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The joint effects of fire and herbivory on hardwood regeneration in central Texas woodlands

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ABSTRACT

Oaks (*Quercus* spp.) are not regenerating in forests and woodlands in central Texas and elsewhere. This has been attributed to fire suppression. However, overabundant white-tailed deer (*Odocoileus virginianus*) can also limit oak regeneration. We hypothesized that both fire re-introduction and protection from deer would increase the number and growth of hardwood seedlings, saplings, and sprouts in a central Texas woodland co-dominated by Texas red oak (*Quercus buckleyi*) and Ashe juniper (*Juniperus ashei*). We measured the separate and joint effects of prescribed fire and deer herbivory on the number, size, and growth of Ashe juniper and hardwoods, tree mortality, and canopy cover. We collected data one year before and three years after deer-fence construction and a prescribed fire. Fire stimulated re-sprouting in oak and other hardwoods, but had no detectable effect on their seedlings or saplings, even three years later. Deer exclusion increased the number of seedlings transitioning to the sapling size class. Both fire and deer exclusion together were required to increase average sprout height above the browseline. The apparent adaptations of native hardwoods to fire are the strongest evidence we have for an important role for fire pre-settlement. Our results also indicate that fire suppression in central Texas and other parts of the south-central US is causing a shift, not to more mesic-adapted species as observed in the eastern US, but to juniper (*Juniperus* spp.), which is at least as xeric-adapted as oak. Therefore, thinking about the "oak regeneration problem" needs to be expanded beyond "mesophication" to incorporate the shift to juniper in drier regions. It is likely that deer control is necessary to allow fire to have positive effects on the regeneration of oaks and other hardwoods in this region and wherever deer are over-abundant. Moreover, the negative effects of deer herbivory on oak growth may partially account for reported failures of single fires alone to promote hardwood regeneration elsewhere.

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1. Introduction

The importance of surface fire in maintaining the composition and dynamics of forests and woodlands is not yet well understood, but is an active topic of research (e.g., Ryan et al., 2013; Stambaugh et al., 2014). Currently, fires are suppressed in many forests and woodlands. One of the hypothesized effects of this fire suppression is a shift in species composition, specifically the current failure of oak (*Quercus* spp.) regeneration in many forests and woodlands in the United States (Brose et al., 2013; Nowacki and Abrams, 2008). Oaks are failing to regenerate in forests and woodlands of the eastern United States (US) (Arthur et al., 2012), the Ozark Mountains in the central US (Dey and Hartman, 2005), parts of the western US (Tyler et al., 2006), and parts of Texas (Doyle, 2012; Russell and Fowler, 2002).

In woodlands on the eastern Edwards Plateau of central Texas, Texas red oak (*Quercus buckleyi*) and Plateau live oak (*Q. fusiformis*) are not regenerating, while Ashe juniper (*Juniperus ashei*) is increasing in abundance (Diamond and True, 2008; Murray et al., 2013). Another juniper species, eastern red cedar (*Juniperus virginiana*), is also replacing oaks in the Ozark Mountains and Cross Timbers regions of the US (Burton et al., 2010; DeSantis et al., 2011; Hanberry et al., 2014). We propose the term 'juniperization' to describe the phenomenon of increasing juniper density and cover, leading to oak regeneration failure. Juniper species are also increasing in grasslands and savannas in the central US (Briggs et al., 2005), and in woodlands, shrublands and savannas in the western US (Romme et al., 2009), but we are concerned here only

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with increases in juniper combined with oak regeneration failure in woodlands.

If fire suppression is responsible for the failure of oak regeneration, re-introducing fire should promote oak regeneration. We tested whether a prescribed surface fire in a Texas red oak–Ashe juniper-dominated woodland would increase the regeneration of Texas red oak and other hardwood species and decrease Ashe juniper abundance. Because re-introducing surface fire in woodlands where fire suppression has substantially reduced fine fuels is difficult, and is potentially dangerous due to the risk of catastrophic crown fire (Agee and Skinner, 2005), thinning of Ashe juniper saplings was done before the prescribed burn.

The process of juniperization is related to, but different from, the better-studied process of mesophication in the eastern United States (Abrams, 1992). Mesophication is also caused by fire suppression, but it involves the replacement of relatively shade-intolerant, fire-tolerant oaks by shade-tolerant, fire-sensitive maples (*Acer* spp.) and similar species (Nowacki and Abrams, 2008; Rentch et al., 2003). Although for different reasons, both maple leaves and juniper needles are poor fuels, and decrease the probability of surface fires (Kreye et al., 2013; Shang et al., 2004; Twidwell et al., 2009).

However, unlike mesophication, juniperization increases the risk of catastrophic crown fire (Reemts and Hansen, 2013) and greatly reduces herbaceous diversity (Yager and Smeins, 1999). While maples are more mesic-adapted than eastern oak species, junipers are in general more xeric-adapted than the oaks they replace. For example, the distribution of Ashe juniper extends further to the west than that of Texas red oak (Turner et al., 2003). Many juniper species have ecological roles related to their tolerance of relatively xeric habitats: they colonize open sites such as savannas and pastures, are drought-tolerant, and can grow on rocky and shallow soil (Van Auken and McKinley, 2008).

