Fowler and Carden *Fire Ecology* (2024) 20:55
https://doi.org/10.1186/s42408-024-00286-8

Fire Ecology

Association for Fire Ecology

REVIEW

Open Access

Roles of fire in the plant communities of the eastern Edwards Plateau of Texas

Norma L. Fowler[1*] and Rebecca E. Carden[1]

Abstract

Background The eastern Edwards Plateau supports a mosaic of woodlands, savannas, and shrubland in which native plant and animal species are often still dominant. Some woodlands are dominated by a mix of native woody species, including Ashe juniper *(Juniperus ashei*), oak species (*Quercus* spp.), and other hardwoods. Other woodlands are nearly pure Ashe juniper; these are particularly susceptible to crown fires. The savannas were once, and still can be, maintained by surface fires.

Results We hypothesize that frequent surface fires once kept some of the mixed woodlands more open and more diverse (a "lost community") and that these fires would have reduced the abundance of Ashe juniper, which does not resprout from the base, and allowed oak regeneration, which is currently failing. The absence of fire, the current failure of oak regeneration, and high white-tailed deer densities together favor the "juniperization" of woodlands, that is, the conversion of mixed woodlands into nearly pure stands of Ashe juniper.

Surface fires in savannas can sometimes control woody encroachment and the non-native grass King Ranch bluestem (*Bothriochloa ischaemum*), although the particular fire characteristics required are not yet clear. The current lack of fire in savannas favors their conversion to woodlands. Since under present conditions Ashe juniper is the primary encroacher, without fire or mechanical clearing these savannas are also on trajectories towards nearly pure stands of Ashe juniper.

Conclusions Prescribed fire, sometimes paired with mechanical thinning, offers land managers in this region a tool for achieving many goals, including increasing native biodiversity and reducing wildfire danger. However, more study of the effects of fires of different intensities and frequencies in these woodlands, savannas, and shrublands is needed to better inform the use of prescribed fire in this region.

Keywords *Bothriochloa ischaemum*, Edwards Plateau, *Juniperus ashei*, Oak regeneration, Prescribed fire, *Quercus buckleyi*, *Quercus fusiformis*, Savannas, Surface fire, Woodlands

Resumen

Antecedentes El este de la Meseta Edwards mantiene un mosaico de bosques, sabanas, y arbustales en los cuales animales y plantas nativos son todavía dominantes. Algunos de sus bosques están dominados por una mezcla de especies arbóreas nativas incluyendo al enebro de frutos azules (*Juniperus ashei*), robles (*Quercus* spp.), y otros árboles de madera dura. Otros bosques son de enebro puro; éstos son particularmente susceptibles a incendios de copas. Las sabanas fueron, y todavía pueden ser, mantenidas por fuegos superficiales.

*Correspondence:
Norma L. Fowler
nfowler@austin.utexas.edu
Full list of author information is available at the end of the article

Resultados Hipotetizamos que los incendios superficiales frecuentes mantuvieron en el pasado algunos de los bosques mixtos más abiertos y diversos (una "comunidad perdida") y que esos incendios habrían reducido la abundancia del enebro de frutos azules, el cual no rebrota de su base una vez quemado, y habrían permitido la regeneración del roble, que actualmente está fallando. La ausencia de fuego, la falla actual en la regeneración de los robles, y las altas densidades de venados cola blanca han favorecido en conjunto "juniperization", es decir, el incremento en la densidad del enebro en estos bosques y la conversión de bosques mixtos en bosques compuestos casi en su totalidad de enebros. Los fuegos superficiales en las sabanas pueden a veces controlar el incremento de especies leñosas y del pasto tallo azul de Kingranch (*Bothriochloa ischaemum*), aunque las características de los fuegos que se requieren para ello no están todavía claras. La falta de fuego actual en esas sabanas favorece su conversión a bosques. Dado que en las condiciones actuales el enebro de frutos azules es la principal especies leñosa invasora, sin fuegos o tratamientos mecánicos de remoción esas sabanas están también en una trayectoria sucesional hacia rodales puros de enebros.

Conclusiones Las quemas prescriptas, muchas veces apareadas con raleos mecánicos, ofrece a los manejadores de tierras de la región una herramienta para alcanzar varios objetivos, incluyendo el incremento de la diversidad de especies nativas y la reducción en el peligro de incendios. Sin embargo, más estudios sobre los efectos de fuegos de diferente intensidad y frecuencia en esos bosques, sabanas y arbustales son necesarios para mejorar la información sobre el uso de quemas prescriptas en la región.

Introduction

The Edwards Plateau of central Texas, about the size of Indiana, is one of the most biologically diverse regions in the nation (Hamilton et al. 2022). Because of the thin soils and hilly topography, it has been ranched rather than farmed; this plus a pre-settlement history of native grazing and browsing ungulates are the primary reasons why it still supports a set of diverse plant communities dominated by native plant species. The eastern Edwards Plateau has mixed oak–juniper woodlands that are the south-westernmost extension of the oak forests of the Ozarks, juniper woodlands that recall the juniper woodlands of northern New Mexico, and savannas that are in many ways an extension of the southern Great Plains. It also has some shrublands. The potential roles of fire in each of these are complex, as are the effects of fire on preventing or facilitating transitions from one community to another. In recent decades, however, fire has mostly been excluded across the eastern Edwards Plateau.

