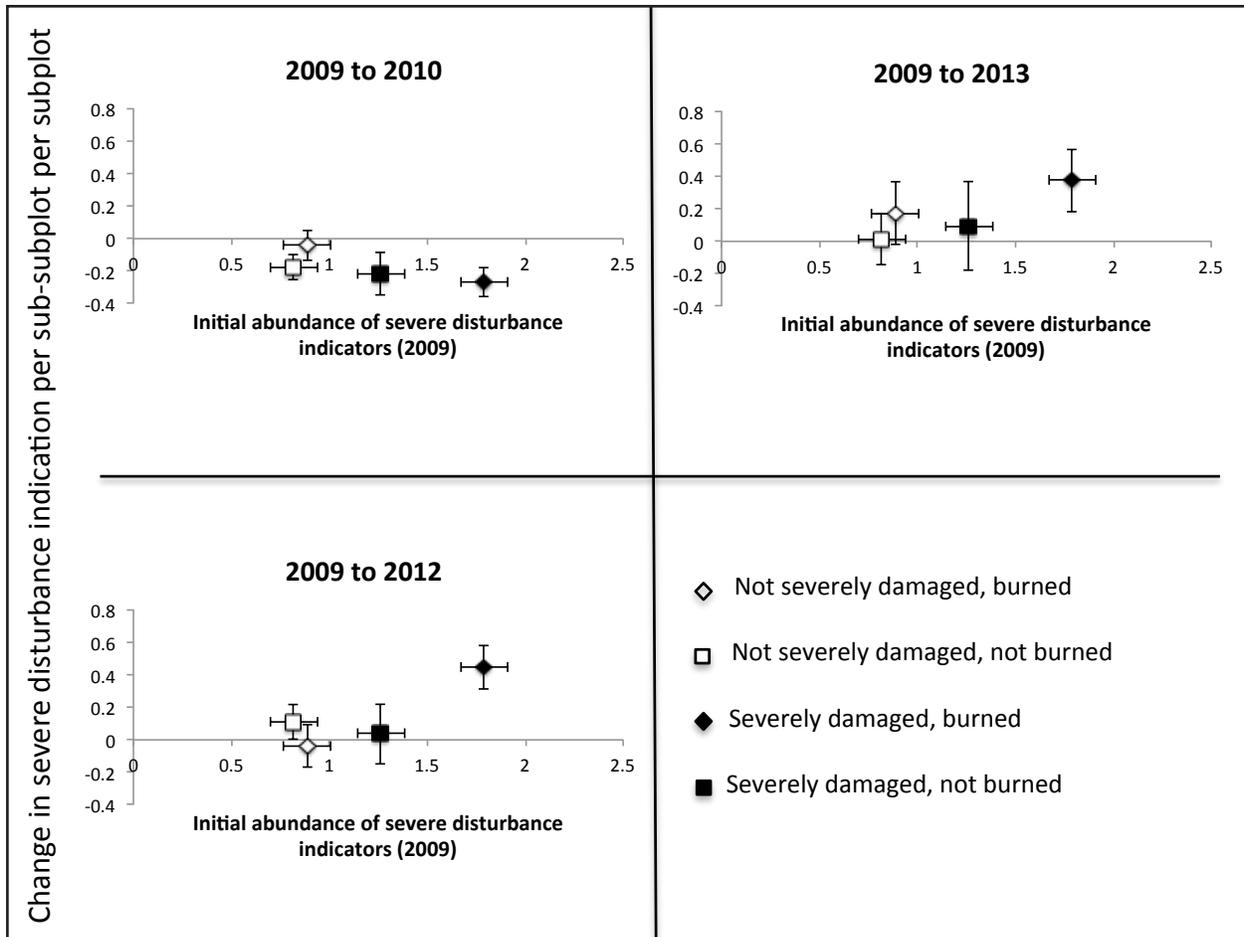
Figure 7. Changes in the weighted summed abundance of severe anthropogenic disturbance indicator species per 5 m × 7.5 m sub-subplot (square-root transformed) per 300 m^2 between 2009 and 2013 among plots that differed in damage severity and prescribed burning (n = 2 severely damaged and burned subplots, 1 severely damaged and unburned subplot, 2 undamaged and burned subplots, and 3 undamaged and unburned subplots). Values are means ± 1 SE.

