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Shocks to the system: community assembly of the oak savanna in a 40-year fire frequency experiment

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Abstract. Fire is a major force driving the evolution of plants and the structure and function of ecosystems globally. It thus likely operates as an important environmental filter that selects for species that have evolved to tolerate and depend on fire. Across a 40-year experimental fire gradient from frequently burned open savanna to unburned dense woodland in Minnesota, USA, we examined the relationships among community assembly, evolutionary history, and functional trait composition. Close relatives had similar abundance patterns across the fire gradient, providing evidence for phylogenetic conservatism in fire adaptation and highlighting the importance of shared ancestry in predicting species responses to fire.

Phylogenetic beta diversity was greatest between the most extreme fire treatments across the gradient, indicating that species in the most contrasting fire regimes were most distantly related. Fire strongly influenced diversity, co-occurrence patterns, and leaf trait means and variances within communities. The most frequently burned communities had the highest species richness, exhibited the most resource-conservative leaf traits, and spanned the greatest number of phylogenetic lineages but harbored more close relatives within those lineages than other communities. In contrast, unburned communities had the lowest species diversity, the most acquisitive leaf traits, and the fewest phylogenetic lineages, but close relatives co-occurred less frequently. The largest difference in abundance between treatments occurred within the Rosales, Asteraceae, Vitaceae, and the Poaceae; woody Rosales were strongly selected for in unburned communities, while composites and grasses of the Poaceae were strongly selected for under frequent burning.

A major climatic perturbation of consecutive hot, dry summers in the late 1980s prompted a significant shift in the functional and phylogenetic composition of communities. Greater than expected turnover in species composition occurred following the drought years, and then again during the subsequent five-year rebound period. Just after the drought year, turnover was greatest among recently diverged taxa, whereas during the rebound period turnover was greater among taxa that diverged deep in the phylogeny. The drought years also caused a short-term shift in functional traits, including declines in specific leaf area and leaf nitrogen content and an increase in leaf length. These results indicate that the phylogenetic and functional trait composition of communities are responsive both to fire gradients and to shocks to the system, such as climatic perturbation.

Key words: Cedar Creek Ecosystem Science Reserve; climatic perturbation; community-weighted means; depth of turnover; fire frequency; functional traits; oak savanna; phylogenetic niche conservatism; phylogeny.

INTRODUCTION

Fire is a major force in the evolution of fire-tolerant and fire-dependent plant species (Keeley 1991, Schwilk and Ackerly 2001, Bond and Keeley 2005) and is a critical driver of ecosystem structure and function globally (Whelan 1995, Pyne et al. 1996, Thonicke et al. 2001, Bond et al. 2005). The frequency and dynamics of fire have important consequences for community assembly (Verdu and Pausas 2007, Peterson and Reich 2008, Silva and Batalha 2010), functional trait composition (Ackerly et al. 2002, Hoffmann et al. 2003, 2005, Silva and Batalha 2009, Willis et al. 2010), and ecosystem function, including productivity and nutrient cycling (Myers 1985, Reich et al. 2001*a*, *b*). In North America, oak savanna is a fire-dependent and endangered ecosystem that once covered nearly one-third of the continental United States (Packard and Mutel 1997). Due to the expansion of agriculture, major shifts in land use and changes in land management practices with Euro-American settlement (including fire suppression), the oak savanna has been reduced to a tiny fraction of its original area. Oak savannas represent a major

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Plate 1. Spring burning in a 40-year fire frequency experiment in the oak savanna at Cedar Creek Ecosystem Science Reserve (Minnesota, USA). Photo credit: John Haarstad.

ecotone between forest and grassland biomes and have long been studied to investigate issues such as stability, the role of disturbance, and controls on community composition and ecosystem function. Intermediate-frequency fire regimes are commonly found to be important in maintaining savannas (Gleason 1913, Glitzenstein et al. 1995, Peterson and Reich 2001, Varner et al. 2005, Hoffmann et al. 2009). Reductions in fire frequency caused both by land use change and fire suppression have been implicated in loss of savanna ecosystems and succession toward closed-canopy and fire-intolerant species (Dickman 1978, Wright and Bailey 1982, McPherson 1997, Anderson et al. 1999). Fire is likely to interact with other abiotic factors, including climate, to impose environmental filters on the establishment and population dynamics of species (Danz et al. 2011). These environmental filters may be expected to have consequences for the phylogenetic and functional composition of communities (Cavender-Bares et al. 2004*a*, *b*, Verdu and Pausas 2007). If fire adaptations are conserved through evolutionary history, closely related species may sort similarly across fire frequency gradients.

The objective of this paper was to investigate the role of fire dynamics and climatic perturbation through time on shifts in the phylogenetic and functional composition of communities across the grassland–forest ecotone. The study is conducted in the context of a large-scale 40-year fire frequency experiment designed to test the role of fire in restoring the Midwestern oak savanna (see Plate 1). This time frame spans a range of climatic variability. Climate was mildly variable from the 1980s to the present, but extreme high temperatures occurred over three consecutive growing seasons in the late 1980s, accompanied by severe drought. This is known to have had major effects on regional ecosystems (Haddad et al. 2002, Dovciak et al. 2005).

Previous studies in this woodland system have found shifts in composition, including an increase in basal density of woody species and canopy closure with decreasing fire frequency (Peterson and Reich 2001). Contrasting fire frequency also influences light availability and light heterogeneity within stands, leading to divergent patterns of community phylogenetic structure (Willis et al. 2010). At the ecosystem level, decreasing fire frequency accelerates N mineralization and N cycling driven by increased detrital production, improved detrital quality, and increased moisture, caused by a roughly 50–50 mixture of direct impacts and those flowing from changes in vegetation composition (Reich et al. 2001*b*, Dijkstra et al. 2006).

Information about the shared ancestry of organisms, often associated with functional similarity of species, has proven to be illuminating about biodiversity in ways that go beyond simply counting numbers of species (e.g., Faith 1994, Webb 2000, Cavender-Bares et al. 2004*a*, Cadotte et al. 2008). Individual traits are likely to vary in the extent to which they are phylogenetically conserved (Ackerly and Reich 1999), and trait lability may vary with phylogenetic scale (Cavender-Bares et al. 2006, 2009). At some phylogenetic scale, however, phenotypic and functional traits, including those that relate to ecological niches, generally show greater similarity among species with greater shared ancestry (Harvey and Pagel 1991, Blomberg and Garland 2002, Wiens and Graham 2005, Donoghue 2008, Wiens et al. 2010).

Given that species with shared functional attributes and shared ancestry may have similar responses to the environment, environmental filters are predicted to have consequences for both the functional (Weiher and Keddy 1999, Weiher et al. 1999) and phylogenetic structure of communities (Webb et al. 2002, Cavender-Bares and Wilczek 2003). Some efforts to detect consequences of environmental filtering on community structure have detected strong functional effects independent of species evolutionary history (e.g., Silva and Batalha 2010, Milla and Reich 2011). However, in many cases, both are detected, with functional consequences helping to illuminate mechanisms by which phylogenetic community structure is influenced (Cavender-Bares et al. 2004*a*, Kraft and Ackerly 2010, Willis et al. 2010, Knapp et al. 2012, Savage and Cavender-Bares 2012). Frequently, information on functional traits may be limited or lacking, particularly for species rich communities (e.g., Webb 2000, Strauss et al. 2006, Cadotte et al. 2010, Davies et al. 2010), or the functional traits critical for community assembly may be unknown. Phylogenetic information thus offers integrative information on shared ancestry and potentially on species functional similarity that can provide insights on the drivers of community structure and responses of communities to environmental change (Webb et al. 2002, Kraft et al. 2007, Cavender-Bares et al. 2009, Vamosi et al. 2009).

In this study, we investigated the evidence for phylogenetic conservatism in fire frequency niches by examining whether species that have descended from a recent common ancestor sort similarly across a 40-year fire frequency gradient. If species with high shared ancestry are similarly selected for by a given fire regime, and if species adapted to contrasting environments are drawn from different lineages across the phylogeny, then increasing differences in fire regime between communities should increase phylogenetic beta diversity, or phylogenetic dissimilarity between communities (sensu Bryant et al. 2008, Graham and Fine 2008, Sander and Wardell-Johnson 2011). We thus predicted turnover across the extremes of the gradient to occur between lineages that diverged deep in time, but turnover among communities within similar environments to occur among close relatives that share similar adaptations. We also examined the extent to which shocks to the system, such as major climatic perturbations, cause temporal turnover in phylogenetic and functional composition beyond that expected at random. Finally, we examined the extent to which both fire regime and climatic perturbation drive shifts in functional and phylogenetic components of diversity.