In this paper, we review the roles of fire in these woodland, savanna, and shrubland communities. The importance of fire in creating and maintaining diverse savannas and shrublands in the region is widely recognized, although many details remain unclear. In contrast, the past and potential roles of fire in the woodlands of this region are far less understood. We argue that woodland surface fires potentially have important roles to play, including fostering oak regeneration and supporting native biodiversity. At a landscape level, we argue that fire is therefore critical to restoring and maintaining a mosaic that includes diverse woodlands, savannas dominated by native grasses and forbs, and shrublands. Fire management via prescribed burns can provide many benefits in the region, including the maintenance of a heterogeneous landscape with multiple community types that maximizes native biodiversity.

As it is in many parts of the eastern USA, oak regeneration is failing in the woodlands of the eastern Edwards Plateau (Russell and Fowler 1999). Fire effects on oak populations have been studied in the woodlands of the Ozark and Cross Timbers regions of the south-central USA (e.g., Cutter and Guyette 1994; Dey and Hartman 2005; DeSantis et al. 2011; Stambaugh et al. 2014a; Knapp et al. 2015) and in forests further east (reviewed in Brose et al. 2013). We argue below that the mixed oak–juniper woodlands of the eastern Edwards Plateau are similar to the oak forests elsewhere in that the rarity of surface fires is, at least in part, responsible for oak regeneration failure. Under present conditions, these woodlands are increasingly dominated by the native Ashe juniper (*Juniperus ashei* J. Buchholz), which benefits from fire exclusion. We have called this process "juniperization" (Andruk et al. 2014). Woodlands that are dominated by Ashe juniper are particularly susceptible to crown fires (Thomas et al. 2016).

Surface fires also once played a critical role in the maintenance of savannas on the eastern Edwards Plateau, most importantly by preventing or restricting encroachment of Ashe juniper and other woody species (Fowler and Simmons 2009). In this, the eastern Edwards Plateau resembles the southern Great Plains (e.g., Briggs 2002; Scholtz et al. 2018), although the encroaching juniper species there is eastern redcedar (*Juniperus virginiana* L.). Other juniper species are encroaching on savannas and grasslands in many areas in the western USA (e.g., Miller and Rose 1999; Brockway et al. 2002; Johnson and

Miller 2006; Bradley and Fleishman 2008). In central Texas, as elsewhere, prescribed fire is a possible tool to manage woody encroachment. Fires in savannas on the eastern Edwards Plateau are also being actively studied to determine whether and how they can best be used to promote native grass and forb diversity.

Definition and description of the eastern Edwards Plateau

The Edwards Plateau of central Texas is a region of shallow soils over early Cretaceous limestone formations, approximately 380 km east-to-west and 220 km north-to-south (Fig. 1). On its eastern and south-eastern margins, it is sharply defined by the Balcones Fault Zone, a series of inactive faults that separate the harder early Cretaceous limestone formations of the Plateau from the softer, younger Austin Chalk on the east and Eocene formations on the southeast. To the north, the eastern Edwards Plateau has a relatively sharp boundary with the Llano Uplift (Mason and Llano Counties), which has quite different geology, soils, and biota. For the purposes of this paper, we consider the eastern Edwards Plateau to extend from the western portions of Williamson, Travis, Hays, Comal, and Bexar Counties through Gillespie, Kerr, Real, and northern Uvalde and Medina Counties (Fig. 1). To supplement the limited literature on the eastern Edwards Plateau, we also include some results from studies conducted on the western Edwards Plateau (Texas A&M Sonora Station) and at Fort Cavazos (formerly Fort Hood), which is located in the Western Cross Timbers (Lampasas Cut Plain) north of the eastern Edwards Plateau (Griffith et al. 2004).

In most of the Edwards Plateau, the limestone bedding layers are remarkably flat. The topography has therefore been created by erosion. Steep hillsides and narrow canyons and arroyos are common, but there is little overall variation in elevation. In general, the soils are very thin and there are exposed outcrops of the limestone bedrock, and the region supports ranching rather than crop farming. As a result, until recently there was no wholesale loss of natural ecosystems, in contrast to, for example, the former cotton-farming region east of the Plateau. However, housing