Brewer *et al.* 2012). The increase resulted from the fact that many of these perennial species were already present, but at low densities, most likely having been suppressed by shade prior to canopy damage. Canopy reduction created the environmental conditions necessary to promote the natural increase of species indicative of fire-maintained open habitats (Clewell and Aronson 2013). Such a result mirrors responses to experimental canopy reduction and biennial fires in a more mesic oak-dominated forest in the loess plains of northern Mississippi (Brewer *et al.* 2015). Such responses provide support for the fire tolerance hypothesis and are consistent with a

primary restoration goal in oak-pine woodlands and forests of the eastern United States (Smith 1994, Taft 1997, Laatch and Anderson 2000, Hutchinson *et al.* 2005, Ruffner and Groninger 2006, Phillips and Waldrop 2008, Kinkead *et al.* 2013).

Canopy reduction associated with tornado damage did not change the abundance of forest indicators as a group. Hence, the increase in open-habitat indicators and ruderals did not come at the expense of forest indicators. Some of the species that responded positively to the treatment were indicators of both open habitats and forests (e.g., Bosc's panicgrass). The group responses, however, obscured some

responses of individual forest-indicator species that were not predicted. For example, one forest indicator, longleaf wood oats, increased dramatically following tornado damage in the severely damaged plot. I found no clear evidence of declines by any forest indicators (see also Brewer *et al.* 2012). The lack of decline by species indicative of closed-canopy forests following canopy reduction was somewhat unexpected and requires some explanation. One possibility is that species that truly require closed-canopy conditions simply were not present in the groundcover of these forests prior to tornado damage. Hence, many of the forest indicators present in these forests are perhaps best described as light-flexible forest herbs (*sensu* Collins *et al.* 1985). Classification of some of these species as closed-canopy forest indicators may be inaccurate and an artifact of modern fire exclusion. Indication scores were derived from habitat occurrence described in regional flora manuals, all of which were based on observations made during or after modern fire exclusion. I argue that many light-flexible forest species could also be accurately described as open forest or open woodland species but were classified as closed-forest species due to the lack of open forests and woodlands in the modern landscape.

Although, in the long term, repeated surface fires will be necessary to maintain the open canopy conditions necessary to favor species indicative of fire-maintained open habitats, I found very weak direct effects of fire on groundcover vegetation over the six growing seasons following tornado damage. The lack of significant effects of fire on open habitat indicators as a group may in part be due to a lack of replication and thus statistical power. Repeated fires (with or without canopy damage) appeared to favor a few species (e.g., Bosc's panicgrass and creeping lespedeza), but additional study with greater replication and continued burning is necessary to see if additional species will respond positively to fire alone.

Contrary to the predictions of the disturbance sensitivity hypothesis, I found no evidence that repeated fires negatively affected forest indicative herbs at the sites studied here. In fact, the forest indicator openflower rosette grass increased in response to fire between 2009 and 2013. Matlack (2013), who criticized the use of fire in mesic deciduous forests (within which he includes mixed oak-pine forests of the southern Appalachians, and the eastern interior Coastal Plain), argued that most forest plant species lack the adaptations to fire (e.g., smoke-cued germination, resprouting from rhizomes) necessary to respond positively to fires. It is possible that the sites studied here occurred on soils that were not as moist or fertile as those envisioned by Matlack and therefore lacked many of the forest specialists that would have responded negatively to frequent fires. If true, the disturbance sensitivity hypothesis may need to be refined and restricted to more mesic ecosystems (e.g., mesic floodplain terraces and steep ravines). Groundcover herbs in the forests studied here were tolerant of low- to moderate-intensity surface fires, perhaps because many species were perennials with rhizomes, deep taproots, or belowground bud or seed banks that were protected from damage by such fires (e.g., *Helianthus* spp., *Desmodium* spp., *Lespedeza* spp.*, Dichanthelium* spp.). It may not be true that oak-dominated forests lack fire-adapted herbs. Narrowleaf silkgrass (*Pityopsis graminifolia* [Michx.] Nutt) is associated with oak and oak-pine forests of the interior Coastal Plain and Highlands of the southern US and occurred at the sites studied here. I previously showed that this species exhibited increased flowering in response to fires or simulated fires during the peak season of coincidentally high lightning frequency and extended rain-free intervals (mid- to late summer, early fall; Brewer 2009).