Previous studies of the effects of prescribed surface fire on oaks have had mixed results (Barnes and Van Lear, 1998; Brose et al., 2007; Dey and Hartman, 2005; Lanham et al., 2002). A recent review (McEwan et al., 2010) and meta-analysis (Brose et al., 2013) found that single dormant-season fires are often insufficient to increase oak regeneration. Multiple fires combined with overstory thinning are generally more successful than single fires (Hutchinson et al., 2012), but results vary widely. Oaks readily resprout following fire (Clark and Hallgren, 2003) but it is unclear if prescribed fire increases rates of germination, seedling establishment, or the growth of advanced regeneration. Where community composition and structure have been altered beyond historical conditions, a transition from one stable state to another may have occurred (Briske et al., 2006). If so, the simple reintroduction of fire alone may not be enough to restore oak regeneration and other factors may need to be taken into account (Arthur et al., 2012; McEwan et al., 2010).

One of the other factors that may limit oak regeneration is ungulate herbivory. The density of white-tailed deer is extremely high in central Texas (Mostyn, 2001), as it is in many parts of the eastern US. Herbivory by white-tailed deer has been demonstrated to limit oak regeneration in central Texas (Russell and Fowler, 2004, 2002) and other plant species elsewhere (Côté et al., 2004; Rooney and Waller, 2003). Therefore we also studied the effects of deer browsing. We expected protection from deer browsing to have a positive effect on oaks and other hardwood species, all of which are eaten by deer, and an indirect negative effect on Ashe juniper, which they rarely eat (Armstrong and Young, 2002). Deer herbivory and a lack of fire are not mutually exclusive explanations for the failure of oak regeneration; it is likely that both are involved, acting either additively or synergistically. Few previous studies have simultaneously examined the effects of both fire and deer herbivory on oak recruitment despite strong evidence that both are important drivers of plant community trajectories (but see (Collins and Carson, 2002). We therefore designed this experiment to detect interactions between the effects of fire and deer, as well as their separate effects.

2. Materials and Methods

2.1. Study system

The woodlands of the eastern Edwards Plateau in central Texas are drier than any of the ecosystems in the eastern US in which oak regeneration has been studied, including the Ozarks: average annual precipitation at our study site was 91.97-cm (NCDC). We refer to them as woodlands rather than as forests to reflect their low stature (rarely > 10 m) and relatively open canopy. These woodlands are common on hillsides throughout the eastern Edwards Plateau. They are co-dominated by Texas red oak and Ashe juniper; other hardwood species such as black cherry (*Prunus serotina*) and possumhaw (*Ilex decidua*) are minor components. 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 et al., 2013). The estimated fire return interval for post-oak (*Quercus stellata*) woodlands in northeast Texas prior to 1820 (i.e., prior to settlement), is 6.7 years (Stambaugh et al., 2011); central Texas woodlands probably had a similar fire frequency.

We conducted the study at Balcones Canyonlands National Wildlife Refuge (BCNWR), located on the eastern Edwards Plateau of central Texas. A two-way factorial experiment ($N = 5$, 20 total 11-m radius, 0.038 ha plots) with burning and deer herbivory as treatments was set up in May 2009 (Fig. 1a). The study site is long and narrow because Texas red oak–Ashe juniper woodland typically occurs in narrow horizontal bands along slopes, as it did in our study site. The site had no recorded history of management or fire since 1970. Deer densities at BCNWR averaged 1 deer/11.33 ha from 2005 through 2009 (spotlight deer surveys, C. Schwope, pers. comm), lower than the region-wide average of 1 deer/1.62 ha (Lutes et al., 2006; Mostyn, 2001).

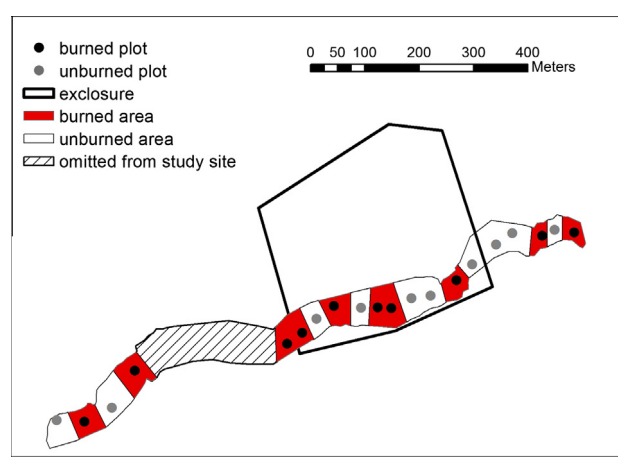

Fig. 1a. Map of the study site. Deer exclosure shown as black square. (Note: exclosure extends beyond the study area because the results presented here are part of a larger study). Burned areas (red) contain burned plots (black points). If two burned plots were adjacent, the entire area between them was burned. Unburned areas (white) contain unburned plots (gray). The hatched area was omitted from the study site because there were no overstory hardwood trees present in that region (only juniper). There were $N = 5$ plots per burning fencing combination (20 total plots). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.2. Experimental design