By investigating the dynamics of communities through time under long-term experimentally manipulated disturbance regimes, we seek to address long-standing questions on the controls of diversity and composition of the prairie–oak savanna–woodland mosaic and to provide critical knowledge relevant to the management of biodiversity and ecosystem services of a once prominent ecosystem. In doing so, we address critical questions about the phylogenetic conservatism of ecological niches (Donoghue 2008, Wiens et al. 2010) and the importance of evolutionary history in driving species responses to environmental change (Edwards et al. 2007, Willis et al. 2008).

METHODS

Site and study system

The study was located at the Cedar Creek Ecosystem Science Reserve (hereafter Cedar Creek), a 2300-ha reserve and National Science Foundation (NSF) Long Term Ecological Research site on the Anoka Sand Plain in eastern Minnesota, USA (see Plate 1). The terrain is relatively flat, and soils are infertile, excessively drained, fine-to-medium sands. The climate is humid continental, with warm summers and cold winters. Mean annual precipitation is 79 cm, with 64% of this total occurring during the active growing season (May–September; Reich et al. 2001*b*). Episodes of prolonged drought occurred in the late 1980s and the mid-1990s. The most striking climate period from 1982 to 2011 was 1986–1988. This period included the three hottest summers during the period, one of the three driest summers, and both the hottest and driest two-month and one-month periods. Moreover, the hottest and driest two-month periods were coincident (June–July 1988) and the single driest month (the fifth hottest of the 112 in the record) was followed by the single hottest month. Of over 4000 days in this record, 11 of the 25 hottest were in 1988. Marked impacts of this 1986–1988 hot dry period on the dynamics of Anoka sand plain vegetation have been documented previously (Haddad et al. 2002, Dovciak et al. 2005).

A prescribed burning experiment was initiated at Cedar Creek in 1964 to characterize responses to varying fire frequency and to restore and maintain oak savanna vegetation (Peterson and Reich 2001). An area of 300 ha was divided into 19 management units of 2.4 to 30 ha, and each was assigned a burn frequency treatment, ranging from nearly annual burns to complete fire exclusion, creating a gradient from open savanna to closed forest. Prescribed burns were conducted in April or May, after the snow melted but before leaf out. Typical burning conditions included air temperatures of 15°C to 25°C, relative humidity of 25% to 45%, and winds of 20 km/h. Fire behavior varied with weather conditions and fuel loads, but fires were generally of low intensity, with mean flame lengths of 1 m (Reich et al. 2001*b*). We characterized the burn units and the 375-m^2 sample plots within them into five categories: the unburned control ("Fire 0"); low frequency (approximately once per decade; "Fire 1"); medium frequency (2–3× per decade; "Fire 2"); mid-high frequency (4–5× per decade; "Fire 3"); and high frequency (7–8× per decade; "Fire 4").

Land use history across the burn units was relatively homogeneous; by the mid-20th century, most were dominated by semi-native woodland that had never been plowed, but had likely been periodically grazed and experienced limited selective logging (largely for firewood). Baseline vegetation data were not collected prior to the start of the prescribed fire program in 1964. There are no reliable fire records prior to this time period, but fire exclusion was an important management objective in the prior decades and was apparently achieved. Prior to 1938, these stands likely burned periodically. Aerial photos taken between 1938 and 1964 show increasing total canopy cover resulting from expansion of tree crowns and new tree growth (Reich et al. 2001*b*).

Community sampling

Permanent 0.375-ha plots (50 × 75 m) were established in the savanna burn units, each consisting of four parallel 50-m sampling transects placed 25 m apart. Eleven plots were established in 1984, three more were added in 1990, and 11 additional plots were added in 1995. Understory communities were surveyed every five years since the mid-1980s. In each plot, percent cover of all vascular plant species was assessed at sample points placed at 10-m intervals along each transect (a total of 24 sample points per plot). These cover values represent abundance in terms of both density and biomass. Cover values were summed across sample points by species within plots to estimate total abundance in each 375-m^2 community. To assure uniform taxonomic identities across years, given changing investigators over time, in a small number of cases, we used generic identification for genera that showed unlikely species level shifts between years. Ferns were excluded from all analyses due to the long-branch problem (Kembel and Hubbell 2006) that made communities with ferns extreme outliers in terms of community phylogenetic composition. There was one conifer in the study system, *Juniperus virginiana*. Exclusion of this species had no significant consequences for any of the results, and it was included.

Phylogeny construction

We used three literature-based phylogenies resolved manually with branch lengths estimated using minimum fossil ages (Supplement 1). The first phylogeny, referred hereafter as the CCphy tree (shown graphically in Appendix C) was assembled using the Angiosperm Phylogeny Group III tree (R20091110) as a backbone phylogeny and resolving the family and generic relationships manually (Supplement 2 and Appendix B). Nodes were dated based on minimum fossil ages and divergence-time estimates available in the literature (Supplement 2, including: Manos et al. 1999, Wikstrom et al. 2001, Chaw et al. 2004, Anderson et al. 2005, Bell et al. 2010, Bouchenak-Khelladi et al. 2010), using the BLADJ algorithm in Phylocom (Webb and Donoghue 2005). The second was assembled collectively by members of the Ecophylogenetic Working Group, hereafter referred to as the EcoPhyWG tree, and the methods are explained in Beaulieau et al. (2012this issue). Sources and nodes were annotated using the program Phylografter (Ree 2009). The ~14 000 species phylogeny was pruned for the 237 taxa represented in the Cedar Creek fire frequency data set. The third tree, previously reported in Willis et al. (2010), was constructed based on the Davies et al. (2004) backbone tree using Phylomatic (Webb and Donoghue 2005). Higher taxa were resolved based on available literature, and minimum fossil ages were used to date nodes. The CCphy tree is more resolved than the EcoPhyWG tree and slightly updated from the Willis et al. (2010) tree. It is used for all of the analyses presented.

Species functional traits

A suite of functional traits, including leaf morphometric traits, leaf N concentration, and plant height, were used to provide univariate and multivariate measures of functional diversity at the community level and to estimate abundance-weighted community means across treatments and through time. Green leaf areas and masses, and N concentrations (using standard methods), were measured in mid-summer for several individuals of all species representing >1% of cover on 8–11 subplots in each of 12 plots. Upper canopy foliage was sampled from each individual and the percentage of canopy openness of each subplot was measured (Reich et al. 2001*a*). Maximum plant height was determined from both field collections and available literature. Leaf morphology and plant height were previously reported in Willis et al. 2010; N concentrations are from P. Reich (*unpublished data*). The trait matrices are incomplete due to rarity of some species. Leaf morphological traits were available for 107 species; plant height for 86 species, and leaf nitrogen for 95 species. Species trait data represent >~80% biomass in the plots.

Data analysis

Community diversity.—We used several metrics of community diversity, including species richness (number of species per community), phylogenetic species variance (PSV; a measure of phylogenetic diversity independent of species richness; Helmus 2007), mean phylogenetic distance weighted by abundance (MPD; Webb 2000), and mean nearest phylogenetic taxon distance weighted by abundance (MNTD; Webb 2000). PSV, MPD, and MNTD were calculated using the Picante package in R (Kembel et al. 2010). While many metrics are available, these were chosen to capture a range of aspects of biodiversity. PSV ranges from zero to one, where a PSV of one indicates that species in a community are from disparate parts of the tree, and values of zero indicate perfect relatedness (or perfect trait similarity). Similarly, MPD provides a measure of mean phylogenetic diversity by taking the mean phylogenetic distance between individuals normalized by those distances when species identities are randomized across the tips of the phylogeny. MNTD is similar to MPD, but uses phylogenetic distances between closest relatives, emphasizing evolutionary relatedness encompassing the branch tips of the phylogenetic tree (Webb 2000). Diversity of functional traits was calculated using PSV based on hierarchical clustering of univariate or multivariate traits (Petchey and Gaston 2002) as implemented by Cadotte et al. (2009). Univariate traits were maximum plant height and leaf nitrogen concentration. The multivariate trait was the first principal component axis loadings of a principal components analysis that included leaf area, leaf length, specific leaf area, and leaf area per perimeter, each standardized to a mean of 0 and variance of 1. All diversity indices were compared to null models in which species abundances were randomized across communities, constraining species total biomass, but not the number of species per community. Standardized effect sizes (SES) were calculated as

$$\mathrm{SES} = (\bar{x}_{\mathrm{obs}} - \bar{x}_{\mathrm{null}})/\mathrm{SD}_{\mathrm{null}}$$

where x_{obs} is the observed mean diversity, x_{null} is the mean of the simulated values, and $\mathrm{SD}_{\mathrm{null}}$ is the standard deviation of the simulated values.