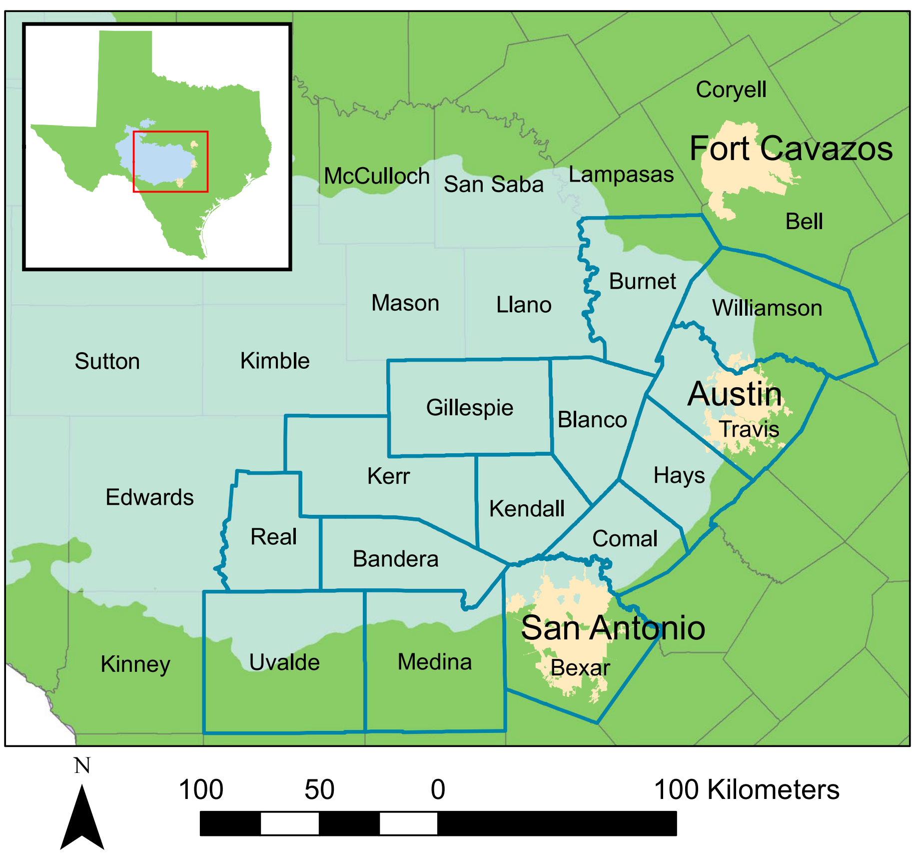

Fig. 1 The Edwards Plateau (shaded light blue) of central Texas is approximately 380 km east–west × 220 km north–south in central Texas. The eastern Edwards Plateau, as defined here, is approximately 23,000 km^2 (about the size of New Jersey). Counties that include portions of the eastern Edwards Plateau as defined in this paper are outlined in bold. Edwards Plateau polygon downloaded from Texas Parks and Wildlife Department (n.d.)

developments, commercial areas, and their associated infrastructure are rapidly replacing ranches in the region, especially near Austin and San Antonio. Much of the region can now be described as wildland-urban interface.

Plant communities

At this time, the major upland plant communities of the eastern Edwards Plateau are (A) mixed oak–juniper woodland, (B) low diversity stands of Ashe juniper, (C) oak savanna, and (D) oak–sumac shrubland (Amos and Gehlbach 1988; Diamond 1997) (Figs. 2 and 3). Riparian forests are also present, especially in moist canyons (Van Auken et al. 1979; Diamond 1997). It has been proposed that these riparian forests did not burn frequently due to their mesic character (Yao et al. 2012). This paper is limited to the upland communities. True grasslands (i.e., tracts without woody plants) are relatively uncommon and usually due to recent brush removal; we have pooled them with savannas for simplicity. Fire certainly played important roles in these savannas and shrublands, discussed below. We will also argue that surface fires once played a role in the mixed woodlands, perhaps to the extent that it created (E) a sixth, "lost community," one