Initial data were collected in summer 2009 from all 20 plots before any treatments were imposed, using FIREMON (Fire Effects Monitoring and Inventory Protocol), a standard methodology used in fire-effects research (Lutes et al., 2006). Seedlings (woody plants <1.5-m tall that were not part of a larger individual) were sampled in a 3.57-m radius (0.004 ha) circle in the center of each plot, while saplings and mature trees were sampled 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. We recorded species, number of stems in each DRC (diameter at root crown) class and height to the nearest 0.1-m of each sapling (woody individuals >1.5-m tall, with a DRC < 10.16-cm) and mature tree (woody plants with a DRC ⩾ 10.16-cm). In summer 2009 each mature tree was tagged with a unique number. The diameter at breast height (DBH) was measured at the tag in 2009 and subsequent years. A sprout was defined as stem with a DRC < 5.08-cm that arose from the base of a mature tree; sprouts were present pre-fire and post-fire. 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. We calculated average sprout height per tree as the average of the tallest sprout in each of the two DRC classes of sprouts.

In February 2010 a deer exclosure was constructed in the middle of the site, containing 10 of the 20 plots (Fig. 1a). Five plots inside and five plots outside the exclosure were randomly assigned to be burned. All Ashe juniper saplings were cut in the plots that were to be burned (Fig. 1b). The resulting woody debris was spread out within those plots; an effort was made to avoid piling debris around mature trees. The resulting arrangement of slash would best be represented for fire behavior modeling as SB1, Low Load Activity Fuel, using Standard Fire Behavior Fuel Models (Scott and Burgan, 2005). A second vegetation survey of all plots was done in summer 2010 after cutting and fence construction, using the methods described above. On December 15, 2010 the prescribed fire was implemented by burning "contour strips" using hand ignition with drip torches to minimize fire intensity (Table 1, Fig. 1b). Fire effects varied throughout the study area, but would best be characterized by moderate fire intensity: the sub-canopy was scorched but the upper canopy remained intact. Some of the study area experienced moderate/high fire intensities: the upper canopy was also scorched. Post-fire vegetation was sampled again in summer 2011 and 2012. In 2012 we quantified browsing rate on sprouts by counting the number of deer-browsed and unbrowsed stems. A stem on a given sprout or sapling was considered browsed if at least one branch of current year growth was browsed by deer. In summer 2013 all seedlings and hardwood saplings were re-sampled. Browse was quantified on saplings but not sprouts in 2013.

Fig. 1b. Picture of the ignition pattern. The prescribed fire was implemented by burning "contour strips" using hand ignition with drip torches. Length between contour strips was modified, depending on surface fuel load and slope, to maintain consistent fire behavior. Note the cut Ashe juniper saplings as fuel.

Hemispherical canopy photographs were taken in each of the 20 plots at 9 locations per plot with a hemispherical lens (Sigma 8 mm f/3.5 EX DG circular fish eye lens) in 2011. The photographs were taken after leveling the camera on a tripod less than 0.5 m above the ground. The photographs were converted into binary images (canopy cover/sky) using Gap Light Analyzer (GLA) imaging software (Frazer et al., 1999). Canopy cover, from 0% (no canopy cover) to 100% (total canopy cover), was calculated from the binary images using GLA, converted to canopy openness (=100 − canopy cover), and then averaged for each plot. We used hemispherical canopy photography to better understand how fire affects canopy cover and hence, light availability, an important factor in oak regeneration.

2.3. Statistical analysis

Each response variable was analyzed with one or more generalized linear models (Table 2). SAS 9.2 PROC GLIMMIX was used in all instances. Distributions differed, but in all cases we used the standard link function for that distribution: a log link function with the Poisson and negative binomial distributions and a logit link function with the binomial distribution, and an identity link function with the normal distribution. If the response variable was a count (e.g., number of seedlings), we initially assumed a Poisson distribution. If we then found that the count data were over-dispersed (Pearson χ^2/df much greater than 1) we used a negative binomial distribution. If the response variable was survival (0 = dead, 1 = alive) or browsing (0 = unbrowsed, 1 = browsed), we used a binomial distribution. If the response variable was height or canopy openness we used a normal distribution. Due to some problems with convergence, all of our models used treatment (3 df) to represent the four treatment combinations: control, burn-only, fence-only, burn-fence. The separate effects of burning, of fencing, and of their interaction were tested with the appropriate contrasts (1 df each). Random effects were included, nested as appropriate. Year was considered a repeated effect with the subject of plot within treatment. The covariance structure that minimized the Pearson χ^2/df was selected individually for each model. The Kenward Roger degrees of freedom approximation was used in all models. In any analysis with a significant treatment *x* year interaction effect, comparisons were made among years within treatments and were adjusted with Tukey–Kramer for multiple comparisons.

