

Conflicting Short and Long-Term Management Goals: Fire Effects in Endangered Golden-Cheeked Warbler (*Setophaga chrysoparia*) Habitat

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Abstract—Decades of fire suppression have significantly altered the vegetation structure and composition of savannas, woodlands, and forests. The presence of endangered species and other species of conservation concern in these fire-suppressed systems makes re-introducing fire more challenging. In oak-juniper woodlands of central Texas, we are presented with the challenge of re-introducing fire to attempt to increase oak regeneration, while simultaneously not substantially altering the vegetation structure and composition of the burned areas to avoid degrading habitat that is currently occupied by an endangered species, the golden-cheeked warbler (*Setophaga chrysoparia*). This bird breeds in Texas red oak (*Quercus buckleyi*) and Ashe juniper (*Juniperus ashei*) woodlands with an average combined canopy cover greater than 70 percent. To better understand the effects of fire on golden-cheeked warbler habitat, we examined the effects of four different wildfires on canopy cover and on the abundance and sizes of hardwoods and of Ashe juniper. Burned sites differed in fire frequency, fire seasonality, and time since fire. Burned sites had fewer Ashe juniper seedlings, saplings, and mature trees. Texas red oak and other hardwood trees and saplings sprouted after fire, but effects on hardwood seedlings were mixed. In the short-term, burned areas retained enough canopy cover to maintain golden-cheeked warbler habitat, but in the long-term, if oak regeneration failure continues in fire suppressed areas, these woodlands will likely become Ashe juniper woodlands and no longer provide quality habitat. It may be that more intense and severe fires are needed to sufficiently increase light availability and hence oak seedling abundance. We propose that pre-settlement vegetation was a fire-driven shifting mosaic of oak-savanna, shrubland, and oak-juniper woodland. Savanna and shrubland may mature into oak-juniper woodland under fire suppression, and more intense fires in oak juniper woodland may result in savanna or shrubland. If this proposition is correct, permanent designation of endangered species habitats to specific sites may be unattainable, as the suitability of habitat is dynamic and dependent on the natural fire cycle. We expect that conflicts between short and long-term management goals will increase in the future as stressors such as fire suppression, invasive species, and climate change continue to interact and drive novel plant and animal community dynamics.

Introduction

The presence of endangered species presents significant challenges to the use of prescribed fire and other management interventions such as invasive species removal (Lampert and others 2014; Severns and Moldenke 2010). Decades of fire suppression have altered the habitat of many endangered species. Efforts to restore the natural fire regimes in habitats where fire has been suppressed have included the use of prescribed fire to restore jack pine (*Pinus banksiana*) to produce habitat for the endangered Kirtland's warbler (*Dendroica kirtlandii*) (Payne and others 2012) and open pine woodlands for the endangered red-cockaded woodpecker (*Picoides borealis*) (US Fish and Wildlife Service 2003). In both of these examples the birds were not currently occupying the burned sites at the time of the prescribed fire. However, in our study system, oak-juniper woodlands of central Texas,

we are presented with the challenge of re-introducing fire after decades of fire suppression while simultaneously not substantially altering the vegetation structure and composition of the burned areas so that we do not degrade habitat that is currently occupied by an endangered species. Here, fire is being used to maintain, rather than create or restore, breeding habitat. Our situation is in some ways closer to the challenges faced by many managers when there are conflicting uses of the same site at the same time. For example, efforts to remove invasive tamarisk (*Tamarix* spp.) to restore native riparian vegetation are complicated by the use of the invasive tamarisk by the endangered willow flycatcher (*Empidonax traillii extimus*) (Dudley and Bean 2012).

Conflicting Management Goals

In many cases, as described above, decades of fire suppression have changed the vegetation so much that the target endangered species no longer occupies that area. However, in oak-dominated forests, woodlands, and savannas, fire suppression reduces light availability, causing a failure of oak (*Quercus* spp.) regeneration while leaving