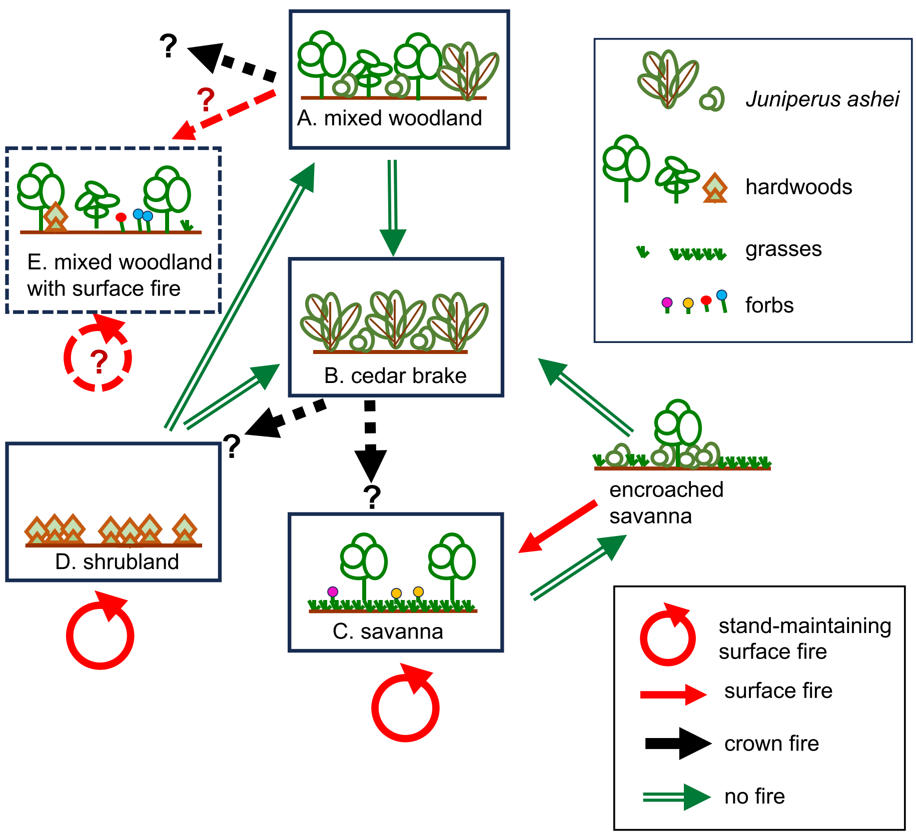

Fig. 2 Simplified scheme of upland communities (boxes) of the eastern Edwards Plateau of Texas and their dynamics (arrows). Solid arrows and outlines represent well-documented communities, transitions, and processes; dashed outlines, dashed arrows, and question marks represent hypothesized or unknown communities, transitions, and processes. **Communities:** *(A) Mixed woodlands* are commonly co-dominated by species of oaks, especially Texas red oak (*Quercus buckleyi*), and Ashe juniper (*Juniperus ashei*). *(B) Cedar brake* is the local name for a nearly-pure stand of Ashe juniper. *(C) Savannas* commonly have Plateau live oak (*Quercus fusiformis*) as the dominant tree species, a rich herbaceous flora, and Ashe juniper as the commonest woody encroaching species. *(D) Shrublands* are commonly dominated by species of sumac (*Rhus* spp.) and shin oak (*Q. sinuata*). We hypothesize that an additional community existed, *(E) mixed woodlands with surface fire*, that differed from current mixed woodlands in having less Ashe juniper, in supporting oak and other hardwood regeneration, and in having higher shrub and herbaceous diversity. **Dynamics:** The role of surface fire (circular solid red arrows) in maintaining savannas (C) and shrublands (D) is widely accepted. Without fire, savannas (C) and mixed woodlands (A) are on paths (double-line green arrows) towards cedar brakes (B), savannas due to woody plant encroachment and mixed woodlands due to the scarcity of hardwood regeneration. Whether the trajectory of a shrubland (D) in the absence of fire is towards a mixed woodland (A) or a cedar brake (B) (double-line green arrows) likely depends on how much Ashe juniper it initially has or acquires. We hypothesize that surface fire could convert current mixed woodlands (A) to mixed woodlands with surface fire (E) (dashed straight red arrow), and maintain them in that state (dashed circular red arrow). The eventual effects of crown fire on mixed woodlands (A) and cedar brakes (B) are uncertain (dashed black arrows)

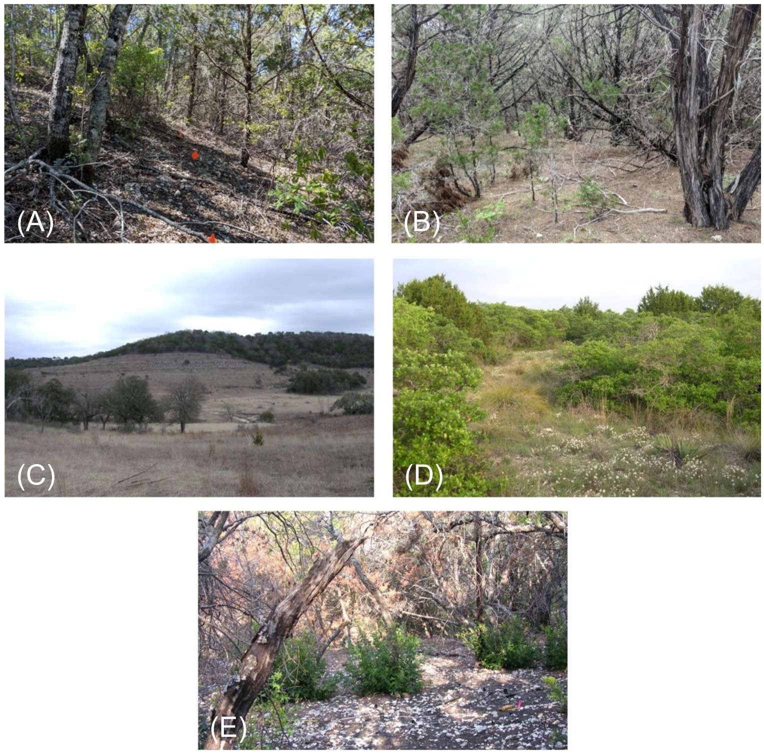

Fig. 3 Images of four upland plant communities of the eastern Edwards Plateau: **A** mixed woodland, **B** cedar brake, **C** savanna, and **D** shrubland. The fifth image is a picture taken 6 months after an experimental fire in a mixed woodland (Andruk et al. 2014) to represent how surface fire might be used to restore the hypothesized "lost community" (**E**): mixed woodland with surface fire. Shrubland photograph (**D**) by C. Reemts

that was much more open than mixed woodlands are now.

The division between woodland (A, B, and E in Fig. 2) and savanna (C in Fig. 2) is somewhat arbitrary in this region, as it is elsewhere: there is a continuum from closed-canopy woodland with few or no glades, to woodland with many large glades, to savanna with clusters of woody plants, to nearly open grassland (Van Auken 2000; González 2010). Ashe juniper is both a dominant in many woodlands and the most common woody encroacher in the savannas (Diamond 1997; Fowler and Simmons 2009). This native species occurs from northern Mexico through Texas, and sparsely in Oklahoma, Arkansas, and southern Missouri, but it is especially common on the eastern Edwards Plateau (Sullivan 1993; US range map: USDA NRCS 2014). Like eastern redcedar, Ashe juniper does not resprout after it is burned, and therefore is favored by the absence of fire (Fuhlendorf et al. 1996; Reidy et al. 2016; Short et al. 2019).

In mixed woodlands (A in Figs. 2 and 3), Ashe juniper co-dominates with native hardwood species, most commonly Texas red oak (*Quercus buckleyi* Nixon & Dorr). Texas persimmon (*Diospyros texana* Scheele), elbowbush (*Forestiera pubescens* Nutt.), Lindheimer's silktassel (*Garry ovata* Benth.), possumhaw (*Ilex decidua* Walter), black cherry (*Prunus serotina* Ehrh.), cedar elm (*Ulmus crassifolia* Nutt.), and other native woody species are also frequently present (Van Auken et al. 1981; Diamond 1997; Barnes et al. 2008). On the sides of canyons and other mesic sites, additional species such as bigtooth maple (*Acer grandidentatum* Nutt.), redbud (*Cercis canadensis* L.), and Mexican buckeye (*Ungnadia speciosa* Endl.) may also be present (Barnes et al. 2008). These oak–juniper woodlands provide breeding habitat for the endangered golden-cheeked warbler (*Setophaga chrysoparia*), which requires mature Ashe juniper and mature oaks (Pulich 1976; Groce et al. 2010; Marshall et al. 2013).