We examined the effects of fire and deer herbivory on numbers of seedlings, saplings, and sprouts (Table 2). There was a marginally significant treatment *x* year interaction effect ($P = 0.0505$) on oak seedling numbers, apparently due to the drought that occurred in year 3 (year 2011, immediately post-fire, 49% decrease in total rainfall from the long-term average, Fig. 2). Therefore, we did two additional analyses of oak seedling numbers to see whether they responded to and recovered from the drought similarly (Table 2). The number of oak saplings could not be analyzed separately because there were too many plots with no oak saplings; we therefore pooled all hardwood saplings and dropped the 3 plots that had no hardwood saplings over the entire 5 years. There were too few non-oak hardwood trees to analyze separately. Instead, two chi-square tests were used to test whether the numbers of non-oak hardwood sprouts were equal in burned or fenced areas pre-treatment and post-treatment (2 × 2 contingency table, burning or fencing *x* time).

Table 1
Fuel and weather conditions on the date of the prescribed burn, December 15, 2010. Rh, relative humidity. ERC, energy release component. Ignition began at 13:00 and finished at 17:40. Plots were burned from east to west (Fig. 1). 100-h Fuel moisture was 13.5%; 1000-h fuel moisture was 14.7%. The Keetch–Byram Drought Index, KDBI was 487 (61%). The fire was burned upslope using contour strips. If two plots next to each other were supposed to be burned, the area between them was also burned (Fig. 1). There was a 'buffer' around each group of treated plots such that the area immediately surrounding burned plots was also burned while the area surrounding unburned plots was also unburned.

Time	Temp (°C)	Rh (%)	Midflame wind speed	1-h Fuel (%)	10-h Fuel (%)	ERC
13:00	22.78	45	3	8.3	10.1	15
14:00	23.89	41	4	7.5	8.8	19
15:00	24.44	39	3	7.9	7.8	23
16:00	23.89	39	3	9.3	7.3	27
17:00	22.78	42	2	10.3	7.2	28

Table 2
Generalized linear models used in the analysis. tr, treatment combination (control, burn-only, fence-only, burn-fence); plot(tr), plot nested within treatment; tree(plot), tree nested within plot. Cov struc, residual covariance matrix structure: CS, compound symmetry; VC, variance components; AR(1), autoregressive.

Dependent variable	Species	Distribution	Independent	Random effects	Repeated effect	Cov struc
Seedling #	Oak	Negative binomial	tr, year, tr × year	plot(tr)	Year	CS
Seedling # (years 2 & 3)	Oak	Negative binomial	tr, year, tr × year, year 1 covariate	plot(tr)	Year	CS
Seedling # (years 4 & 5)	Oak	Negative binomial	tr, year, tr × year, year 3 covariate	plot(tr)	Year	CS
Seedling #	Black cherry	Negative binomial	tr, year, tr × year	plot(tr)	Year	CS
Seedling #	Juniper	Poisson	tr, year, tr × year	plot(tr)	Year	VC
Sapling #	Hardwoods	Negative binomial	tr, year, tr × year	plot(tr)	Year	VC
Sapling height	Hardwoods	Normal	tr, year, tr × year, year 1 covariate	plot(tr)	Year	VC
Sapling browse	Hardwoods	Binomial	tr	plot(tr)	–	–
Tree survival (separately for years 2, 3 and 4)	Oak	Binomial	tr, DBH, tr × DBH # sprouts, tr × # sprouts	plot(tr)	–	–
Tree survival (separately for years 2, 3 and 4)	Juniper	Binomial	tr, DBH, tr × DBH	plot(tr)	–	–
Sprout #	Oak	Negative binomial	tr, year, tr × year	plot(tr) tree(plot)	Year	AR(1)
Sprout height	Oak	Normal	tr, year, tr × year, year 1 covariate	plot(tr) tree(plot)	Year	AR(1)
Sprout browse	Oak	Binomial	tr	plot(tr) tree(plot)	–	–
Canopy openness	–	Normal	tr	–	–	–

3. Results

3.1. Tree survival

We define top-kill as the death of an oak stem that reaches the tree canopy. The fire top-killed some mature tree oaks (woody plants with a DRC ⩾ 10.16-cm): 94.15% of oaks survived in unburned areas, while only 72.83% did so in burned areas in year 3 (2011) ($P = 0.0183$). Larger oaks were more likely to survive to year 4 (2012) ($P = 0.0204$); the average DBH of dead trees was 15.77-cm, 17.61-cm of live trees. None of the top-killed oaks died; all of them had sprouts. We expected that the top-killed oaks, which were significantly smaller, might produce more sprouts (Vesk, 2006), but sprout number after the fire was not significantly related to oak survival. There was a strong trend ($P = 0.0701$) for oak sprouts to be browsed more often in burned plots (80.44 ± 2.79% browsed) than in unburned plots (70.84 ± 3.73% browsed). The fire did kill some juniper trees: significantly more juniper trees were dead in burned areas than in unburned areas in year 4 (2012, 1.5 years after fire): 79.05% of juniper trees were alive in burned areas compared to 98.90% in unburned areas ($P = 0.0035$). Larger juniper trees, as measured by DBH, were more likely to survive to year 3 (2011) ($P = 0.0106$) and to year 4 (2012) ($P = 0.0408$).