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the existing oak-dominated canopy intact (Brose and others 2013; Nowacki and Abrams 2008; Russell and Fowler 2002). Oak regeneration failure is widespread. It is occurring in forests and woodlands of the eastern United States (US) (Arthur and others 2012), the Ozark Mountains in the central US (Dey and Hartman 2005), parts of the western US (Tyler and others 2006), and parts of Texas (Doyle 2012; Russell and Fowler 2002). On the Edwards Plateau of central Texas, the endangered golden-cheeked warbler (*Setophaga chrysoparia*) breeds in woodlands that contain mature Texas red oak (*Quercus buckleyi*), which is not regenerating, and Ashe juniper (*Juniperus ashei*), with an average total canopy cover greater than 70 percent (Groce and others 2010). Animals like the golden-cheeked warbler that forage predominately in the canopy can persist relatively unaffected in areas where oak is failing to regenerate. However, once enough overstory oak individuals die and are not replaced, the area will become unsuitable for the golden-cheeked warbler. Oak regeneration failure has therefore been identified as a threat to the golden-cheeked warbler (Groce and others 2010).

The restoration of oak regeneration, and consequently the re-introduction of fire, is therefore essential to the long-term persistence of the golden-cheeked warbler. Nevertheless, in the shorter-term, the areas targeted for the re-introduction of fire must maintain current golden-cheeked warbler habitat quality. Therefore, the current challenge is to try to restore oak-regeneration while not decreasing canopy cover below the 70 percent threshold that golden-cheeked warblers prefer. Although conflicts between fire management goals and conservation efforts for animal species of concern are common (Bisson and others 2003; Perry and others 2009), this situation is unique, to our knowledge, in that the target endangered species will eventually benefit in the long-term from the use of fire, but there is a definite limit on how severely an area can be burned in the short-term. However, as land managers increasingly confront conflicting short- and long-term management goals (in our system, open canopy for oak regeneration versus closed canopy for current animal habitat), similar challenges will become more common.

Central Texas Woodland

In central Texas woodlands, Texas red oak and Plateau live oak (*Q. fusiformis*) are not regenerating, while Ashe juniper (*Juniperus ashei*) is increasing in abundance (Murray and others 2013; Van Auken 2008). Therefore, the current fire suppression seems to be converting these woodlands from oak-dominated systems to juniper-dominated ones. We introduced the term 'juniperization' to describe the phenomenon of oak regeneration failure combined with increasing juniper density and cover (Andruk and Fowler 2014). Juniperization is also occurring as eastern red cedar (*Juniperus virginiana*) replaces native oaks in the Ozark Mountains and Cross Timbers regions of the US (Burton and others 2010; DeSantis and others 2011; Hanberry and others 2014), potentially causing conservation conflicts similar to the ones in central Texas.

Ashe juniper is a non-resprouting multi-stemmed tree. It is killed by high-intensity wildfires and has low re-establishment after such fires (Reemts and Hansen 2013, 2008). In contrast, Texas red oak resprouts after both low- to moderate- intensity prescribed fires (Andruk and Fowler 2014; Andruk 2014) and high-intensity wildfires (Reemts and Hansen 2013). Other common native hardwoods in these woodlands include black cherry (*Prunus serotina*), cedar elm (*Ulmus crassifolia*), and Texas persimmon (*Diospyros texana*); all three resprout after fire (Andruk and Fowler 2014). The pre-settlement fire frequency in these woodlands is unknown. Historic documents suggest that frequent fires maintained much of central Texas as savanna (Bray 1904). These fires were likely frequent, low-intensity surface fires that occurred primarily in dry years (Murray and others 2013). The estimated fire return interval for post-oak (*Q. stellata*) woodlands in northeast Texas prior to 1820 (i.e., prior to settlement) is 6.7 years (Stambaugh and others 2011); central Texas woodlands probably had a similar fire frequency.

Objectives

At the time of this study, the use of prescribed fire in golden-cheeked warbler habitat was usually not allowed (but see Andruk and Fowler 2014). We therefore studied the impacts of wildfires at four sites that had burned accidentally. Study sites differed in fire frequency, fire severity, time since fire, and prior management history. We measured the effects of fire on the number, size, and growth of Ashe juniper and hardwood individuals. We were particularly interested in whether Texas red oak recruitment had been restored in burned areas, and whether fire reduced the canopy cover below 70 percent, making burned areas potentially unsuitable for golden-cheeked warblers.