Woodlands dominated by Ashe juniper (B in Figs. 2 and 3) often result from woody encroachment in savannas and are locally called cedar brakes (cedar is a local common name for Ashe juniper) (Fowler and Simmons 2009). Encroachment is primarily by the expansion and subsequent merging of clusters of woody plants rather than by the establishment of isolated individuals, although Ashe juniper individuals also become established in open grassland (Fowler 1988; González 2010). In the absence of fire or mechanical clearing to halt woody plant encroachment, the continuum from grassland to woodland becomes a successional sequence (Fowler and Simmons 2009). This process can create near-monocultures of

Ashe juniper with only a few remnant oaks (Fuhlendorf et al. 1996; Fowler and Simmons 2009) and a sparse or absent herbaceous layer (Fuhlendorf et al. 1997; Wayne and Van Auken 2010).

Like the woodland–savanna continuum, the distinction between mixed woodlands (A in Fig. 2) and cedar brakes (B in Fig. 2) is somewhat arbitrary, as the proportion of Ashe juniper varies widely among stands. At present, most of the large Ashe juniper trees in all communities have an open-grown, branched-at-base morphology (Smeins and Fuhlendorf 1997), suggesting that they originally grew in a savanna or in a woodland with a much more open canopy. In addition, many Ashe juniper populations have size distributions that are consistent with young stands (Van Auken 1993; Van Auken and McKinley 2008). The cedar brakes are not old-growth forests (Diamond 1997), despite recent claims that they are (e.g., McGreevy 2021). We do not know whether cedar brakes, if left undisturbed and unburned, would remain in their present condition, or if they would remain dominated by Ashe juniper but transition to large trees with erect single-trunk morphology, or transition to diverse mixed woodlands, or have some other trajectory (Fig. 2).

Many savannas (C in Figs. 2 and 3) of the eastern Edwards Plateau support rich communities of native grasses and forbs with a few scattered individuals or clusters of woody plants. The most common savanna oak is Plateau live oak (*Quercus fusiformis* Small). In contrast, honey mesquite (*Prosopis glandulosa* Torr.) is uncommon, being limited by the shallow soils of the Plateau, although it is common to the south, east, and north of the Plateau and on the Llano Uplift. Common native savanna grasses include silver bluestem (*Bothriochloa laguroides* (DC.) Herter), Texas winter grass (*Nassella leucotricha* (Trin. & Rupr.) Pohl), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), and species of three-awn grasses (*Aristida* spp.) and grama grasses (*Bouteloua* spp.) (Fowler and Dunlap 1986). The non-native King Ranch bluestem grass (*Bothriochloa ischaemum* (L.) Keng) is a common invasive species in savannas.

Shrublands (D in Figs. 2 and 3) are not common but are important as nesting habitat for the recently de-listed black-capped vireo (*Vireo atricapilla*) (Grzybowski et al. 1994; USFWS 2018). Common shrubs in this community include shin oak (*Quercus sinuata* Walter) and sumac species, including flameleaf sumac (*Rhus lanceolata* (A. Gray) Britton) and evergreen sumac (*R. virens* Lindh. Ex A. Gray) (Diamond 1997). Like most hardwoods in central Texas, these shrub species resprout after fire.

The distribution of these communities on the landscape is determined by past land management, especially the history of land clearing and fire, as well as by topography (Cartwright 1966; Wink and Wright 1973; Smeins 1980; Diamond and True 2008; Murray et al. 2013). These may be correlated: it is easier to clear flatter sites, for example. Savannas are somewhat more common in flatter areas than on hillsides and woodlands are more common on hillsides than in flatter areas, but grassy slopes and flat woodland sites are certainly not uncommon (Diamond and True 2008). Topographic location is important for Texas red oak, which commonly occurs in a band around some hillsides just below the hilltop or mesa top (Van Auken et al. 1981). This band is clearly visible in years when Texas red oak leaves turn red for a time in the fall. But Texas red oak can also be found growing scattered elsewhere in woodlands.

Past eastern Edwards Plateau landscapes

In many parts of the world, a knowledge of past plant communities and fire regimes is available to guide land managers and to inform community ecology. However, the relative amounts of woody and herbaceous cover in this region in the past, the scale of the patches of each, their position across the landscape, and whether or not the landscape was a shifting mosaic are all uncertain. Pollen and phytoliths from the best cave record in the region (Hall's Cave) include substantial amounts of hackberry (*Celtis* spp.), juniper, oak, grass, and Asteraceae pollen and C4 grass phytoliths throughout the past 2000 years (Cordova and Johnson 2019). This suggests that both woodland and savanna were present throughout this period.

Past land management practices by Indigenous populations in this region are essentially unknown by present non-Indigenous scientists and land managers. The effects of Indigenous people probably changed substantially as Indigenous populations were reduced by Old World diseases (Denevan 1992; Snow 1995; Ryan et al. 2013). Indigenous land management practices likely changed again when peoples with horse- and bison-based cultures (Apache and Comanche) arrived in the region, perhaps around 1700 (Newcomb 1961; Carlisle 2020; Lipscomb 2020; but see Taylor et al. 2023). These tribes are known to have deliberately set fires in this region, and it seems likely that they used fire extensively to maintain savannas as bison habitat (Foster 1917; Smeins 1980).