3.2. Seedlings

The number of oak seedlings (individual stems < 1.5-m) was highly dependent on year ($P < 0.0001$, Fig. 2a), significantly decreasing in year 3 (2011). That year was exceptionally dry, with a 49% decrease in total rainfall from the long-term average. However, treatments did not significantly affect oak seedling response to the drought (years 2 (2010) and 3 (2011), Table 2, $P = 0.066$) or recovery from the drought (years 4 (2012) and 5 (2013), Table 2, $P = 0.747$). There was a significant treatment *x* year interaction effect on black cherry seedlings ($P < 0.001$): seedling numbers increased from an average of 1.2 seedlings per plot in year 3 (2011) to 48.2 seedlings per plot in year 4 (2012) in the burned-only plots and remained high in the following year. There was a significant treatment *x* year interaction effect on juniper seedlings (Table 2, $P < 0.0068$). Fire killed 89.1% of juniper seedlings. There were still significantly fewer juniper seedlings in burned plots in year 5 (2013) than in year 1 (2009), indicating a slow recovery (Fig. 2b).

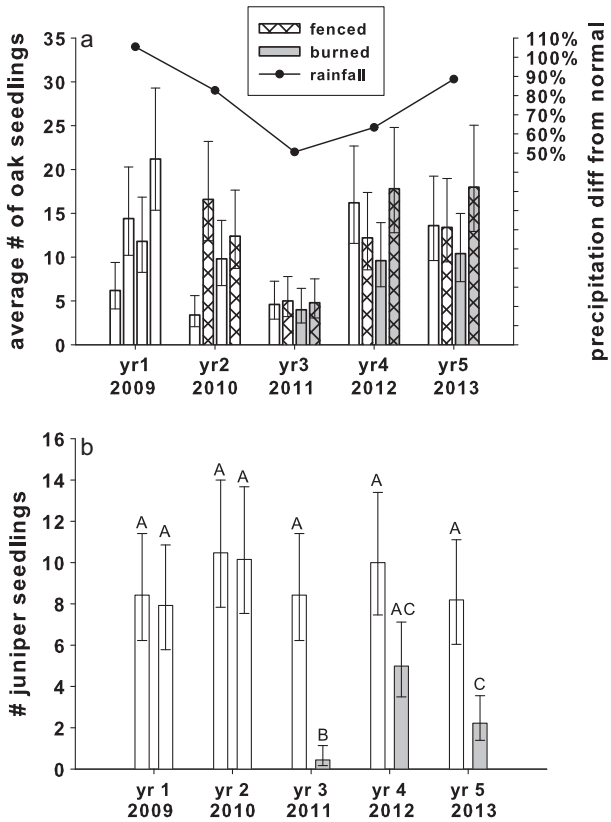

Fig. 2. The effects of year and treatment on average seedling numbers at BCNWR, 2009–2013. Bars are grouped by year on the *x*-axis. Seedlings are individual stems (not connected to a larger adult) <1.5 m. (a) The fire killed juniper seedlings; letters indicate significant differences between years within treatments and (b) error bars are back-transformed ±1 SE.

3.3. Saplings

There was a significant treatment *x* year effect on pooled hardwood saplings (Table 2, $P = 0.0109$). There were more hardwood saplings in the fenced-only plots, reaching significance four years after fence construction (year 1 (2009) vs. year 5 (2013) contrast, $P = 0.044$, Fig. 3). The number of hardwood saplings in the burned-fenced treatment decreased by more than half in 2011, probably in response to both fire and drought (year 1 (2009) vs. year 3 (2011) contrast, $P = 0.043$, Fig. 3). However, recovery was dramatic: there were 2.5 times more hardwood saplings in year 5 (2013) than at the start of the experiment (year 1 (2009) vs. year 5 (2013), $P < 0.0001$, Fig. 3). Sapling numbers in the burned-only plots were initially low and never changed significantly, but did show a slight trend of decrease and increase over time. Treatment did not have a significant effect on hardwood sapling height, but average height tended to decrease in both fenced treatments due to the influx of new individuals into this size class. Browsing rates on burned hardwood saplings were higher (61.25 ± 3.85% browsed) than on unburned saplings (51.04 ± 5.10% browsed), but not significantly so ($P = 0.1617$). No new juniper saplings appeared in the plots after they were cut.

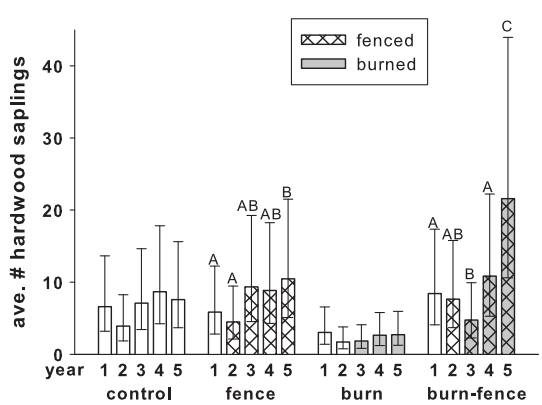

Fig. 3. The effects of years (2009–2013, labeled 1–5 on the *x*-axis) and treatment on the average number of pooled hardwood saplings. Saplings are stems >1.5-m tall with a diameter at root crown (DRC) <10.16-cm. Letters indicate significant differences between years within treatments. Error bars are back-transformed ±1 SE.