Matlack (2015) argued forcefully that fire-intolerant species currently occur in mesic deciduous forests and that recent invasion by

these species following modern fire exclusion (as suggested by Nowacki and Abrams 2008) was unlikely, given the short time scale of modern fire exclusion relative to the low rates of dispersal and colonization of fire intolerant species (Matlack 1994). He therefore concluded that fire was not a historically important factor in mesic deciduous forests. It is important to recognize that Matlack and Nowacki and Abrams are not referring to the same "fire-intolerant" species. Matlack is primarily considering poorly dispersed forest herbs (Matlack 1994), whereas Nowacki and Abrams (2008) are primarily considering widely dispersed tree species, such as red maple. In north Mississippi, invasion of upland oak forests from adjacent floodplains, mesic terraces, and steep ravines by red maple and fire-sensitive pioneer tree species such as sweetgum and winged elm (*Ulmus alata* Michx.) following modern fire exclusion is entirely plausible (Brewer 2001). Furthermore, to call red maple, sweetgum, and winged elm fire-intolerant species is not entirely accurate. The ability of these fire-sensitive tree species to resprout following fire could have prevented their complete elimination in the face of frequent fires, historically. Their slow regrowth following topkill by fire compared to oaks (Brose *et al.* 1999, Hutchinson *et al.* 2012, Cannon and Brewer 2013), however, likely prevented their escaping a "fire trap" (*sensu* Bond and Midgley 2001), relegating them to a sprout bank. Their persistence as sprouts prior to modern fire exclusion could partly explain their rarity among witness trees in fire prone areas during General Land Office surveys but also could have contributed to their subsequent rapid increase following fire exclusion. The resulting increase in canopy closure reduced the abundance of herbaceous species indicative of open woodlands and some light-flexible forest herbs, both of which (as shown in the current study) are tolerant of repeated fires.

Although additional study at other sites is necessary, the results of the current study, along with those of Brewer *et al.* (2015), lead to me to suggest that fire-intolerant forest herbs are largely absent from upland oak and oak-pine forests on gentle slopes. If such herbs ever were present, they were likely eliminated by frequent fires, cultivation, and grazing that occurred prior to modern fire exclusion (Hutchinson *et al.* 2005). Today, fire-intolerant forest herbs most likely are restricted to cool, moist microclimates associated with floodplains and mesic terraces or steep ravines. Irrespective of fire, such microclimates likely provide a more suitable growing environment for some mesophytic herbs (e.g., spring ephemerals) than those associated with more exposed uplands with moderate slopes or poorer soils of the coastal plain of north Mississippi. In addition, the former areas are today, and were historically, located in portions of the landscape that were not frequently visited by fire (Frost 1998; Mola *et al.* 2014). I therefore propose that fire-intolerant or fire-sensitive herbs historically were and currently are most likely restricted to areas that, prior to modern fire exclusion, were more or less closed-canopy forests on steep ravines or rich floodplains and terraces dominated or co-dominated by fire-sensitive tree species. More research is needed, however, to discover which forest herbs are truly fire-intolerant.

An encouraging result of this study was the lack of a generally positive response of ruderals to fire. Although some ruderals responded positively to fires, others did not. Low-intensity surface fires are not severe disturbances, and thus in one sense they should not be expected to favor ruderals or other species dependent upon soil disturbances or other lethal factors (Grime 1979, Roberts 2007, Brewer and Bailey 2014). There were some native ruderals that initially responded positively to canopy reduction by the tornado, but then declined over time (e.g., American burnweed and dogfennel). The decline in these species coincided with a significant increase in perennial ruderals moderately indicative of severe disturbances, such as sawtoothed blackberry. The net effect of these changes was no

general decline or increase in ruderals over time as a function of either canopy reduction or fire.