Phylogenetic beta diversity.—While there are multiple approaches for calculating phylogenetic beta diversity or phylogenetic dissimilarity between communities (e.g., Bryant et al. 2008, Morlon et al. 2011, Sander and Wardell-Johnson 2011, Swenson et al. 2012), we used the comdistn function in Picante (Kembel et al. 2010), in which a pairwise community distance matrix was computed based on the mean nearest taxon distance between species pairs across plots, weighted by species abundance. This provides a matrix of intercommunity phylogenetic beta diversity values. From this matrix, we used Primer version 5 (Clarke and Warwick 1994, PRIMER-E 2001) to compute a nonmetric multidimensional scaling (NMDS) ordination and to conduct a nonparametric analysis of similarity (ANOSIM) to test for differences between fire treatments, averaged across years. The ANOSIM tests whether the phylogenetic beta diversity (or phylogenetic dissimilarity) between treatments or years is greater than expected at random.

Phylogenetic depth of species turnover.—In a related approach, we examined the species turnover at sequential depths in the phylogeny. This allows identification of the historical time interval in which changes in turnover between treatments (or years) is greatest. In combination with mapping abundances, it reveals the lineages most important in turnover between community groups. Bray-Curtis dissimilarity between communities was calculated using the Vegan Community Ecology package in R (Oksanen et al. 2011), collapsing taxa at 20-million-year intervals through the phylogeny, adapting the approach used in Cavender-Bares et al. 2004*a*. At each successive phylogenetic depth, the tree was trimmed to include only the ancestral taxa at that depth, and abundance was summed for all collapsed taxa at each interval. Thus, the number of taxa was reduced at each slice through the phylogeny. To account for this change in numbers of taxa, a null model was generated in which species distributions were randomized across communities constraining total biomass per species. These methods are explained and illustrated further in Appendix A.

Bray-Curtis dissimilarity was computed between the unburned control and the four fire treatments by averaging biomass values of species across all survey years in each treatment. Dissimilarities between treatments greater than the null for a given phylogenetic depth indicate greater turnover in species composition between unburned and burned communities than expected if species distributions were random. Dissimilarity between consecutive census years was computed by averaging biomass values per species across all fire treatments. The null model randomized species biomass values across communities and years for the two comparison years, constraining total biomass per species. Communities in the analyses were constrained to those common to both years. Dissimilarities between years greater than the null indicate greater changes in community composition for a given phylogenetic depth than expected at random. Dissimilarities less than the null indicate greater continuity in species composition between sample years than expected.

Test for phylogenetic conservatism.—We tested for phylogenetic signal in functional traits and in species responses to fire and drought by examining variation in species mean trait values or species relative abundances using the *K* statistic (Blomberg et al. 2003) using the Kcalc function (written by S. Blomberg and D. Ackerly) implemented in Picante. *K* relates the observed variance among traits to that expected among traits of species descended from a common ancestor. *K* values of 1 are equivalent to trait evolution expected under a Brownian motion model evolution. *K* values of 0 have no phylogenetic signal. We tested whether observed *K* values were significantly different than expected at random by comparing them to a null model in which species identities were randomized 999 times across the tips of the phylogeny (null model 1). We also compared whether observed values were significantly different than 1 by generating a Brownian motion null model in which traits were evolved on the phylogeny (using the rTraitCont function in APE [Paradis et al. 2004]) 999 times with a rate of evolution calculated from the data (using the fitContinuous function in Geiger [Harmon et al. 2008]; null model 2). We assume that a K value significantly greater than that expected at random (null model 1) provides evidence for phylogenetic conservatism in traits or in species response to environmental factors. A K value not significantly different from 1 (null model 2) would indicate that patterns of trait evolution show phylogenetic signal consistent with Brownian motion evolution, a higher level of conservatism (Losos et al. 2008).

To test for phylogenetic conservatism in species responses to fire frequency, we calculated K for species' relative abundance, averaged across all years, in each of the fire treatments. Total species abundances in the Cedar Creek oak savanna system might themselves have phylogenetic signal, and this must be tested to determine whether phylogenetic signal across the fire gradient can be linked to a nonrandom sorting process. A significant K for abundances within treatments and nonsignificant K in total abundances across all treatments can be interpreted as evidence that species abundance patterns are nonrandom and that evolutionary history influences how species sort across the gradient. We also tested whether there was an increase in phylogenetic signal in species abundances following the severe drought years of the late 1980s to evaluate whether species with shared ancestry respond similarly to climatic perturbation.

Community-weighted means for functional traits.— Species mean functional traits values were used to calculate community trait means, weighted by abundance (CWM) as follows:

$$\mathrm{CWM} = \sum_{i}^{n} T_i P_i$$

where T_i is the species mean trait value for species i and P_i is the proportional abundance of species i in the community (Garnier et al. 2004). These community-weighted means incorporate only a single mean trait value per species, and therefore do not consider intraspecific variation in traits across the fire frequency gradient. Changes in values among treatments and over time thus reflect changes in species composition and abundance, but not plastic or genetically based intraspecific variation that might be expected across environments. Standardized effect sizes for trait values across the treatments calculated relative to a null model where species distributions were randomized across communities showed nearly identical patterns to the observed values and are not shown.

RESULTS

Overall, we found that closely related species sort more similarly across the fire frequency gradient than expected at random and showed greatest phylogenetic beta diversity at extremes of the gradient; species turnover occurred particularly between lineages that diverged deep in the phylogeny (80–140 million years ago [mya]; Fig. 1). Phylogenetic community structure and community-weighted functional trait means differed between fire treatments and shifted in response to climatic perturbation. Temporal phylogenetic beta diversity, or turnover through time, also spiked and then recovered in response to the drought.

Community diversity and composition

Mean species richness per 375-m^2 plot was significantly lower in the unburned treatment than in any of the burn treatments (Figs. 1A and 2A), and was below the 95% CI for the null expectation based on random species distributions (not shown). Species richness was relatively stable through time, varying from a mean of 33–39 species/plot in the unburned treatment and 42–60 species/plot in the burn treatments. Phylogenetic species variance (PSV), which is independent of species richness, was also lowest in the unburned plots (as was MPD; Appendix B) and below the 95% CI for the null expectation. Mean PSV per plot was relatively stable through time, except in the unburned treatment, where it decreased somewhat after 1995 (Fig. 2B). Abundance-weighted MPD followed a similar trend as PSV, with lowest values in the unburned plot (Appendix B). In contrast, the abundance-weighted mean nearest taxon distance (MNTD) per plot was higher in the unburned treatment than in any of the burn treatments and was lowest in the highest frequency burn treatment in most years (Fig. 2C). Moreover, MNTD showed a marked dip in 1990 in the unburned treatment, followed by a subsequent increase. Variance in MNTD within treatments was also lowest in 1990. Patterns of phylogenetic community structure were similar using the alternative phylogenies and are compared in Appendix E.

Community diversity calculated based on functional traits showed complicated patterns through time, and treatments were not always clearly differentiated (Appendix B). The multivariate measure of leaf trait diversity was lowest in the two highest frequency burn treatments, except in 1990, when the highest frequency burn treatment showed the greatest variation in leaf functional diversity (Fig. 2D). This pattern was repeated for diversity in leaf nitrogen concentration (Appendix B). Diversity in maximum plant height tended to be lowest in the unburned treatment and in the highest frequency fire treatment, with higher height diversity in the intermediate fire treatments (Appendix B). Standardized effect sizes for diversity metrics calculated relative to a null model where species distributions were randomized across communities showed nearly identical patterns to the observed values (Appendix B). Using abundance-weighted measures vs. species occupancy values had only a marginal influence in interpreting the effects of fire. However, the shifts in diversity and composition in 1990 after the severe drought were much