3.4. Sprouts

Fire significantly increased the number of oak sprouts (stems with a DRC < 5.08-cm) per tree in year 3 (2011, i.e., 6 months post-fire) in both burned-only and burned-fenced plots (Fig. 4). Some sprouts died in year 4 (2012), significantly so in the burned-only treatment (year 3 (2011) vs. year 4 (2012) contrast, $P = 0.0006$). Sprout numbers increased in all treatments between year 1 (2009) and year 2 (2010). Fenced-only trees continued to add new sprouts in year 3 (year 1 (2009) vs. year 3 (2011) contrast, $P < 0.0001$), while control trees did not. Diameter at breast height (DBH) was not a significant predictor of oak sprout number ($P = 0.1211$). Fencing significantly increased sprout height in both fenced-only and burned-fenced plots (Fig. 4). Fire and fencing together were required to increase average sprout height above the probable browseline of 1.5 m (Fig. 4, dotted line). All hardwood species in the study site sprouted after fire (Table 3). Burning significantly increased the total number of non-oak hardwood sprouts (Table 4). The proportion of hardwood sprouts in fenced and unfenced plots did not significantly differ ($\chi^2 = 1.31$, $P = 0.252$).

Canopy openness, 100 minus canopy cover, was 31.42 ± 1.77 in burned plots, significantly greater than the canopy openness in unburned plots, which was 20.95 ± 1.77 ($P < 0.0001$). There was no significant effect of fence or fire × fence on canopy openness.

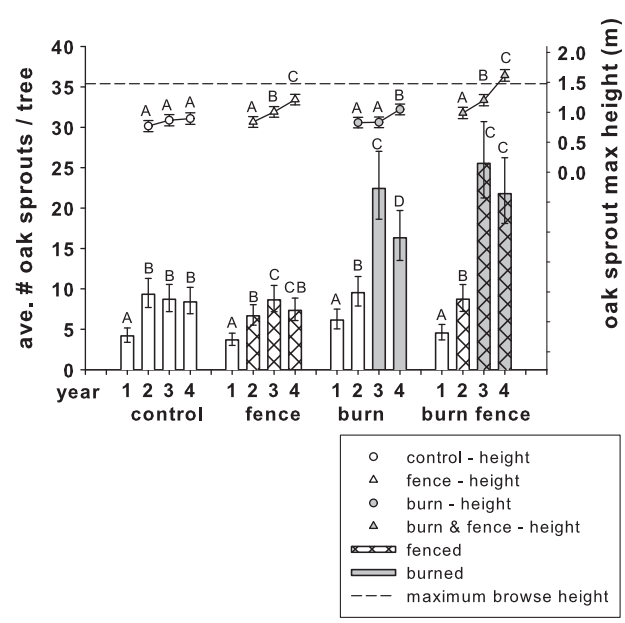

Fig. 4. The effects of years (2009–2012, labeled 1–4 on the *x*-axis) and treatment on average number of oak sprouts per tree (bars) and their average height (lines & points) at BCNWR. Sprouts are stems connected to a mature tree with a DRC < 5.08-cm. There was a significant treatment *x* year interaction in the analysis of oak sprout number ($P < 0.001$). Letters indicate significant differences between years within treatments. Error bars are back-transformed ±1 SE.

Table 3
Hardwood species in the study plots. All of these sprouted after the fire.

Species	Common name
Celtis laevigata	Sugarberry
Diospyros texana	Texas persimmon
Fraxinus albicans	Texas ash
Ilex decidua	Possumhaw
Quercus buckleyi	Texas red oak
Frangula caroliniana	Carolina buckthorn
Prunus serotina	Black cherry
Sideroxylon lanuginosum	Gum bumelia
Viburnum rufidulum	Rusty blackhaw

Table 4
Number of non-oak hardwood sprouts in burned and unburned plots pre-treatment and post-treatment at BCNWR 2009–2012. Oak data in Fig. 4; junipers did not resprout.

	Unburned	Burned	725
Pre-treatment (2009 & 2010)	92	247	
Post treatment (2011 & 2012)	152	669	
% change	+65%	171%	$\chi^2 = 150.96$ $P < 0.001$

4. Discussion

4.1. Effects of fire on regeneration; role of fire in central Texas woodlands

The prescribed fire met most of the management goals: it remained a surface fire, it increased light availability, it did not substantially alter canopy composition, and it promoted oak basal sprouting. However, it did not meet the goal of increasing oak regeneration from seed. As has been found after surface fires in other oak-dominated woodlands and forests (Brose et al., 2013; Clark and Hallgren, 2003; McEwan et al., 2010), this fire stimulated re-sprouting in other hardwood species as well as oaks, and killed small junipers. Unexpectedly, it had no detectable effect on the number of small hardwood plants, including oaks (individual plants < 1.5 m tall, 'seedlings' in the FIREMON protocol and this study) or on hardwood sapling (individual plants > 1.5 m tall with root crown diameter [DRC] < 10.14 cm) abundance or height even three years later. In contrast, Brose et al. (2013) reported that fires tend to decrease oak sapling numbers and increase oak seedling numbers. A combination of drought and insufficient advance regeneration may have been responsible for the lack of effects on seedlings and saplings in our study, as discussed below.

