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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.

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).

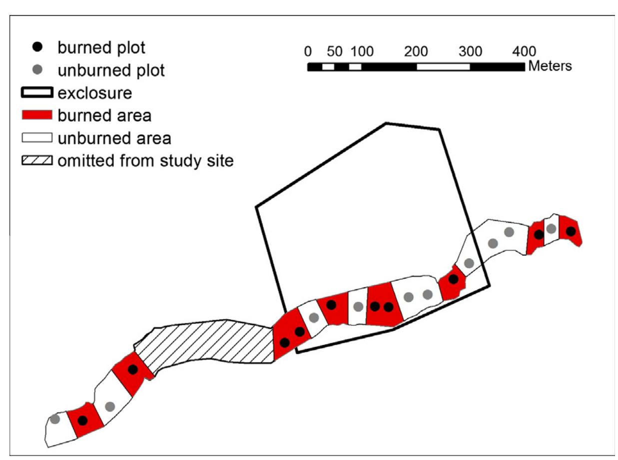

Fig. 1a. Map of the study site. Deer exclosure shown as black square. (Note: exclosure extends beyond the study area because the results presented here are part of a larger study). Burned areas (red) contain burned plots (black points). If two burned plots were adjacent, the entire area between them 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.)