Methods

Experimental Design and Surveys

We surveyed vegetation response to wildfire at four woodland sites in Balcones Canyonlands National Wildlife Refuge (table 1). Woodlands of this type are common on hillsides on the limestone-derived soils on the eastern Edwards Plateau (Van Auken 2008). We call them woodlands because their canopy height rarely exceeds 10 m. Each site contained an area that was burned and a paired unburned control area. Each site burned when a nearby prescribed fire in a savanna escaped its intended boundary. See table 1 for a description of the study sites, which we name 'two-fires,' 'one-fire-old,' 'one-fire-recent,' and 'one-fire-thin' to reflect their fire history. The one-fire-thin site had numerous large-diameter Ashe juniper stumps. We interpreted this to be evidence of past cutting and removal of large Ashe juniper trees. There were no stumps in the other sites. Control areas had slopes and aspects similar to their paired burned areas. Within each of these four sites, we randomly located two 11-m radius plots in the burned area, and two additional 11-m radius plots in the adjacent unburned control area, for a total of 8 burned and 8 unburned plots. This

Table 1. The four sites surveyed in this study. Each was burned when a nearby-prescribed fire escaped its intended boundary at Balcones Canyonlands National Wildlife Refuge.

Site	Date of fire(s)	Fire season
two-fires	Feb. 1998, Jan. 2009	dormant season
one-fire-old	Mar. 2006	growing season
one-fire-recent	Jan. 2009	dormant season
one-fire-thin	Mar. 2009	growing season

design includes spatial variation at two scales: site level (site: 3 df; site X burn: 3 df) and plot level (plot, which was nested within burn treatment X site: 8 df).

Vegetation surveys were completed using FIREMON (Fire Effects Monitoring and Inventory Protocol), a standard methodology used in fire-effects research (Lutes and others 2006). All of the sites were surveyed in June 2009, except for the one-fire-recent site (table 1), which was sampled in June 2010. Seedlings (woody plants < 1.5-m tall that were not part of a larger individual) were surveyed in a 3.57 m radius (40 m²) circle in the center of each plot, while saplings and mature trees were surveyed in the entire 11 m radius plot. We recorded species and height class (0-0.2 m, 0.2-0.4 m, 0.4-0.8 m, 0.8-1.2 m, or 1.2-1.5 m) of each seedling. Species, number of stems in each DRC (diameter at root crown) class, and height to the nearest 0.1 m were recorded for each sapling (woody individual > 1.5 m tall, with a DRC < 10.16 cm) and mature tree (woody plant with a DRC ≥ 10.16 cm). We also measured DBH (diameter at breast height) of each mature tree. A sprout was defined as stem with a DRC < 5.08 cm that arose from the base of a mature tree (woody plant with a DRC ≥ 10.16 cm). The number of sprouts in each DRC class and the height of the tallest sprout in each DRC class were recorded for each mature tree.

Canopy photographs were taken at 9 locations per plot in 2 sites (two-fires, one-fire-recent) with a fisheye lens (Sigma 8mm f/3.5 EX DG circular fisheye lens). The photographs were converted into binary images (canopy vs. sky) using the program Gap Light Analyzer. Canopy openness was calculated from binary images and compared between sites and between burned and unburned areas.

Statistical Analyses

We used a generalized linear model with a Poisson distribution and log link to analyze the effects of fire, site, and their interaction on the number of Ashe juniper seedlings and saplings, Texas red oak seedlings, pooled non-oak hardwood seedlings, pooled hardwood saplings, and pooled hardwood sprouts. Pooled non-oak hardwoods include all hardwood species except for Texas red oak. Pooled hardwood saplings and sprouts contain all hardwood species, including Texas red oak. The generalized chi-square / degrees of freedom was used to assess fit to the Poisson distribution.

We used analysis of variance (ANOVA) to analyze the effects of fire, site, and their interaction on hardwood sapling

and sprout height. We calculated a weighted average sprout height for each mature tree, by weighting the height of the tallest sprout in each DRC class by the number of sprout stems in its DRC class. Ashe juniper sapling height could not be analyzed because there were too few sapling individuals in the burned plots.