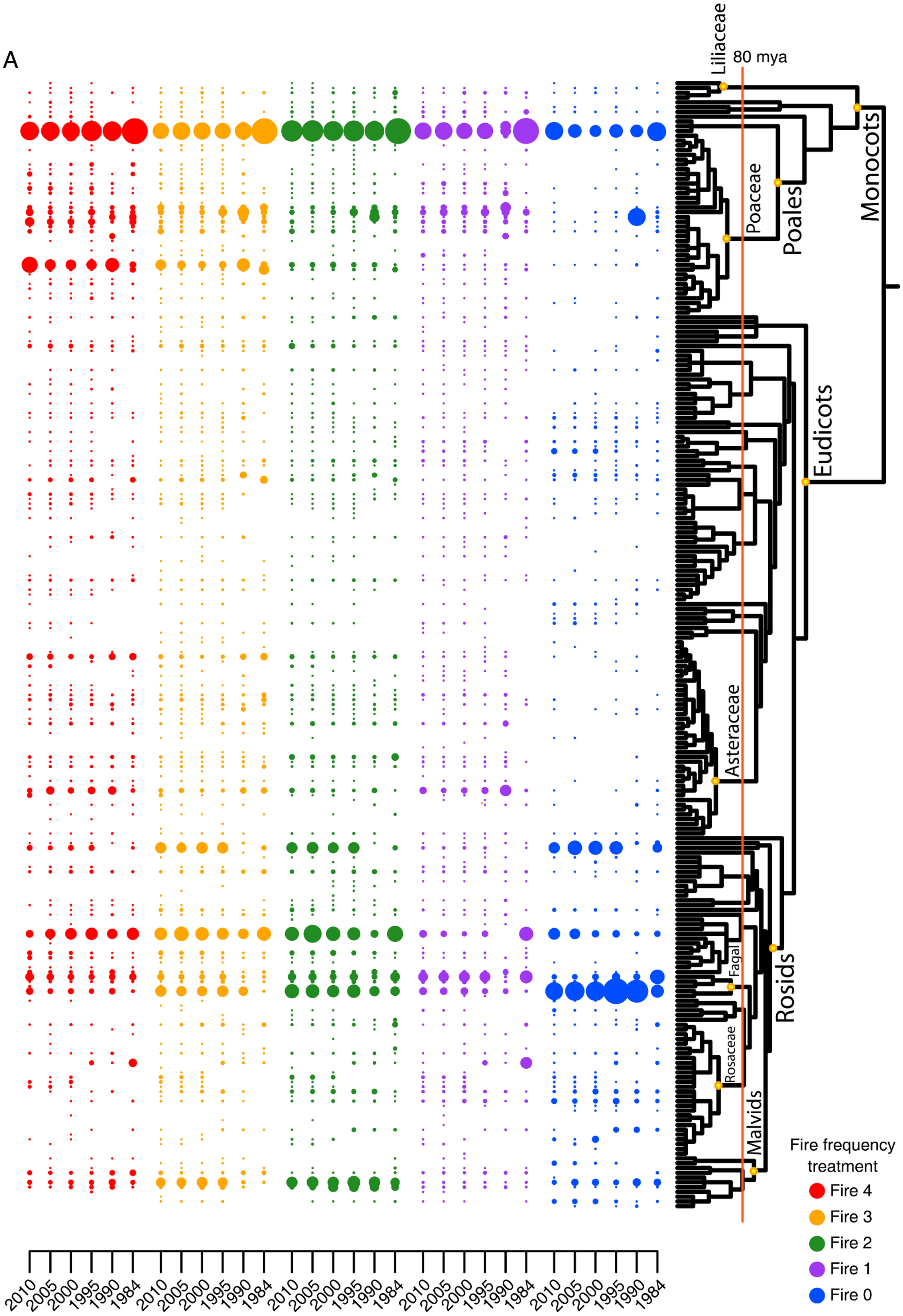

FIG. 1. (A) Relative abundance of species in the oak savanna across the experimental fire frequency gradient from 1984 to 2010 arranged on the CCphy phylogeny. The *y*-axis shows the years of the study for each treatment. Colors show fire frequency treatments: blue, unburned control (Fire 0); purple, low frequency, burned every 10 or 11 years (Fire 1); green, intermediate frequency, burned every 6 or 7 years (Fire 2); orange, intermediate high frequency, burned every 3 or 4 years (Fire 3); red, highest frequency, burned every 1 or 2 years (Fire 4). Circle sizes are proportional to relative abundance. Nodes corresponding to several important clades are labeled. The red line is drawn through the phylogeny at a depth of 80 million years ago (mya), corresponding to the phylogenetic depth where the change in turnover between treatments is greatest, as seen in Fig. 4B. Only angiosperms are shown, given few species and low abundances of other taxa. The complete phylogeny with species names can be viewed in Appendix B.

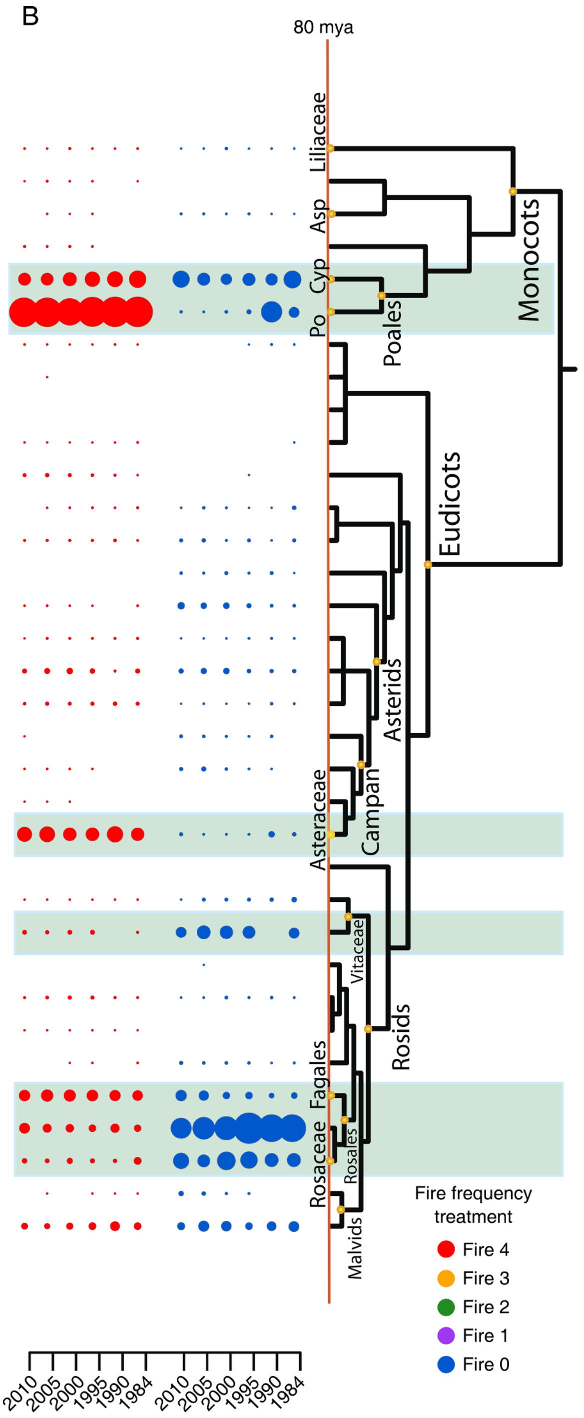

FIG. 1. Continued.

← (B) The same phylogeny is shown sliced at 80 mya. Relative abundances are shown for each clade at this phylogenetic depth. For brevity, only the unburned treatment and the most frequently burned treatment are shown. Fire treatments are color-coded as in panel (A). Clade abbreviations are as follows: Campan, Campanulids; Po, Poaceae; Cyp, Cyperaceae; Asp, Asparagaceae; and Fagal, Fagales.

stronger using abundance-weighted measures. These results indicate that much of the impact of climatic perturbation was on population size rather than species-level persistence.

Functional trait composition in response to fire and drought

Functional trait composition responded to fire frequency in a manner consistent with expectation based on previous work considering the functional attributes known to be selected for under fire suppression or frequent fire (Reich et al. 2001*b*, Hoffmann et al. 2004, 2005, Silva and Batalha 2010, Willis et al. 2010). Species maximum plant height was highest in the unburned plots and lowest in the most frequently burned plots (Fig. 2E). This shift corresponds to the expected increasing dominance of woodland species in the unburned communities and increasing dominance of grasses, herbs, and shrubs in the burned savanna communities. Leaf length was shortest in the unburned plots relative to mean values in all of the fire treatments (Fig. 2F). The shorter leaf size accompanied the reduction in grasses with canopy closure in the woodland communities, consistent with other studies of fire frequency and community structure (e.g., Hoffmann et al. 2005, Silva and Batalha 2010).

Specific leaf area (SLA) and the percentage of leaf nitrogen (leaf %N) were highest in the unburned communities and tended to be lowest in the highest frequency burn treatment. Higher specific leaf area and leaf nitrogen content with increasing fire correspond to greater canopy closure and shading in the woodland understory relative to the savanna, as well as accumulating impacts over time of greater N cycling in closed woodland than open savanna plots (Reich et al. 2001*b*). These trends indicate a shift toward species that invest in light and carbon harvesting in the unburned woodland and in photoprotection, desiccation tolerance, and N competition strategies in the fire-promoted open savanna. Such functional traits shifts would be expected across this fine-scaled ecotone, based on known significance of these functional attributes (e.g., Niinemets 2001, Wright et al. 2001, Reich et al. 2003*a*, *b*, Poorter et al. 2006, Valladares and Sanchez-Gomez 2006).