The first good written descriptions of the vegetation by Lindheimer, Olmsted, and Roemer are from the mid-1800s and are consistent with a mosaic landscape but do not tell us much about relative woody and herbaceous cover, patch size, relationship of vegetation with topography, and other quantitative properties of the landscape (Olmsted 1857; Roemer 1935; Goyne 1991). Bray (1904a,b) also described a mosaic landscape.

Ranching was introduced in the mid-1800s and likely led to a period of intense overgrazing and consequent soil erosion, as it did elsewhere in the western USA (e.g., Bahre 1991). Since then, grazing has favored encroachment by reducing fine fuels and competition from grasses, but has also provided an economic motivation to mechanically remove woody plants. Ashe juniper and other woody plants were also cut for fence posts, building materials, and other uses from the mid-1800s onward. It is therefore plausible that the present ratio of savanna to woodland is similar to what it was in the past (e.g., Diamond and True 2008). However, the majority of authors say that a period of woody encroachment from the late 1800s onwards, caused by a lack of fire, has led to a much higher ratio of woodland to savanna than was present before settlement by non-Indigenous peoples (e.g., Bray 1904a,b; Buechner 1944; Fuhlendorf and Smeins 1997; Stambaugh et al. 2014b; Van Auken et al. 2023). A minority opinion is that the eastern Edwards Plateau was almost all woodland before 1800 (O'Donnell 2019). Some recent initiatives to fight woody plant encroachment so as to restore grasslands (e.g., Twidwell et al. 2013), however appropriate for eastern redcedar encroachment in parts of Oklahoma and north Texas, do not necessarily fit the eastern Edwards Plateau without modification.

Due to these uncertainties about historic fire regimes and plant communities in this region, present communities and their responses to fire are one of the best sources of information about what landscapes may once have been. They are also one of the best sources of information to guide management plans and to identify target plant communities. We review that literature below.

Roles of fire in eastern Edwards Plateau woodlands

Woodland fire characteristics

The long-term frequency of fires of all types in woodlands on the eastern Edwards Plateau is uncertain, but has very likely changed over time with changes in climate and people (Murray et al. 2013). As in many parts of the country, the frequency of wildfires in this region is predicted to increase as the climate changes (Gao et al. 2021; Nielsen-Gammon et al. 2021).

Due to high fuel loads and fuel continuity, combined with periods of hot, dry weather, wildfires are often crown fires in these woodlands. The canopies of Ashe juniper trees extend to the ground (Smeins and Fuhlendorf 1997; Hicks and Dugas 1998), creating vertically continuous ladder fuels that facilitate a surface fire transition to torching in the tree crowns. Common tree species differ in their ability to sustain crown fires: Ashe juniper has higher crown fuel density than Texas red oak, while live oak and shin oak are intermediate (Thomas et al. 2016). Ashe juniper is therefore most likely to sustain a crown fire. Ashe juniper will ignite when the moisture content of needles is < 80% (McCaw et al. 2018). This happened in 2011, when drought, wind, and low humidity combined to create favorable conditions for fire (Nielsen-Gammon 2012), and there were a number of significant wildfires in the region.

The possible role of low- or mixed-severity surface fires in mixed oak–juniper woodlands is uncertain. There is some direct evidence of surface fires in these communities. Murray et al. (2013) found fire scars dating from 1917 to 2001 on Texas red oak at the Balcones Canyonlands National Wildlife Refuge, indicating that woodlands there did have surface fires during that period. They found a period of high fire frequency from 1950 to 1959, which were also years of severe drought. However, the oaks were not old enough to estimate a long-term fire return interval (Murray et al. 2013). The potential behavior and effects of such surface fires are an active area of research. We argue that these fires could play an important role in maintaining diverse native plant communities in woodlands in this region.

Woodland surface fires, deer, and oak regeneration

Oak regeneration is failing on the eastern Edwards Plateau, as it is in many other places. A multi-site study documented that both live oak and Texas red oak were failing to regenerate. Mature trees were abundant, and seedlings (both species), basal sprouts (Texas red oak), and root sprouts (live oak) were also present, but saplings and small trees were almost absent (Russell and Fowler 1999). This pattern was duplicated in a study of live oak at a different site (Barnes et al. 2008). There is also evidence that some of the other oak species and other hardwoods such as bigtooth maple, Texas ash (*Fraxinus albicans* Buckley), and black cherry are also not recruiting saplings (Van Auken and McKinley 2008; Van Auken et al. 2023). Ashe juniper seedlings and saplings, in contrast, are abundant in woodlands in this region (Van Auken 1993; Van Auken et al. 2004). These findings suggest that when mature oaks and other hardwood species die, they will be replaced in the canopy by Ashe juniper.

It is likely that a lack of surface fire is one of the factors causing the failure of oak regeneration. Most mature oak trees on the eastern Edwards Plateau became established in the first half of the twentieth century (Russell and Fowler 2002; Murray et al. 2013). There are several possible explanations for this. Older individuals may be absent due to harvesting or present but not recognized because they had resprouted after being cut. Conditions in the first half of the twentieth century in this region may have been especially favorable for oaks due to reduced competition and higher light levels following widespread harvesting of oaks and Ashe juniper (Bray 1904a; Cartwright 1966; Diamond 1997). If there were woodland surface fires at that time, they would have favored resprouting oaks and other hardwoods over Ashe juniper, which does not resprout after fire (Reidy et al. 2016). Surface fires in woodlands are now very rare. In addition, white-tailed deer (*Odocoileus virginianus*) populations were very low in the first half of the twentieth century, which likely also contributed (Russell and Fowler 2002). Deer densities in central Texas are now among the highest in the country and oaks are among the species they readily browse (Armstrong and Young 2000; TPWD 2023).