Management Implications

Restoring fire to oak-dominated ecosystems in the eastern United States has the potential to increase groundcover plant diversity, both in terms of increased species richness and, more importantly, increased abundance of regional endemics indicative of rare habitats. Prescribed burning alone, however, most likely will not greatly increase diversity in the short term. Ideally, frequent prescribed burning should be coupled with overstory canopy reduction, while being particularly mindful of minimizing disturbance of the groundcover vegetation when felling or removing trees (Brewer *et al.* 2012). In areas where timber harvest is not practical, prescribed burning could be implemented in anticipation of, or following, natural wind-throw disturbances (e.g., tornadoes, derechos, hurricanes) to restore groundcover vegetation of fire-maintained open woodlands. Alternatively, more intense prescribed fires that cause some overstory canopy damage might produce similar results to those caused by the combined effects of fire and wind-throw damage. Although there are good reasons to be cautious about the application of fire to oak-dominated ecosystems in the eastern United States (Brewer *et al.* 2015), there are also consequences to inaction. Given our incomplete knowledge of how fire will interact with different soil types, land-use histories, and climate change, a prudent approach to fire management in Eastern oak and oak-pine ecosystems would be experimental application of fire with appropriate controls.

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Appendix 1. Procedure for calculating habitat indicator scores and weighted summed abundances of habitat indicators.

Step 1. Generating a regional species × habitat presence-absence matrix from regional flora manuals. Manuals used included:

Clewell, A.F. 1985. Guide to the vascular plants of the Florida Panhandle. Florida State University Press, Tallahassee, USA.

Godfrey, R.K., and J. Wooten. 1979*a*. Aquatic and wetland plants of southeastern United States: monocotyledons. University of Georgia Press, Athens, USA.

Godfrey, R.K., and J. Wooten. 1979*b*. Aquatic and wetland plants of southeastern United States: dicotyledons. University of Georgia Press, Athens, USA.

Jones, R.L. 2005. Plant life of Kentucky: an illustrated guide to the vascular flora. University Press of Kentucky, Lexington, USA.

Radford, A.R., H.A. Ahles, and C.R. Bell. 1968. Manual of the vascular flora of the Carolinas (with updates by A. Weakley). University of North Carolina Press, Chapel Hill, USA.

I included species that either I or my co-workers encountered throughout Mississippi, a total of 404 species.

Step 2. Pooling specific habitats (as named and identified in the floral manuals cited in Step 1) into three general habitat categories of interest: Fire-Maintained Open Habitats (open habitats), Forests, and habitats characterized by Severe Anthropogenic Disturbance (disturbed habitats).

Open habitats specifically included open woods, mesic open woods, dry open woods, semi-open dry woods, low open woods, sparsely wooded areas, dry open oak woods, prairies, acid prairies, barrens, bogs (i.e., fire-maintained bogs of the southeast USA), bog margins, borders of bays and shrub bogs, depressions in bogs and pine savannas, depressions in flatwoods or pine savannas, poorly drained pinelands and pine savannas, flatwoods, sandhills, savannas, pine savannas, pine seepage slopes, moist edges of scrub oak-pine barrens, wet pine flatwoods, and wet pine savannas. I assumed that non-native species were not indicative of any of these habitats, regardless of whether they had become naturalized within these habitats.

Forests specifically included woods, oak-hickory forests, mesic woods, rich or loamy woods, shady and mesic slopes, mesic slopes, hammocks, beech woods, calcareous hammocks, coastal hammocks, woods with basic or neutral pH soil, woods with acid soils, forested bluffs, floodplain and bottomland forests, wet woods, low woods, upland woods, alluvial woods, ravine bottoms and slopes, wet calcareous hammocks, wet limestone hammocks, ridgetop woods, dry woods, wooded river banks, pine-oak-hickory woods, pine-oak woods, wooded stream banks, banks of streams draining bays, creek swamps, cypress depressions, cypress swamps, forested wetlands, acid swamps, rocky woods, sandy woods, seepage areas in woodlands, springs, and titi swamps. As with open habitats, non-native species were assumed not to be indicative of any of these native forested habitats.