Compared with 1984, SLA and leaf %N declined markedly in 1990 (following the severe drought years) in most fire treatments, and leaf length as well as perimeter per leaf area (not shown) increased markedly (Fig. 2F–H). Maximum height also declined sharply in the low-frequency fire treatment. These dynamic changes result from abundance losses in species with high water use strategies and abundance increases in species with drought tolerance attributes during a relatively short time window follow the multiyear climatic perturbation. These trait shifts were transient

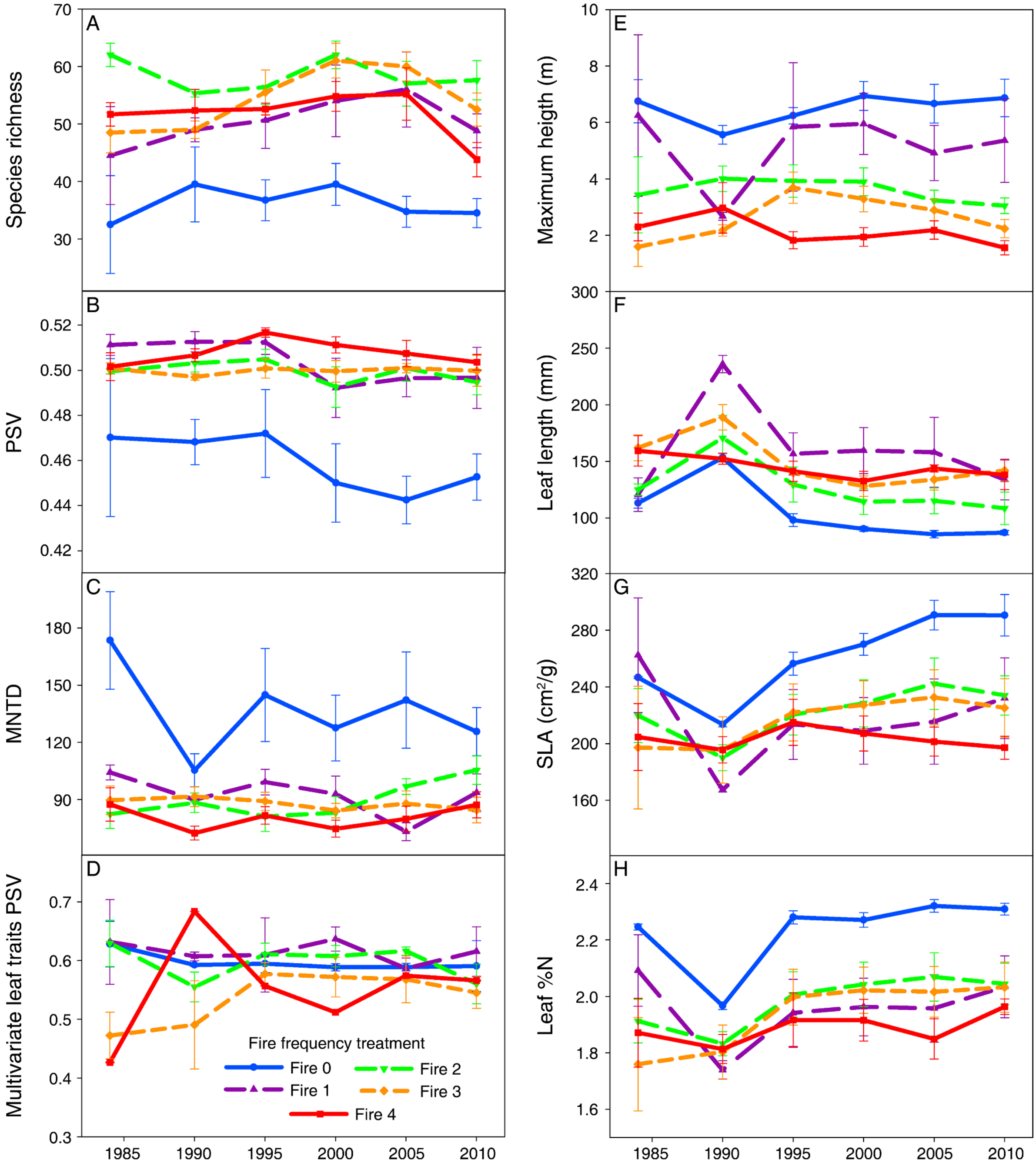

FIG. 2. (A–D) Metrics of diversity for oak savanna understory communities at Cedar Creek Ecosystem Science Reserve, Minnesota, USA, averaged for unburned communities and in communities treated with increasing fire frequency from 1984 to 2010: (A) species richness (number of species per 375-m^2 sample plot averaged across all plots in each treatment); (B) phylogenetic species variability (PSV), a measure of mean phylogenetic diversity that ranges from 0 (low phylogenetic diversity) to 1 (high phylogenetic diversity); (C) mean nearest taxon diversity (MNTD) a measure of species relatedness to their closest relatives; and (D) functional diversity for a multivariate measure of leaf traits using PSV calculated for hierarchical clustering of specific leaf area, leaf perimeter per area, leaf length, and leaf area. Functional diversity for plant height, multivariate leaf traits, and leaf nitrogen concentration, along with their effect sizes, calculated relative to a null model, are shown in Appendix B. Mean phylogenetic distance is also given in Appendix B for comparison. (E–H) Community-weighted means from 1984 to 2010 in each fire frequency treatment for four plant traits: (E) maximum plant height, (F) leaf length, (G) specific leaf area (SLA), and (H) the percentage of leaf nitrogen (leaf %N). Community-weighted means are calculated from species mean values for the trait multiplied by the proportional abundance of each species in the community. In all panels, values are calculated per plot and averaged across all plots in each treatment. See Fig. 1 for fire frequency treatment definitions. Error bars are ±SE.

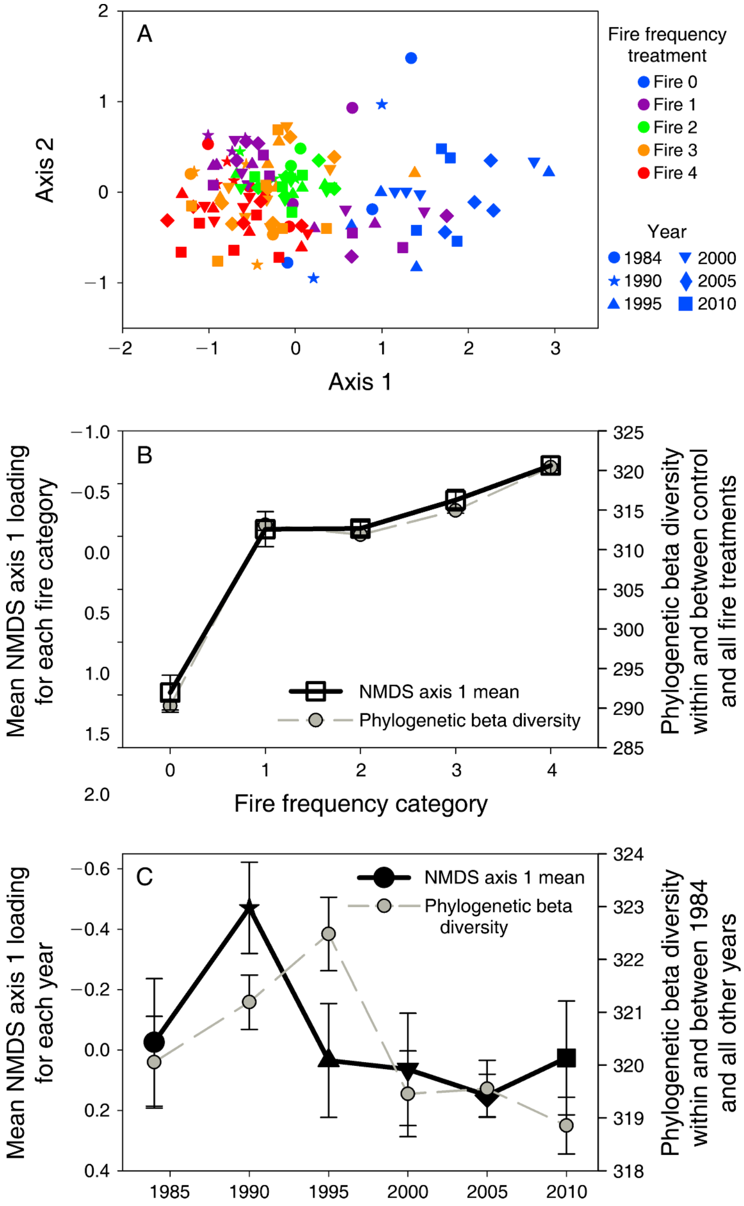

FIG. 3. (A) Nonmetric multidimensional scaling (NMDS) ordination based on pairwise, abundance-weighted, mean nearest-taxon phylogenetic distances between communities in different fire treatments and over time. Color indicates fire frequency treatment (see Fig. 1 for definitions), and the symbol shape indicates the year. (B) Values of the first axis of the NMDS ordination averaged across all years and plotted against fire frequency treatments. Superimposed on these values are the phylogenetic beta diversity values, calculated as the phylogenetic distances between nearest taxa in pairs of communities (375-m^2 plots), for each pairwise comparison between unburned communities and the fire treatments. The value plotted for "0" is the phylogenetic beta diversity between communities within the unburned control. (C) Values of the first axis of the NMDS ordination averaged across all fire treatments and plotted against survey years. Symbols are the same as in panel (A). Superimposed is the phylogenetic beta diversity between 1984 and all other years, calculated as in panel (B). The value plotted for 1984 is the average phylogenetic beta diversity between all pairs of communities for 1984. Error bars are ±SE.

though, as values returned to near-1984 values from 1995 to 2010.