Similar explanations have been proposed for oak regeneration failure in the central and eastern USA (Abrams 1992). Frequent surface fires are hypothesized to favor oaks by opening forest structure and increasing light availability (Knapp et al. 2015). Frequent fires may also favor oaks because many oak species resprout readily after fire (Clark and Hallgren 2003; DeSantis and Hallgren 2011) and may resprout more vigorously than other hardwoods, especially after multiple fires (Dey and Hartman 2005; Burton et al. 2010; Short et al. 2019). Trends in white-tailed deer populations elsewhere in the country are thought to be similar to trends on the eastern Edwards Plateau (McEwan et al. 2011). In Oklahoma and likely elsewhere, fire suppression and drought probably interact to accelerate the effects of oak regeneration failure: in the absence of fire, mature canopy oaks that are killed by drought are more likely to be replaced by abundant fire-sensitive, drought-tolerant competitors, most notably (in Oklahoma) eastern redcedar (DeSantis et al. 2011).

Field experiments on the eastern Edwards Plateau have suggested that introducing surface fires in mixed woodlands and reducing deer densities would increase oak regeneration, especially in combination. A study of prescribed surface fire in mixed woodlands found that surface fires reduced the densities of Ashe juniper seedlings and saplings, as well as hardwood saplings, 16 months later (Reidy et al. 2016). Six years after the fire, though, Ashe juniper seedling and sapling densities were still reduced, but hardwood sapling density was significantly higher in plots with the highest fire severity than in unburned plots (Reidy et al. 2021). Yao et al. (2012) also reported more oak saplings in severely burned than in unburned woodland sites. Russell and Fowler (2004) found that oak seedlings were more likely to grow into the sapling size class where deer were excluded. Andruk et al. (2014) initiated a study in 2009 to examine the joint effects of deer exclusion (via fencing) and prescribed fire in a mixed woodland. Fire was preceded by mechanical thinning of small Ashe juniper to prevent a crown fire. There was some scorch and some top-kill of Texas red oak and other hardwoods, with excellent resprouting from all hardwood species present (Fig. 3E). The pre-fire thinning, combined with the fire, reduced vegetation cover 0.5 m above the surface to approximately 70%, as planned. By 2011, the tallest re-spouts were, on average, in the fenced-and-burned plots, and only in that treatment had they grown above the reach of deer browsing. We concluded that both deer browsing and light limitation due to a closed canopy are inhibiting oak regeneration (Andruk et al. 2014). Carden et al. (unpublished report to USFWS) re-surveyed these plots in 2021 and found that Ashe juniper saplings were still rare in the burned plots, that Texas red oak saplings were most common in the fenced-and-burned plots, and that saplings of possumhaw, which was uncommon in 2009, had become abundant by 2021 in the fenced and fenced-and-burned plots. Possumhaw is preferred by deer (Armstrong et al. 1991) and unfenced plants are often heavily browsed. Both the long-lasting effects of fire and ongoing deer browsing were important in determining the composition of this woodland community.

The results of these experiments suggest that woodlands in this region may require surface fires or some other form of periodic disturbance, plus a reduction in deer densities, to restore hardwood regeneration and to control Ashe juniper. Otherwise, under current conditions, they appear to be on trajectories to become increasingly dominated by Ashe juniper (A → B in Fig. 2). Ashe juniper does not resprout after fire and is the least palatable of all the woody species in these communities (Armstrong et al. 1991). We called this trajectory "juniperization" (Andruk et al. 2014). Juniperization is somewhat similar to, but not the same as, the mesophication trajectory observed in the northeastern USA (Nowacki and Abrams 2008). Unlike maple and beech, Ashe juniper is relatively drought-tolerant (Northup et al. 2021). It produces vertically continuous canopy foliage and dense, persistent duff (Fuhlendorf et al. 1997; Smeins and Fuhlendorf 1997). Both its needles and duff will burn when their water content is low enough. The result of juniperization is not a fire-proof mesic forest, but a cedar brake highly susceptible to crown fire.

The study of the potential role of surface fires in the woodlands of the eastern Edwards Plateau is the southwestern fringe of a much larger effort to understand the role of surface fires in oak woodlands and forests of the central and eastern USA (Abrams 1992; Nowacki and Abrams 2008; McEwan et al. 2011; Arthur et al. 2012; Alexander et al. 2021). Prescribed fire is being studied, and used, to promote oak regeneration in many different places in this larger region. A review of this literature is beyond the scope of this paper. The studies most comparable to studies of the eastern Edwards Plateau are from woodlands where oak regeneration failure is occurring concomitant with an increase in the abundance of eastern redcedar, including the Ozark region of Arkansas and Missouri (e.g., Dey and Hartman 2005; Chapman et al. 2006; Fan et al. 2012; Hanberry et al. 2014; Knapp et al. 2015) and the Cross Timbers of southern Kansas, Oklahoma, and northern Texas (e.g., Rice and Penfound 1959; DeSantis et al. 2010; Sparks et al. 2012; Stambaugh et al. 2014a; Cory et al. 2019). One theme in this larger literature is to determine what a forest or woodland with repeated surface fires would be like.