Habitats associated with severe anthropogenic disturbance specifically included disturbed areas, waste places, areas with ruderals, fallow fields, wet fields and pastures, ditches, borrow pits, lawns, paths, old home sites, gardens, ditch banks, disturbed soils in wet areas, wet disturbed sandy soils, sandy-peaty ditches, roadsides, railroads, and pastures. In contrast to open and forest habitats, non-native species were not assumed non-indicative of severely disturbed habitats.

Appendix 1, continued. Procedure for calculating habitat indicator scores and weighted summed abundances of habitat indicators.

Step 3. Calculating proportional similarity in species composition between each pooled general habitat category of interest and each specific habitat type not within the pooled habitat category of interest. I conducted a separate analysis for each of the three pooled habitat categories of interest. Proportion similarity calculated as Sørensen's quotient of similarity:

$$Q = \frac{2c}{(s_s + s_g)}$$

where Q is the quotient of similarity between a specific habitat and the general pooled habitat category of interest, c is the number of species common to both the specific habitat and the general pooled habitat category, s_s is the number of species in the specific habitat, and s_g is the number of species in the general pooled habitat category.

Step 4. Calculating unrefined habitat indication scores for each species for each of the three general habitat categories of interest. I accomplished this step by taking the species × habitat matrix (with some specific habitats pooled into the general habitat category of interest) and replacing the 1s (presences) with the proportional similarity between each specific habitat with the general habitat category of interest (calculated in Step 3). From the new matrix, I then calculated weighted averages of the proportional similarity scores for each species. This procedure yielded an unrefined indication score for each general habitat category of interest for each species.

Step 5. Refining habitat indication scores. To account for overlap among the general habitat categories of interest and therefore to quantify each species' association with each general habitat category of interest independently of the other two, for each species, I subtracted from the indication score for a given general habitat category the average of the indication scores of the two remaining general habitat categories. I assumed that a species with positive difference was a good indicator of the habitat of interest. I considered those native species with high refined open-habitat indication scores desirable restoration targets and those native species with high refined forest indication scores desirable conservation target species. I considered those species (native and non-native) with high refined disturbed-habitat indication scores to be undesirable ruderal or "weedy" species.

Step 6. Calculating weighted summed abundances of samples (sub-subplot) for each general habitat category of interest. I used the refined habitat indication scores and the abundances of all species with positive indicator scores for the habitat of interest to calculate weighted summed abundances and thus weighted fidelities of the sub-subplot to each general habitat category of interest.

The most desirable responses to treatments included:

1. an increase in weighted summed abundance of open habitat indicators combined with a decrease or no change in weighted summed abundance of ruderals, and
2. an increase or lack of change in weighted summed abundance of forest indicators combined with a decrease in weighted summed abundance of ruderals.

Undesirable responses to treatments included:

1. an increase in weighted summed abundances of ruderals combined with a decrease or lack of increase in weighted summed abundances of either open habitat indicators or forest indicators;
2. a decrease in weighted summed abundance of forest indicators combined with no increase in weighted summed abundance of open habitat indicators; and
3. no increase in weighted summed abundance of open habitat indicators.

Appendix 2. Refined habitat indication scores for herbs and vines encountered at the Tallahatchie Experimental Forest. Nomenclature follows USDA Plants Database.