Phylogenetic beta diversity among treatments and years

The NMDS ordination of intercommunity phylogenetic distances between nearest taxa over all years, a measure of the phylogenetic beta diversity, showed differentiation among treatments. The most frequently burned plots occurred in the bottom left quadrant, and the most infrequently burned plots appeared predominantly in the right half of the plot (Fig. 3A). Fire-treated communities were more tightly clustered in the ordination than the unburned plots, indicating greater phylogenetic similarity among burned communities than among unburned ones. The differentiation between unburned and burned communities (and also, but less so, among burned communities differing in fire frequency) is evident when the loadings from the first axis are averaged across all years and plotted relative to fire frequency category (Fig. 3B). These relative differences in the first NMDS axis were highly similar to the mean phylogenetic beta diversity among unburned plots and between the unburned plots and each fire category (Fig. 3B). Differentiation across years also occurred (Fig. 3C), with a loading in 1990 of −0.47 ± 0.15 (mean ± SE) across all fire treatments, which is lower than all other years (ranged from −0.025 ± 0.21 in 1984 to 1.5 ± 0.07 in 2005). Phylogenetic beta diversity means for all plots within 1984 (the initial survey year) and between 1984 and all other years showed a similar pattern, with the exception that the highest phylogenetic beta diversity was between 1984 and 1995, after which time communities showed declining phylogenetic beta diversity indicating greater phylogenetic similarity to the initial survey year.

ANOSIM results for differences between fire treatments averaged across years with 999 permutations of the distance matrix, showed significant differentiation between the unburned treatment and the most frequently burned treatment (Fire 0 vs. Fire 4, $R = 0.832$, $P = 0.001$). All burn treatments were significantly different than the unburned treatment (e.g., 0 vs. 3, $R = 0.75$, $P = 0.001$; 0 vs. 2, $R = 0.86$, $P = 0.001$; 0 vs. 1, $R = 0.52$, $P = 0.001$), but intermediate fire treatments were not significantly differentiated (2 vs. 3, $R = -0.06$, n.s.; 3 vs. 4, $R = -0.04$, n.s.) or were significantly differentiated, but had low R values (e.g., 1 vs. 2, $R = 0.24$, $P = 0.004$; 1 vs. 4, $R = 0.286$, $P = 0.002$; 2 vs. 4, $R = 0.31$, $P = 0.001$). R and P values largely corresponded to the magnitude of difference between fire frequency categories so that the unburned plots and the most frequently burned plots were the most differentiated, while the intermediate frequency treatments were the least differentiated. For comparisons across years for the full data set, ANOSIM showed significant differentiation between 1990 and all other years (Appendix D).

Phylogenetic depth of species turnover between fire treatments and over time

Turnover in species composition between unburned communities and all fire treated communities (averaged across years using Bray-Curtis dissimilarity at different phylogenetic depths) was large (dissimilarity high) and resulted from contrasting fire frequency niches among lineages that diverged deep in the phylogeny (Fig. 4A, B). The greatest turnover occurred between the unburned and most frequently burned plots, consistent with the ANOSIM analysis from the phylogenetic distance matrix. In this comparison (Fire 0 vs. Fire 4), the dissimilarity declined sharply starting at 80 mya, as seen most clearly from the standardized effect sizes (Fig. 4B), indicating that this is a critical depth for localizing clade-level niche differences related to fire. Dissimiliarity continued to decline to 140 mya. The largest drop in dissimilarity occurred between 80 mya and 140 mya, encompassing the origins of the monocots and eudicots. At the 80-mya cutoff (Fig. 1B) the Rosales, Fagales, Vitaceae, Asteraceae, and Poaceae are the clades that contribute most prominently to turnover between treatments. Turnover between fire treatments of different frequency was substantial (but much less than comparing burned and unburned vegetation), and changes in dissimilarity through successive depths in the phylogeny were flat or continuously declining, indicating that turnover occurred across the phylogeny among taxa that diverged recently as well as anciently. Between consecutive sampling years, turnover was greater than expected only between 1984 and 1990 among taxa at the tips of the phylogeny and between 1990 and 1995 among clades that diverged deep in the phylogeny (Fig. 4C, D). In the other consecutive year pairs, dissimilarity was lower than the null expectation of random species distributions across years, indicating continuity in community composition between years.

Phylogenetic conservatism in species sorting across the fire frequency gradient

The K value for species abundances averaged across fire treatments and years was 0.11 with the observed K value >410/999 null values (null model 1), indicating no phylogenetic signal in species abundances, on average, in the oak savanna understory (Table 1). There was significant phylogenetic signal in species distributions across the fire gradient, however. The K value for species relative abundance in the unburned treatment was 0.25 (observed phylogenetic signal, Kobs > 997/999 null values, $P = 0.003$). Similarly, the K for species relative abundance in the highest frequency burn treatment was 0.24 (Kobs > 996/999 null values, $P = 0.004$). Observed K values did not fall within the 95% confidence interval for Brownian motion evolution (null model 2). This was true for all K values in Table 1, and null model 2 results are not shown. Thus, phylogenetic signal in the unburned and most frequently burned communities was greater than expected at random, but not as high as would be expected if species abundance patterns had evolved under Brownian motion evolution.

Abundance values in any given year, averaged across all fire treatments, showed no phylogenetic signal, with the exception of 1995, which was marginally significant ($K = 0.14$, Kobs > 925, $P = 0.076$; Table 1). This survey year corresponds to the recovery period after the drought, during which period phylogenetic beta diversity also spiked (Fig. 3C). The marginally significant K indicates that niche conservatism played some role in which species were able to colonize after the drought.

Several functional traits (including plant height, leaf length, leaf %N, and perimeter per leaf area) also had significant K values relative to null model 1, although specific leaf area did not (Table 1). As before, observed