Some hardwood individuals had their main stem (DRC ≥ 10.16-cm) killed by fire; many of these individuals were producing basal sprouts after the fire (i.e., they were top-killed). We used a generalized linear model with a binomial distribution and logit link (logistic regression) to analyze the effect of fire, site, species (Ashe juniper, Texas red oak, pooled non-oak hardwoods), and the interaction of fire and species (fire X species) on the proportion of mature trees whose main stem was alive. A separate analysis was done to examine the effect of fire, the number of living sprouts per tree, and their interaction on the proportion of living hardwood trees whose main stem was alive. This was done to determine whether hardwood trees whose main stem was killed by fire were more likely to have a greater number of sprouts. In both of these analyses, a random factor 'plot' was included to account for the nesting of plot within site X fire. Plot was included because the dependent variable was the number of sprouts per tree; hence there were multiple observations per plot. Plot was not included in other analyses because there was one observation per plot (e.g., number of seedlings). In analyses that included plot, the denominator degrees of freedom for the F-tests was 8, that is, the degrees of freedom associated with plot.

We used an ANOVA to analyze the effect of fire, site and their interaction on canopy openness. Percent canopy openness, i.e., 100 minus percent canopy cover, was log-transformed to meet normality requirements.

In all of the above analyses, if site was significant, pairwise comparisons between sites were made. If fire X site was significant, we compared burned and unburned plots within each site with the Tukey-Kramer HSD test.

Results

There was no significant main effect of fire on Texas red oak seedling abundance: the number of red oak seedlings did not differ significantly between fire treatments. Sites differed significantly in red oak seedling abundance ($P = 0.0037$). There was also a significant fire X site interaction effect on red oak seedling abundance ($P = 0.027$, figure 1). There were significantly fewer Texas red oak seedlings in the burned than in the unburned area of the one-fire-recent site ($P = 0.0342$) and the one-fire-thin site ($P = 0.0043$). There were significantly more Texas red oak seedlings in the burned than in the unburned area of the one-fire-old site ($P = 0.0056$). There was no significant effect of fire, site, or their interaction on Ashe juniper seedling abundance. Although sites differed in non-oak hardwood seedling abundance ($P = 0.0218$), the two treatments (burned v unburned) did not differ significantly in their effects on non-oak hardwood seedling abundance; the fire X site term was also not significant in the analysis of non-oak hardwood seedling abundance.

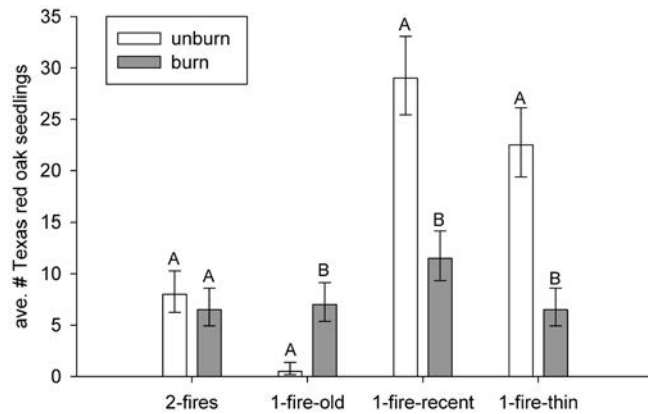


Figure 1—There was a significant fire x site interaction effect on Texas red oak seedling abundance ($P = 0.027$). Seedlings are individual woody plants < 1.5 m tall. Graph shows average number of seedlings per 11-m radius plot. Letters indicate significant differences between unburned and burned areas within each site. Bars represent ± 1 SE.

There were significantly more pooled hardwood saplings in burned plots than unburned plots ($P = 0.0005$, figure 2a). Sites differed in pooled hardwood sapling number (averaging across burned and unburned plots, $P = 0.0034$): the two-fires site had significantly more hardwood saplings than the one-fire-thin site ($P = 0.029$), as did the one-fire-recent site ($P = 0.042$), and the one-fire-old site ($P = 0.027$). There was no significant fire X site interaction. There were significantly fewer Ashe juniper saplings in burned plots than in