Species	Open habitat indicator score	Forest indicator score	Severe disturbance indicator score
Acalypha gracilens A. Gray and *virginica* L.	0.04	−0.36	0.32
Ageratina altissima (L.) R.M. King & H. Rob.	−0.43	0.79	−0.36
Agrimonia rostellata Wallr.	−0.43	0.80	−0.38
Ambrosia artemisiifolia L.	−0.37	−0.40	0.78
Andropogon virginicus L.	−0.02	−0.08	0.10
Antennaria plantaginifolia (L.) Richardson	−0.38	0.73	−0.36
Aristida longespica Poir.	−0.17	−0.20	0.36
Aristida purpurascens Poir.	0.13	−0.21	0.08
Aristolochia serpentaria L.	−0.29	0.47	−0.18
Asclepias variegata L.	0.30	−0.23	−0.07
Asplenium platyneuron (L.) Britton, Sterns and Poggenb.	−0.01	0.01	0.00
Carex spp. L.	NA	NA	NA
Chasmanthium laxum (L.) Yates	−0.05	0.04	0.00
Chasmanthium sessiliflorum (Poir.) Yates	−0.27	0.36	−0.09
Chrysopsis mariana (L.) Elliott	−0.08	0.15	−0.06
Cirsium carolinianum (Walter) Fernald & B.G. Schub.	0.30	−0.40	0.10
Clitoria mariana L.	0.37	−0.25	−0.12
Conyza canadensis (L.) Cronquist	−0.37	−0.40	0.78
Coreopsis major Walter	−0.26	0.16	0.10
Cyperus echinatus (L.) Alph. Wood	−0.13	−0.13	0.26
Desmodium laevigatum (Nutt.) DC.	0.04	−0.04	0.00
Desmodium nudiflorum (L.) DC.	−0.43	0.76	−0.33
Desmodium paniculatum (L.) DC.	0.00	−0.03	0.03
Desmodium rotundifolium DC.	0.06	0.21	−0.27
Desmodium viridiflorum (L.) DC.	0.00	−0.03	0.03
Dichanthelium acuminatum (Sw.) Gould & C.A. Clark var. acuminatum	0.04	−0.12	0.07
Dichanthelium acuminatum (Sw.) Gould & C.A. Clark var. lindheimeri (Nash) Gould & C.A. Clark	0.16	−0.28	0.12
Dichanthelium boscii (Poir.) Gould & C.A. Clar*k*	0.13	0.19	−0.32
Dichanthelium commutatum (Schult.) Gould	0.20	0.13	−0.33
Dichanthelium dichotomum (L.) Gould	−0.22	−0.17	0.39
Dichanthelium laxiflorum (Lam.) Gould	0.00	0.15	−0.15
Digitaria filiformis (L.) Koeler	0.02	−0.03	0.01
Dioscorea villosa L.	−0.29	0.38	−0.09
Elephantopus tomentosus L.	−0.40	0.20	0.21
Erechtites hieraciifolius (L.) Raf. ex DC.	−0.32	−0.03	0.35
Eupatorium capillifolium (Lam.) Small	−0.22	−0.23	0.45
Eupatorium serotinum Michx.	−0.03	−0.02	0.04
Euphorbia corollata L.	0.04	−0.19	0.14
Eurybia hemispherica (Alexander) G.L. Nesom	0.16	−0.21	0.05
Galactia volubilis (L.) Britton	0.09	0.02	−0.11
Galium circaezans Michx.	−0.25	0.38	−0.13
Galium pilosum Aiton	−0.18	0.10	0.08
Gamochaeta purpurea (L.) Cabrera	−0.06	−0.33	0.39
Gentiana villosa L.	0.09	0.02	−0.11
Helianthus hirsutus Raf.	−0.05	0.00	0.05
Helianthus microcephalus Torr. & A. Gray	0.06	−0.09	0.03
Heuchera americana L.	−0.16	0.28	−0.12
Hieracium gronovii L.	−0.08	−0.10	0.19
Houstonia purpurea L.	−0.14	0.10	0.04
Hypericum hypericoides (L.) Crantz	−0.41	0.77	−0.36
Hypoxis hirsuta (L.) Coville	0.37	−0.16	−0.21
Ionactis linariifolius (L.) Greene	0.22	0.15	−0.37
Lactuca canadensis L.	−0.32	−0.03	0.35
Lespedeza hirta (L.) Hornem.	0.17	−0.26	0.09
Lespedeza violacea (L.) Pers.	−0.03	−0.07	0.10
Lespedeza procumbens Michx.	−0.03	−0.07	0.10
Lespedeza repens (L.) W.P.C. Barton	0.05	−0.05	0.00

Appendix 2, continued. Refined habitat indication scores for herbs and vines encountered at the Talla-hatchie Experimental Forest. Nomenclature follows USDA Plants Database.