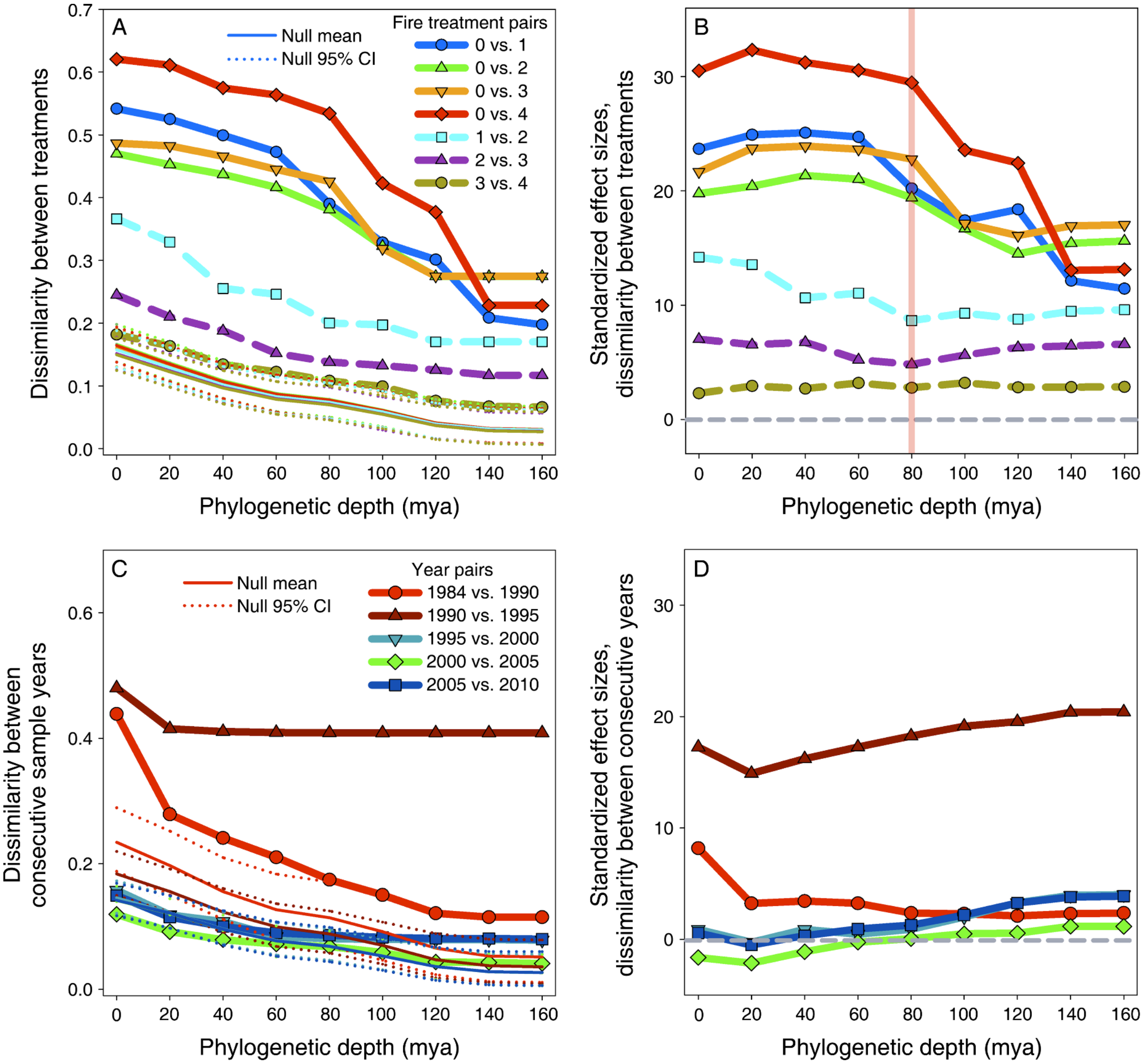

FIG. 4. Phylogenetic depth of species turnover between unburned and fire-treated communities, averaged across years (upper panels), and between consecutive sample years, averaged across fire treatments (lower panels), relative to null models in which species biomass values are randomized across communities and total species richness and number of occupancies is constrained. (A) Bray-Curtis dissimilarity (*d*) between unburned communities (Fire 0) and all fire treatments: Fire 0 vs. Fire 1 (blue), Fire 0 vs. Fire 2 (green), Fire 0 vs. Fire 3 (orange), and Fire 0 vs. Fire 4 (red) and between Fire 1 vs. 2 (cyan), Fire 2 vs. 3 (purple) and Fire 3 vs. 4 (olive green), averaged across years and plotted for taxa across increasing phylogenetic depth. The mean (solid lines) and 95% confidence intervals (dotted lines) for null models for each pairwise treatment comparison are shown computed by randomized species biomass values across communities, constraining biomass totals per species. Colors of the null models correspond to each pairwise treatment comparison but are highly overlapping. (B) Standardized effect sizes for the same comparisons as in panel (A): (obs *d* – null mean *d*)/SD null. The pink line indicates the phylogenetic depth (80 mya) where dissimilarity starts to decrease most rapidly between the unburned communities and the communities subject to high fire frequency. At this depth, the clades that contribute most to dissimilarity can be easily identified in Fig. 1A. (C) Bray dissimilarity for consecutive year pairs plotted for taxa at increasing phylogenetic depth; 1984 vs. 1990 (red); 1990 vs. 1995 (dark red); 1995 vs. 2000 (dark green); 2000 vs. 2005 (light green); 2005 vs. 2010 (blue). Null models are computed by randomization of species biomass values across communities in both years with biomass totals per species constrained. Calculations for observed and null dissimilarities are constrained to communities common to both years in each pair. Colors of the null models correspond to each pairwise year comparison. (D) Standardized effect sizes for panel (C).

K values for all traits, except SLA, indicate that trait values were more similar among close relatives than expected at random, but not as conserved as would be expected under Brownian motion evolution. Thus, phenotypes that might influence how species sort across the fire frequency gradient were phylogenetically conserved, at least in comparison to a random expectation.

Table 1. Phylogenetic signal in (A) species functional traits, (B) in species abundances in all communities and within each fire treatment, and (C) in species abundance in each year.

A) *Functional traits*:

Trait	Kobs	K.mean.null	Sim > obs	K.ses	*P*
Plant height	0.29*	0.11*	4*	5.35*	0.005*
Leaf length	0.35*	0.19*	23*	2.34*	0.024*
Specific leaf area (log)	0.20	0.18	211	0.63	0.212
Leaf N concentration	0.28*	0.18*	10*	3.28*	0.011*
Perimeter per area ratio of leaf	0.35*	0.19*	8*	3.00*	0.009*

B) *Species abundance (averaged for all years)*:

Community	*K*	K.mean.null	Sim > obs	K.ses	*P*
All communities	0.11	0.14	410	0.02	0.411
Unburned communities	0.25*	0.10*	2*	5.18*	0.003*
Low-frequency burning	0.11	0.10	146	0.71	0.147
Medium-frequency burning	0.10	0.11	422	−0.27	0.423
Med-high frequency burning	0.10	−0.11	524	0.10	0.525
Most frequently burned communities	0.24*	0.10*	3*	5.52*	0.004*

C) *Species abundance (averaged for all fire treatments)*:

Year	*K*	K.mean.null	Sim > obs	K.ses	*P*
1984	0.11	0.11	399	−0.05	0.400
1990	0.12	0.12	205	0.56	0.206
1995	0.14†	0.10†	75†	0.69†	0.076†
2000	0.14	0.11	116	0.32	0.117
2005	0.13	0.11	215	0.24	0.216
2010	0.13	0.12	199	0.03	0.200

Notes: The observed phylogenetic signal (Kobs) is quantified as Blomberg's *K* and compared to a null model in which species are randomized across the tips of the phylogeny 999 times. K.mean.null is the mean value of the null model. The rank of the observed *K* is given relative to the null observations showing the number simulated that are greater than the observed (sim > obs). The standardized effect size (K.ses) is (Kobs – K.mean.null)/SD null.

* $P < 0.05$; † $P < 0.10$.

Discussion

We found evidence for phylogenetic conservatism in the responses of plant communities to a 40-year fire frequency experiment. Closely related species sorted more similarly than would be expected (from random sorting) across communities that were unburned and frequently burned, indicating conservatism in the environmental niches driven by fire frequency. Functional traits that might influence how species sort across the gradient were also largely phylogenetically conserved. Turnover in composition in response to fire occurred largely among lineages that diverged between 80 and 140 mya, highlighting the deep footprint of evolutionary history on current ecological processes. Large abundance differences between unburned woodlands and frequently burned savanna grasslands were found within the Poales, Campanulids, and Rosales.

Response to climatic perturbation was marked, but only weakly associated with phylogenetic history; turnover before and after a major drought occurred among recently diverged taxa across many branches of the phylogeny and can be attributed largely to spikes or declines in abundance of species rather than to changes in their presence or absence. These abundance shifts altered phylogenetic community structure and trait composition, which subsequently returned to values similar to the pre-drought period.

Phylogenetic niche conservatism across woodland–savanna, fire frequency gradient

Species sorted across the fire gradient in a manner that reflects deep evolutionary history within the angiosperms. Multiple lines of evidence support this conclusion. First, species abundance patterns at both extremes of the gradient (enclosed woodlands at one end and open savanna on the other) had higher than expected *K* values, but total species abundances did not. In other words, species with high fire frequency niches are more closely related than expected at random; likewise, species in unburned niches are more closely related than expected (Table 1). We note that intermediate fire frequencies did not have phylogenetically conserved abundance patterns, suggesting that dispersal across the savanna–woodland mosaic create mixed assemblages of fire-tolerant and intolerant species in conditions where filtering is less severe. Second, we found increasing phylogenetic dissimilarity between communities with greater differences in fire frequency, such that phylogenetic beta diversity was maximal across the treatment extremes (Fig. 3B; ANOSIM results in Appendix D). Lineages most abundant in communities under the highest frequency fire regime diverged from lineages most abundant in unburned communities between 80 and 140 mya (Figs. 1 and 4). In contrast, the turnover between fire treatments of different frequency was much lower and occurred between lineages that diverged more recently.