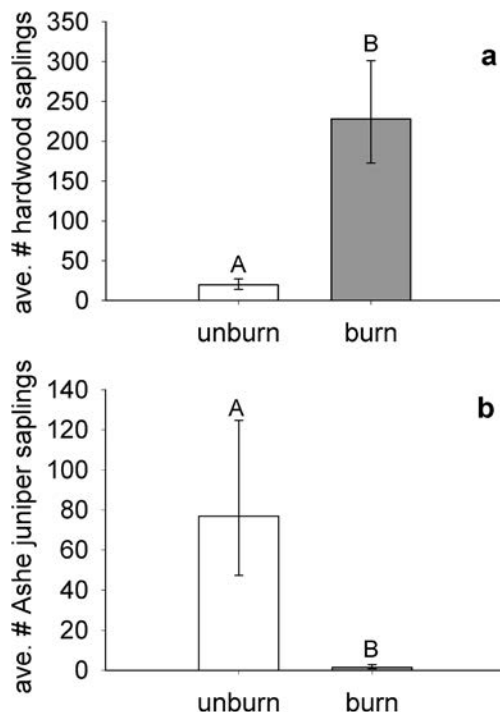


Figure 2—Effects of fire and site on saplings (individuals > 1.5 m tall with a DRC < 10.16 cm). (2a) There were significantly more pooled hardwood saplings in burned than unburned areas ($P = 0.0005$); (2b) there were significantly fewer Ashe juniper saplings in burned than unburned areas ($P = 0.0005$); letters indicate significant differences between groups. Bars represent ± 1 SE.

unburned plots ($P = 0.0005$, figure 2b); there was no significant effect of site or fire X site interaction.

Hardwood saplings growing in the unburned plots were 1.5 times taller on average than those growing in the burned plots ($P = 0.001$); this indicates recent growth of smaller individuals into the sapling size class. Averaging across burned and unburned plots, the one-fire-recent hardwood saplings were significantly shorter than those in other sites ($P = 0.007$). There was no significant fire X site interaction.

A large number of hardwood saplings and mature trees were observed producing sprouts in the burned areas. Woody species that had sprouts in the burned areas included *Ageratina havanensis* (Havana snakeroot), *Baccharis neglecta* (Rooseveltweed), *Cercis canadensis* var. *texensis* (Texas redbud), *Diospyros texana* (Texas persimmon), *Forestiera pubescens* (stretchberry), *Fraxinus texensis* (Texas ash), *Garrya ovata* ssp. *lindheimeri* (Lindheimer's silktassel), *Ilex decidua* (possumhaw), *Ilex vomitoria* (yau-pon), *Juglans microcarpa* (black walnut), *Melia azedarach* (chinaberry, an invasive species), *Mimosa texana* (Texas mimosa), *Ptelea trifoliata* (common hoptree), *Prunus serotina* (black cherry), *Q. buckleyi*, *Quercus sinuata* (shin oak), *Rhus aromatica* (fragrant sumac), *Rhus lanceolata* (flame-leaf sumac), *Sideroxylon lanuginosum* (gum bully), and *Ulmus crassifolia* (cedar elm).

There was no overall effect of fire on the average number of sprouts per tree, but there was a significant fire X site interaction ($P = 0.0002$, figure 3). Mature trees in the burned areas of the two-fires and one-fire-old sites had significantly more sprouts than mature trees in the unburned areas of those sites ($P = 0.0044$ and $P = 0.0035$, respectively, figure 3). There was no significant difference in sprout number between burned and unburned areas in the one-fire-recent site. There was no significant effect of fire, site or their interaction in the analysis of average sprout height. However, the average height of unburned sprouts was 2.44 ± 0.43 m, taller than that of burned sprouts, 1.81 ± 0.25 m, suggesting recent sprout growth in the burned areas.

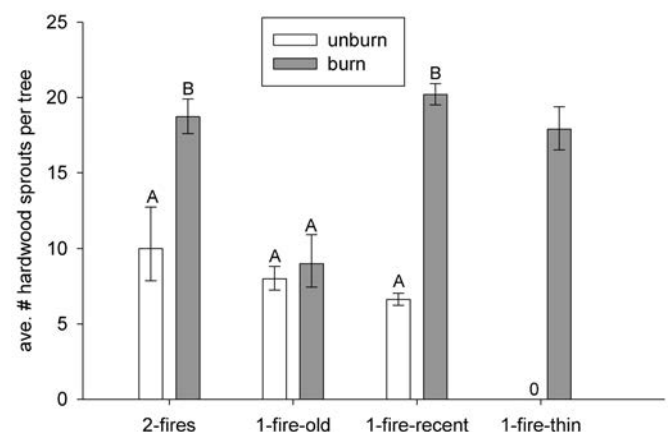


Figure 3—There was a significant fire x site interaction effect on average sprout number per tree ($P = 0.0002$). Letters indicate significant differences between burned and unburned areas within each site. None of the unburned trees in the one-fire-thin site had sprouts; this is indicated by the 0. Bars represent ± 1 SE.