All of the hardwood species in our study site re-sprouted after the fire, especially Texas red oak. Resprouting is an important functional trait that allows trees to persist after fire (Clarke et al., 2013) and may in fact have evolved in response to fire (Keeley et al., 2011). Another important functional trait that allows trees to persist after fire is the ability to survive surface fires. In our study site, no mature hardwood trees died and few lost their entire canopies. Whatever the evolutionary origins of these traits, the fact that all of the hardwood trees in the study survived and resprouted after fire suggests that the central Texas flora may be a product of past fires. In the absence of other evidence for pre-settlement fire frequency and intensity, the apparent adaptations of native hardwood species to fire are among the strongest evidence we have for an important role for fire pre-settlement. Surface fires from adjacent savannas (Fuhlendorf et al., 1996) were probably an important source of pre-settlement woodland fires. Since settlement, and especially in the past 100 years, there have been fewer savanna fires to burn into woodlands (Twidwell et al., 2013). Active fire suppression and the cessation of deliberate burning have also reduced woodland fire frequency (Ryan et al., 2013). Periodic lower-intensity surface fires may have been common pre-settlement, and may be required to achieve the restoration goal of re-creating pre-settlement vegetation.

4.2. Juniperization

Our results support the hypothesis that this decline in fire frequency in central Texas has contributed to the observed failure of oak regeneration and the increase in Ashe juniper. We call this transition from fire-tolerant oak-dominated woodlands to fire-sensitive juniper-dominated woodlands juniperization. This process is widespread; eastern red cedar (*Juniperus virginiana*) has replaced oaks in woodlands of the Cross Timbers (Burton et al., 2010; DeSantis et al., 2011, 2010) and the Ozark Mountains of the US (Hanberry et al., 2014). These changes in species composition are part of a larger trend of decreases in the abundances of fire-tolerant species coupled with increases in the abundance of fire-sensitive species under fire suppression (Hanberry, 2013; Kreye et al., 2013; Stambaugh et al., 2014). For example, fire-sensitive and relatively mesic species such as laurel oak (*Quercus hemisphaerica*), water oak (*Quercus nigra*), live oak (*Quercus virginiana*), and red maple (*Acer rubrum*) have replaced fire-tolerant species such as longleaf pine (*Pinus palustris*) and turkey oak (*Quercus laevis*) in the woodlands of the southeastern coastal plain of the US (Gilliam and Platt, 1999).

Nowacki and Abrams (2008) called the shift from more xeric fire-tolerant oaks to more mesic-adapted species, predominately maples, "mesophication" and argued it should be slow or non-existent in more xeric sites. All of central Texas, like the south-central US in general, is xeric by comparison with the forests that Nowacki and Abrams (2008) were describing, yet the suppression of fire is apparently also creating a shift in dominance throughout this region. This shift is not to mesic-adapted species, but to juniper, which is more xeric-adapted than oak. In both processes the fire-intolerant species (maple; juniper) also reduces the surface fuel load, further decreasing the probability of fires. This initiates a positive feedback loop. Maple tree litter is more shallow and dense that oak litter. It therefore retains more moisture and is less likely to burn and to sustain a fire (Kreye et al., 2013). Similarly, juniper litter is shallower, denser, and less likely to burn than oak litter (Kay, unpublished data). Consequently, lower-intensity wildfires become less and less likely. When wildfires do eventually occur in juniper-dominated woodlands, they are crown fires (Reemts and Hansen, 2013). The risk of catastrophic crown wildfires provides an additional reason for prescribed burning in central Texas woodlands.

4.3. Oak regeneration

The restoration of oak regeneration eventually requires the production of new individuals. Among the variables that prescribed fire can affect are flowering, acorn production, germination, and establishment from seed, and also advanced regeneration; all of these can affect oak regeneration (Arthur et al., 2012). However, oak seedlings did not positively respond to fire in this study. Oak seedling abundance tracked weather conditions, decreasing in the drought, and increasing in subsequent years in all treatments. There are at least four non-mutually exclusive reasons our results differed from some published studies (Brose et al., 2013): (a) insufficient advance regeneration, (b) low to moderate fire-intensity, (c) severe drought (a 49% decrease in total rainfall from the long-term average the first year after fire), and (d) episodic infrequent seedling production.

If the reason why we did not observe more oak regeneration was insufficient advance regeneration, a likely cause is deer herbivory. Even though the density of deer at our study site was not as high as it in some parts of central Texas, it was high enough for us to detect significant fencing effects. However, our study was not designed to provide a quantitative estimate of how much advance regeneration is sufficient.