Third, functional traits that influence how species sort across the gradient, such as maximum height (high values of which are critical to competitive ability capture light in shady woodland conditions) and leaf N concentration (high values of which are critical for photosynthetic light-use efficiency in low-light conditions) also tend to show phylogenetic conservatism (Table 1). Across the fire frequency gradient, species shift from those in the unburned woodland that invest in light and carbon harvesting to those in the fire-promoted open savanna that invest in photoprotection, desiccation tolerance, and N competition strategies. Our previous work in this system revealed conservatism in species light availability niches, analyzed at the 0.5-m^2 scale, and in functional traits associated with light availability (Willis et al. 2010). Conservatism in response to fire frequency may be related to conservatism in response to light and nitrogen availability because increasing fire frequency drives an increase in light and a decrease in nitrogen availability (Reich et al. 2001*a*). Taken together, these studies demonstrate that species ecological distributions across multiple spatial scales are significantly influenced by their evolutionary heritage.

Consequences of fire frequency for community diversity and structure

High-frequency fires alter phylogenetic community structure (Fig. 2B, C) and the phylogenetic composition of communities by allowing recruitment of many species from across major angiosperm lineages, including the Asteraceae, Fagaceae, and Poaceae, which tend to be excluded or reduced in abundance in the absence of fire (Figs. 1 and 4). Differences between burned and unburned communities are large and significant in terms of species richness, overall phylogenetic diversity (PSV), phylogenetic distances between close relatives (MNTD; Fig. 2A–D), community-weighted functional trait means (Fig. 2E–H), and phylogenetic community composition (Fig. 3). Unburned successional woodlands harbor the lowest species richness and lowest overall phylogenetic diversity (PSV), while higher fire frequency treatments harbor greater species richness and phylogenetic diversity (Fig. 2). Plant communities left unburned have the highest phylogenetic distance between close relatives, as indicated by the higher than expected MNTD values. Thus, close relatives tend not to co-occur, a pattern that might be expected if competition for light or nutrients structure these communities (Darwin 1859, Elton 1946, Webb et al. 2002). For example, high abundance of hazelnut (*Corylus*) may preclude recruitment of other taxa in the Fagales (such as oaks [*Quercus*]). Competition is a plausible explanation given the higher density of the vegetation in unburned plots relative to burned plots and the taller maximum height, higher leaf %N, and higher SLA, traits associated with canopy access and competitive growth strategies (sensu Grime 1977). Still, interpreting the higher than expected MNTD in terms of competition requires caution given the multiplicity of factors that may cause the same pattern (Cavender-Bares et al. 2009). In contrast, fire treatments tend to be phylogenetically clustered (low MNTD; Fig. 2C), a pattern expected if close relatives share adaptations for frequent fire disturbance and stresses associated with fire, including high light and reduced water availability. The conservatism in leaf level traits, such as high C:N ratios (low leaf %N) and short aboveground height, suggests that they do.

Functional diversity offers yet another perspective. Intermediate fire frequency treatments harbor the highest functional diversity in most years. Intermediate treatments are the most heterogeneous in terms of light availability (and likely soil N availability), thus allowing contrasting yet successful growth and stress tolerance strategies of taxa distributed in a patchy mix of open savanna and woodland vegetation. It is interesting that these intermediate fire frequencies support the highest functional diversity, but it is achieved with lower phylogenetic diversity than in the highest frequency treatment.

Climatic perturbation and dynamics of communities over time

There are several indications of a marked perturbation in community structure in the late 1980s that is captured in the 1990 sampling. A distinct reduction in the mean nearest phylogenetic taxon distance (MNTD) of communities occurred in 1990 (Fig. 2B) that is not reflected in species richness. The shift in phylogenetic community structure is accompanied by shifts in trait composition for leaf length, specific leaf area, and leaf nitrogen concentration (Fig. 2). The phylogenetic ordination also indicates an important shift in phylogenetic community structure in the 1990 census. We interpret these shifts as a response to the severe and prolonged drought accompanied by record high temperatures that occurred during the growing seasons from 1986 to 1988. Previous studies of the natural grassland and woodland vegetation close to our study site have documented large perturbations in community dynamics in response to this drought period (Haddad et al. 2002, Dovciak et al. 2005). The pattern of increased phylogenetic clustering, indicated by the drop in MNTD across all treatments in 1990 (Fig. 2C), may provide a signal of environmental filtering caused by climatic perturbation. That trait means and phylogenetic community structure tend to recover has implications for understanding the long-term resiliency of the oak savanna system.

The direction of change (prior to or following 1990) in community-weighted trait means support the interpretation of environmental filtering caused by prolonged drought and heat. The increase in leaf length (Fig. 2F) suggests an increase in relative abundance of grasses following the drought. Specific leaf area (SLA) also declined sharply (Fig. 2G). The decline would be predicted in response to drought stress both phenotypically and resulting from shifts in species and their abundance. Plasticity is not considered in this study, and the decline results largely from species shifts in abundance. Abundance of species with thinner, desiccation-intolerant species would be expected to decline in abundance in favor of species with thicker, drought-tolerant leaves (Westoby et al. 2002, Ackerly 2004, Franco et al. 2005). Such stress-tolerant species would likely have lower leaf nitrogen concentrations, a pattern which also is apparent in 1990 (Fig. 2H; Wright et al. 2001, Poorter et al. 2006).

The phylogenetic depth of species turnover through time

Turnover in species composition through time supports our hypothesized community response to climatic perturbation. The beta diversity analysis of species turnover at increasing depths in the phylogeny shows that following the severe drought of the late 1980s, a shift in community structure occurred largely among taxa that diverged relatively recently (<20 mya; Fig. 4A; 1984 vs. 1990). A subsequent shift in community structure between 1990 and 1995 occurred among taxa that diverged at deep levels of the phylogeny (Fig. 4A, B; 1990 vs. 1995). In all subsequent sample years, turnover was less than expected by the null model, indicating greater continuity in composition than expected at random. Our interpretation of this pattern is that drought caused a shift in composition largely among close relatives between 1984 and 1990. Longer term, after climate conditions reversed and as communities recovered from this perturbation (1990 vs. 1995), another major shift in composition occurred among taxa that diverged deep in the phylogeny; a shift that persisted for the rest of the sampling period. This result highlights the importance of long term data in phylogenetic ecology (see also Willis et al. 2008, Cadotte et al. 2012, Norden et al. 2012), in providing novel insights into the signature of evolutionary history in temporal shifts in communities.

Despite these perturbations in phylogenetic community structure and function, there was only weak phylogenetic signal in species abundances following the drought period, averaged across fire treatments. Grasses (Poaceae), in particular, were more strongly selected for following the drought than in other years, but other species selected for or against by the extreme climatic period in the late 1990s were drawn from across the phylogeny. These results invite further investigation on the extent to which responses of natural communities to long-term climate change (cf. Edwards and Donoghue 2008, Willis et al. 2008) will reveal a deep evolutionary footprint.

Conclusion

This study highlights the signature of evolutionary history in species sorting across a major ecotone driven by fire frequency. The phylogenetic and functional differentiation among species that occupy opposite ends of the fire frequency gradient reflects deep evolutionary divergence (>80 mya) and phylogenetic niche conservatism within fire frequency niches. The study also demonstrates community compositional changes at contrasting phylogenetic depths immediately following climatic perturbation and after recovery from perturbation, with apparent long-lasting consequences. Despite persistent compositional shifts, the overall pattern of recovery of trait means and phylogenetic community structure after the climatic "shock" has implications for long-term resilience of the oak savanna system. This pattern was not apparent from simpler measures of community structure, such as species richness. Finally, environmental filtering in response to fire and climatic perturbation is associated with shifts in functional trait composition that provide a mechanistic basis for community change. Taken together, these findings regarding the dynamics of this particular endangered oak savanna ecotone are likely relevant for fire-dominated tree–grass ecotones everywhere.

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SUPPLEMENTAL MATERIAL

Appendix A

Methods for analyzing community turnover at increasing phylogenetic depths (*Ecological Archives* E093-178-A1).

Appendix B

Functional, phylogenetic, and species diversity metrics within communities by fire frequency treatment over time (*Ecological Archives* E093-178-A2).

Appendix C

Graphical presentation of species relative biomass by fire frequency treatment in the Cedar Creek Ecosystem Science Reserve oak savanna across the phylogeny (*Ecological Archives* E093-178-A3).

Appendix D

ANOSIM results (*Ecological Archives* E093-178-A4).

Appendix E

Comparison of phylogenetic diversity metrics calculated from different phylogenies (*Ecological Archives* E093-178-A5).

Supplement 1

Three phylogenetic hypotheses for plant taxa in the Cedar Creek oak savanna communities used in calculating metrics of phylogenetic diversity (*Ecological Archives* E093-178-S1).

Supplement 2

Node ages (in millions of years) used to estimate phylogenetic branch lengths (*Ecological Archives* E093-178-S2).