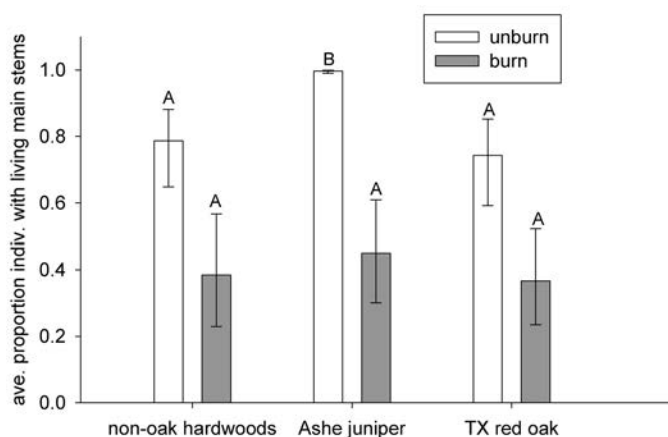


Figure 4—There was a significant fire x site interaction on the proportion of mature hardwood trees with living main stems ($P = 0.0203$). Non-oak hardwoods refer to all hardwood individuals other than Texas red oak (*Quercus buckleyi*). Letters indicate significant differences between burned and unburned areas within each species group. Bars represent ± 1 SE.

Significantly more mature trees ($\text{DRC} \geq 10.16$ cm) had living main stems in unburned areas than in burned areas (94.06 percent as compared to 39.99 percent, $P = 0.0035$). On average, 78.13 percent of the mature hardwood trees with dead main stems had basal sprouts, so these individuals had not completely died, but were instead top-killed. There was no significant relationship between the number of sprouts a mature hardwood tree had and the probability that its main stem was alive.

There was a significant fire X species interaction in the analysis of proportion of mature trees with living main stems ($P = 0.0203$, figure 4). The proportion of living Ashe juniper trees was significantly lower in burned than in unburned areas (figure 4, $P = 0.0051$). Since Ashe juniper does not resprout, trees with dead main stems were completely dead.

The average canopy openness in burned areas was 29.38 percent, significantly more than the 14.94 percent in unburned areas ($P < 0.001$). There was no significant effect of site or fire X site, although plots in the burned two-fires site were more open than those in the one-fire-recent site.

Discussion

Burned areas had fewer Ashe juniper seedlings, saplings, and mature trees. They had more hardwood saplings and sprouts, including Texas red oak. Oaks were also found to sprout vigorously after fire in other studies in central Texas (Andruk and Fowler 2014; Doyle 2012; Reemts and Hansen 2013; 2008; Yao and others 2012), the nearby Cross Timbers region (Burton and others 2010; Clark and Hallgren 2003), and the eastern US (Brose and others 2013). The high sprouting rate of the diverse central Texas hardwood community suggests that these species are adapted to periodic fire. Fires had much less success in promoting oak seedling establishment in this study. Effects on oak seedling establishment in other studies, if present, have also been mixed (Arthur and

others 2012; Brose and others 2013; Green and others 2010). Fire effects on oak seedlings may be mixed because reproduction from seed is extremely rare (mast events), or because very intense and severe fires are required to sufficiently increase light availability and trigger seedling production. We discuss these potential reasons and their implications for the endangered golden-cheeked warbler below.

Reproduction From Seed vs. Resprouting In Oaks

Prescribed fire can increase oak seedling abundance by increasing flowering, acorn production, germination, and establishment, and can also stimulate the growth of existing saplings (advanced regeneration) (Arthur and others 2012). However, fire can limit oak seedling abundance by killing acorns, especially those at the soil surface (Greenberg and others 2012). These opposing mechanisms make it difficult to determine the overall effect of fire on oak seedling abundance. However, it is clear that resprouting is an important functional trait that allows trees, especially oaks, to persist after fire (Clarke and others 2013). In this study, a large number of common central Texas shrubs and trees were observed producing sprouts in the burned areas of which Texas red oak was the most common. Another study found that black-jack oak (*Quercus marilandica*) and post oak (*Q. stellata*) reproduced primarily by resprouting in a Cross Timbers woodland (Clark and Hallgren 2003), indicating that resprouting is an important mechanism of oak persistence in nearby woodlands. In general, resprouting is the dominant method of oak reproduction and persistence (Brose and others 2013; Lawes and Clarke 2011; McEwan and others 2010).