Another, non-exclusive, possible reason for oak regeneration failure is fire intensities too low to increase light availability sufficiently. In our study, the fire was of low to moderate intensity, which may have not been sufficient to promote oak regeneration via seed, although it was evidently enough to promote sprouting. Higher intensity fires increase light availability, which increases oak seedling growth (Green et al., 2010). Multiple fires, in combination with overstory thinning, are generally more effective at restoring oak regeneration than single fires (Brose et al., 2013; Hutchinson et al., 2012), consistent with the hypothesis that oaks need relatively high light conditions for regeneration.

The drought that occurred in 2011, year 3 of our study and 6 months post-fire, probably had multiple negative effects on oaks. It likely reduced post-fire acorn numbers: acorn production is highly dependent on weather, with large variation among individuals and years (Arthur et al., 2012). Because prescribed fires can kill acorns, especially those at the soil surface (Greenberg et al., 2012), oak seedling recruitment was likely dependent upon subsequent acorn crops, which may have been negatively affected by the drought. Seedling recruitment may be higher in our site in the future after the drought ends. As prescribed fire is used to address dominance shifts in more xeric oak-dominated woodlands (DeSantis et al., 2011), negative drought effects will become increasingly important.

Another reason for a possible shortage of acorns is that Texas red oak may have infrequent and highly variable seed production. Acorn production has not been studied in this species, but many North American oak species have large variation in seed production between years (Greenberg, 2000; Healy et al., 1999; Kelly, 1994). In a nearby region, two other oak species (*Q. stellata*, *Quercus marilandica*) were found to have infrequent reproduction from seed (Stambaugh et al., 2014).

Once oak seedlings are established, they must compete with other species that may better survive the fire and/or grow more quickly (Green et al., 2010). In our study, fire killed nearly 90% of juniper seedlings. They did not recover even 2.5 years after the fire, while oak returned to the pre-treatment numbers and black cherry increased. We therefore conclude that juniper seedlings recover more slowly than hardwood seedlings after fires in central Texas, at least in the short-term. Reemts and Hansen (2013) found that juniper recovered more slowly than hardwoods after a high-intensity crown-fire in mixed oak–juniper woodland, finding very few juniper saplings even nine years after the fire. These short and long-term studies demonstrate that fire may be effective at restoring and maintaining low juniper densities.

4.4. Effects of deer

Deer exclusion increased the number of seedlings entering the sapling size class, an important variable because it reflects growth past the probable browse height. The greatest stem growth was in plots that were both burned and fenced. Growing above the browseline is critical: once a palatable plant passes this threshold, it has a much higher probability of becoming a canopy tree. Many preferred browse species are kept below the browseline due to constant browse pressure; this constant removal of biomass and subsequent compensatory growth can deplete a plant's carbon reserve and reduce survival (Côté et al., 2004; Russell et al., 2001).

Deer densities at our study site were relatively high, compared to other parts of the US, although lower than is common in central Texas (Mostyn, 2001). In this region, and the rest of the US, past densities were maintained by human hunting, predators, and reportedly screwworm parasitism (L. Gilbert pers. comm.). The extremely high deer densities in recent decades represent a novel state, which is likely to cause novel vegetation dynamics, especially when fire is re-introduced.

4.5. Interaction of fire and herbivory

Both fire and protection from deer herbivory were required to increase average oak sprout height above the probable browseline of 1.5-m. Although this finding, as far as we are aware, has not been previously reported, we expect it to be general because the mechanisms driving it are general. Fire is well known to trigger oak resprouting and sprout growth rate (Brose et al., 2013; Lanham et al., 2002). Deer are well known to negatively impact hardwood growth (Rooney and Waller, 2003; Russell et al., 2001) and are overabundant in many parts of the US. It is therefore likely that deer control will be necessary to allow fire to have positive effects on the regeneration of oaks and other hardwoods in this region and elsewhere. Moreover, it seems likely that this interaction between fire and deer partially accounts for the failure of fire alone to promote oak regeneration observed in other studies. These historically novel conditions make the use of fire alone an untenable strategy. This mismatch between historical, present, and future dynamics is a general challenge in restoration ecology (Hobbs et al., 2011). Often, as observed here, the simple reintroduction of the historical disturbance regime is not enough to shift vegetation trajectories in the desired direction (Collins and Carson, 2002; Kern et al., 2012).

5. Conclusions

The term juniperization describes the process of decreasing oak abundance coupled with increasing juniper abundance. This process is widespread throughout the south-central US. It is part of a larger trend of decreases in fire-tolerant species and increases in fire sensitive species in forests and woodlands. Although the prescribed fire in this study triggered oak and other hardwood resprouting, it was not sufficient to increase the abundance of hardwood seedlings or saplings. This was partially because deer herbivory strongly limits oak regeneration. Herbivory is an often-overlooked factor that has the ability to modulate community trajectories following disturbance. Future studies that attempt to reintroduce fire in fire-suppressed systems should consider examining multiple factors jointly with fire.

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