Species	Open habitat indicator score	Forest indicator score	Severe disturbance indicator score
Lespedeza virginica (L.) Britton	−0.03	−0.07	0.10
Liatris aspera Michx.	0.05	0.20	−0.25
Lonicera japonica Thunb.			0.28
Maianthemum racemosum (L.) Link	−0.44	0.81	−0.36
Microstegium vimineum (Trin.) A. Camus			0.12
Mikania scandens (L.) Willd.	−0.06	0.18	−0.12
Mimosa quadrivalvis L.	0.06	−0.19	0.13
Monarda fistulosa L.	0.01	0.10	−0.10
Monotropa hypopithys L.	−0.41	0.77	−0.36
Monotropa uniflora L.	−0.41	0.77	−0.36
Orbexilum pedunculatum (Mill.) Rydb.	0.09	−0.07	−0.02
Oxalis stricta L.	−0.30	−0.01	0.31
Oxalis violacea L.	−0.47	0.83	−0.36
Parthenocissus quinquefolia (L.) Planch.	−0.01	0.04	−0.03
Paspalum boscianum Flueggé			0.80
Passiflora lutea L.	−0.05	−0.04	0.09
Pityopsis graminifolia (Michx.) Nutt.	0.02	−0.05	0.03
Pleopeltis polypodioides (L.) Andrews & Windham subsp. polypodioides	−0.02	0.00	0.01
Polystichum acrostichoides (Michx.) Schott	−0.07	0.21	−0.14
Potentilla simplex Michx.	−0.19	0.07	0.12
Pseudognaphalium obtusifolium (L.) Hilliard & B.L. Burtt	−0.03	−0.34	0.37
Pteridium aquilinum (L.) Kuhn	−0.34	0.26	0.08
Rosa carolina L.	0.03	−0.23	0.20
Rubus argutus Link	−0.15	0.06	0.09
Rubus trivialis Michx.	−0.14	−0.13	0.27
Rudbeckia hirta L.	−0.02	−0.06	0.08
Ruellia caroliniensis (J.F. Gmel.) Steud.	0.15	0.02	−0.17
Salvia lyrata L.	−0.06	−0.02	0.07
Sanicula canadensis L.	−0.20	0.05	0.15
Schizachyrium scoparium (Michx.) Nash	−0.02	−0.04	0.06
Scleria reticularis Michx.	0.11	−0.06	−0.05
Scutellaria elliptica Muhl. ex Spreng.	−0.09	0.07	0.01
Silene virginica L.	0.05	0.11	−0.16
Smilax bona-nox L.	−0.14	0.10	0.05
Smilax glauca Walter	−0.08	0.11	−0.03
Smilax rotundifolia L.	−0.05	0.01	0.04
Solanum carolinense L.	0.19	−0.42	0.23
Solidago caesia L.	−0.47	0.84	−0.37
Solidago canadensis L.	−0.01	−0.05	0.06
Solidago odora Aiton.	−0.02	0.04	−0.02
Solidago ulmifolia Muhl. ex Willd.	−0.25	0.45	−0.20
Spiranthes cernua (L.) Rich.	0.06	−0.12	0.06
Stylosanthes biflora (L.) Britton, Sterns & Poggenb.	−0.01	0.00	0.00
Symphyotrichum dumosum (L.) G.L. Nesom	−0.01	−0.01	0.02
Symphyotrichum patens (Aiton) G.L. Nesom	−0.04	−0.02	0.06
Symphyotrichum pilosum (Willd.) G.L. Nesom	0.04	−0.22	0.18
Symphyotrichum racemosum (Elliott) G.L. Nesom	−0.04	0.04	0.00
Symphyotrichum shortii (Lindl.) G.L. Nesom	0.15	0.06	−0.21
Tephrosia virginiana (L.) Pers.	0.07	−0.26	0.19
Toxicodendron radicans (L.) Kuntze	−0.26	−0.01	0.26
Tradescantia ohiensis Raf.	0.09	−0.07	−0.01
Tridens flavus (L.) Hitchc.	0.06	−0.37	0.30
Triodanis perfoliata (L.) Nieuwl.	−0.08	−0.34	0.41
Uvularia perfoliata L.	−0.44	0.81	−0.36
Verbesina helianthoides Michx.	0.29	−0.37	0.08
Viola triloba Schwein.	0.10	0.06	−0.16
Vitis aestivalis Michx.	−0.21	0.16	0.05
Vitis rotundifolia Michx.	−0.02	0.11	−0.09