Due to the predominance of sprouting, oak reproduction from seed is relatively rare. In this study, there were significantly fewer Texas red oak seedlings in the burned areas than in the unburned areas in two of the four sites, presumably because the fire killed them. However, there were significantly more Texas red oak seedlings in the burned area than in the unburned area of the one-fire-old site, which was surveyed 4 years after the fire. It is possible that Texas red oak seedling recovery takes at least 4 years, or that it exhibits mast seed production. In oaks, mast seeding is characterized by large variations in seed production between years and between individuals within a population (Kelly 1994). Masting is common in North American oak forests; for example, large individual and year-to-year variation in acorn production was observed in oak communities in Massachusetts (Healy and others 1999) and southern Appalachia (Greenberg 2000). If Texas red oak exhibits a masting pattern similar to other red oaks, this may explain why we did not observe new oak seedlings: it is possible that we did not survey the plots following a mast year, or that the plots did not contain the “superior producers” that often produce the majority of a population’s acorn crop.

Are Repeated Fires Necessary?

Oaks have high light requirements and consequently may only produce seedlings after a sufficient increase in light availability from a more severe fire. Indeed, multiple

fires in combination with thinning were found to increase oak seedling abundance in southern Ohio, probably due to large increases in light availability (Hutchinson and others 2012). In this study, two fires were not any more successful than one fire in increasing hardwood seedling abundance or sprouting rate. However, a large increase in sprouts was observed after two high-intensity wildfires in another central Texas woodland (Reemts and Hansen 2013). This seems to be true of other oak-dominated communities in the region as well. Repeated prescribed fires increased the cover of shin oak (*Quercus havardii*) in Oklahoma more than single prescribed fires (Harrel and others 2001). Oaks in the Ozark Mountains also vigorously resprouted after repeated fires (Fan and others 2012). These authors argue that repeated fires favor oak in the long-term due to its conservative reproductive strategy. Repeated fires are likely successful because oaks tend to allocate more carbon to root development than shoot development, making them better resprouters than their competitors (Arthur and others 2012; Brose and others 2013). These studies suggest that thinning or multiple fires may be necessary to restore oak regeneration in central Texas woodlands as well. If only fires of greater intensity and severity can promote oak regeneration, then the short-term goal of maintaining habitat for the golden-cheeked warbler (or any other target species) will likely be in conflict with the longer-term goal of promoting oak regeneration.

Management Solutions for Endangered Species

One possible solution is to identify sites that do not presently have the target species, open up the canopy to increase light availability sufficiently, and use them in the future as replacement habitat for the target species when the presently occupied sites are burned. This strategy assumes that sufficiently opening the canopy will successfully restore oak regeneration and the desired structure and composition of the plant community. Even if this is possible, this is a long-term, high-risk solution because we do not know all of the factors that make habitat suitable. It also depends on large areas of protected land not currently occupied by the target species and not already dedicated to another use. In central Texas, this would be sites (a) with enough Texas red oaks to have a good seed source; (b) not currently occupied by golden-cheeked warblers, so that intense and severe fires or thinning could be used; (c) not currently dedicated as habitat for other species of concern; and (d) not used for incompatible recreational or economic uses.

As these conditions are restrictive, another, potentially more realistic scenario, is to relax the assignment of the target species to specific sites; i.e., to stop permanently designating endangered species habitats to specific sites and instead simply ensure that enough total habitat is maintained for each target species (taking into account dispersal limitations, if appropriate). In central Texas, this might involve using the habitat for the endangered black-capped vireo (*Vireo atricapilla*) as a successional pathway to golden-cheeked warbler habitat. The black-capped vireo breeds in fire-maintained shrubland composed of scrubby deciduous trees generally

less than 2 m tall; common plant species include shin oak and flame-leaf sumac (US Fish and Wildlife Service 2007). It seems possible that pre-settlement oak savannas, shrub savannas, shrublands (black-capped vireo habitat), and oak-woodlands (golden-cheeked warbler habitat) existed in a shifting spatial mosaic driven by fire. Therefore, if only intense fires (or thinning) can promote oak regeneration in former woodlands, these areas may have to go through a 'black-capped vireo stage' during the process of restoring mature oak-dominated woodland. If so, management for a shifting mosaic would have the added benefits of recreating potential pre-settlement dynamics.

Land management for bird conservation in oak-savanna and oak-woodland has also been conceptualized as a shifting mosaic in the northern Midwestern US (Mabry and others 2010); they found that site-level restorations for breeding birds were influenced by the composition of the surrounding landscape. Landscape configuration should also be taken into consideration in central Texas. Although shrubland is probably the highest quality habitat for the black-capped vireo, they can also breed successfully in oak-juniper woodlands (Pope and others 2013). The golden-cheeked warbler is also somewhat flexible in habitat preference. Marshall and others (2013) studied golden-cheeked warbler breeding success in Texas red oak and post oak. They found that the proportion of territories that successfully fledged young was higher within Texas red oak habitat, but there were no significant differences between the habitats in nestling survival. Additionally, golden-cheeked warblers exhibit a wide range of preferences for different tree species. They have been observed in habitats that range from 10 to 90 percent Ashe juniper and 10 to 85 percent hardwood trees. Habitats with higher hardwood abundance (75-90 percent) have been found to be positively related to warbler occurrence (Groce and others 2010). However, warblers have also been found to prefer areas with higher Ashe juniper abundance (DeBoer and Diamond 2006). We therefore suggest that the relaxation of the assignment of target species to specific sites may be good policy because (a) evidence suggests that the pre-settlement landscape may have existed in a shifting mosaic of savanna, shrubland, and woodland, and (b) both the black-capped vireo and the golden-cheeked warbler use resources in shrubland and woodland, which could make rigid site assignments less necessary.

Effects of Fire Seasonality

Mature trees growing in sites that burned during the winter dormant season (two-fires, one-fire-recent) had significantly more sprouts than mature trees growing in their respective controls. Trees growing in sites that were burned in the early spring growing season (one-fire-old, one-fire-thin) did not have significantly more sprouts than their controls. These results suggest that dormant season fires trigger more vigorous resprouting than growing season fires in central Texas hardwoods. Plant carbohydrate reserves are generally lowest early in the growing-season after leaf-out (Harrington 1989), possibly explaining why plants that were

burned at this time sprouted less than those burned in the dormant-season. Most prescribed fires in central Texas, and elsewhere, occur in the winter dormant-season when it is typically safer to burn. Growing-season fires are generally of higher intensity than dormant-season fires (Barnes and Van Lear 1998). A meta-analysis found that oaks sprouted at a higher rate than mesophytic species after growing-season fires, but there was no difference in sprout production between these two groups after dormant-season fires (Brose and others 2013). Therefore, contrary to our results, in many regions growing-season fires are more effective than dormant-season fires, especially if the goal is mesophytic species control. Ashe juniper, a more xeric species than Texas red oak, is most flammable during the winter and early spring (Owens and others 1998), suggesting that it will be equally susceptible to winter dormant-season fire and early growing-season fires. Therefore, due to the superior hardwood sprouting rates observed after dormant-season fires in this study, we recommend their use in central Texas woodland restoration projects.

Conclusions

This study is the first step toward understanding how fire structures oak-juniper woodlands. We found that fire generally promotes hardwood sprouting, but effects on seedlings are unclear. More intense and severe fires may be needed to sufficiently increase canopy openness and oak seedling regeneration. If so, the short-term goal of protecting golden-cheeked warbler habitat is in conflict with the long-term goal of maintaining the oak component of that habitat. We suggest that flexible land management is needed to address this conflict. It is likely that the pre-settlement vegetation in this region was a complex spatial mosaic of savanna, earlier successional shrubland, and later successional woodland. This shifting mosaic hypothesis suggests that plant successional trajectories in black-capped vireo habitat may lead to suitable habitat for the golden-cheeked warbler under fire suppression. Conversely, burning in golden-cheeked warbler woodland may create black-capped vireo habitat. This study explored the conflicts between short and long-term management goals. We expect these conflicts to increase as stressors such as fire suppression, invasive species, and climate change continue to interact and drive novel plant and animal community dynamics.

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