A lost community?

The failure of Texas red oak and other hardwood regeneration in the woodlands of the eastern Edwards Plateau, despite abundant mature trees of these species, suggests that there may once have been much more open woodlands in this region that were sustained by regular, mixed-severity surface fires (E in Fig. 2). The creation and maintenance of this community type would probably have resembled the vegetation-fire positive feedback loop that is hypothesized to have maintained oak woodlands across the eastern USA prior to widespread fire suppression (Nowacki and Abrams 2008; Stambaugh et al. 2014a; Alexander et al. 2021). Regular woodland surface fires may have killed small diameter Ashe juniper in woodlands, which are known to be killed by fire in savannas (Noel and Fowler 2007), and thus increased the relative abundance of Texas red oak and other resprouting hardwoods. This change in species composition could have increased the ability of these woodlands to carry surface fire: unlike Ashe juniper, deciduous oaks such as Texas red oak produce large, lobed leaves that curl as they dry and create a deep, porous leaf litter that is highly flammable (Kane et al. 2008). The reduction in Ashe juniper litter and duff and increased light availability in these woodlands would also probably stimulate understory grass and forb growth (Yager and Smeins 1999), as has occurred elsewhere following surface fires (e.g., Burton et al. 2011; Maginel et al. 2019; Vander Yacht et al. 2020). This change in surface fuel bed properties would increase community flammability, and thus the ability of these woodlands to sustain repeated surface fires, further increasing the relative abundance of oaks and other hardwoods (dashed circular arrow under E in Fig. 2). Another desirable effect of this hypothesized community would be more specific to the eastern Edwards Plateau: the lower Ashe juniper abundance would likely also reduce ladder fuels and the risk of a crown fire (Fig. 2).

We do not know how open a woodland would have to be to support hardwood regeneration in this region. However, some of the management being tested in oak woodlands elsewhere in Texas (Sparks et al. 2012) suggests that a woodland open enough to support hardwood regeneration would be different enough from current woodlands to be considered a distinct community that is no longer present: a "lost community" (E in Fig. 2). We suggest that this community would also have been distinct from the savannas in the region in several ways. For example, woody plants would be less likely to be clustered, since extreme clustering is a product of the encroachment process (González 2010).

There is another line of evidence that supports the former existence of this hypothesized lost community. Multiple studies of the endangered bracted twistflower (*Streptanthus bracteatus* A. Gray), an annual wildflower endemic to this region, have found that this is a woodland species that requires more light than it usually gets now to thrive (Zippin 1997; Fowler et al. 2012; Leonard and Van Auken 2013). It is not a savanna species, but it can thrive in gaps in the canopy if it is not over-browsed. It seems likely that this species, likes many of its California congeners, is a fire-follower that would once have had as its primary habitat woodlands in the years soon after a surface fire and then would have been maintained by its dormant seed bank until the next fire.

In Carr's list of 71 plants endemic to the eastern Edwards Plateau, 13%, including bracted twistflower, are identified as growing in partial shade only, and none grow in full shade only (Carr 2022). The lost community would be likely be high-quality habitat for these native partial shade species, in contrast to the full sun species which thrive in savannas. Higher light levels would likely cause the lost community to have a richer herbaceous flora than is common in woodlands now and possibly also greater woody species diversity. Restoration of the lost community would therefore likely help conserve regional plant biodiversity. Unfortunately, this hypothesized community might not be suitable habitat for the endangered golden-cheeked warbler, which requires a closed canopy (Pulich 1976; Groce et al. 2010).

There are practical challenges to reintroducing woodland surface fires in this region. Implementing prescribed surface fire under present conditions may require an initial mechanical thinning of the lower levels of the woody plant fuel profile. This would have the dual effects of removing ladder fuels to reduce the risk of a crown fire and increasing surface fuels that can carry a surface fire. Deer control would also likely be necessary for maximum plant diversity to develop. More research is needed to understand what the best surface fire return interval would be: there would have to be enough time after a fire to allow sufficient litter to accumulate to carry a surface fire that would kill juvenile Ashe juniper, but not so long that ladder fuels would accumulate. Presumably, the fire frequency would have to be routinely adjusted in response to litter buildup, which would be in part a function of precipitation.

The recreation of this hypothesized community (E in Fig. 2) would not be the woody plant encroachment process in reverse. Woody plant encroachment in this region typically involves the formation, lateral expansion, and eventual merging of dense clusters of Ashe juniper and sometimes other woody plants to form a cedar brake (Fowler and Simmons 2009; González 2010). Light levels are low in these clusters as soon as they form (Fowler and Clay 1995). Savanna species are gradually lost in the shrinking glades (Alofs et al. 2014). In contrast, we are suggesting a no-longer-present community in which tree canopies might or might not be continuous, but light levels underneath these canopies would be substantially higher than they are now.

Effects of crown fires in eastern Edwards Plateau woodlands

Crown fires do occur in the woodlands of the region, especially where Ashe juniper is dominant (Bryant et al. 1983), despite active fire suppression. In stands that include hardwoods, there is some evidence from a study at Fort Cavazos that after an intense crown fire a community dominated by resprouting hardwoods, with little Ashe juniper, will eventually develop if soil erosion is not too great (Reemts and Hansen 2008, 2013). The delayed recolonization of Ashe juniper in that case may have been due to a combination of reduced seed source after the crown fire killed most or all dominant Ashe juniper tree and competition from resprouting hardwoods (Reemts and Hansen 2008). Repeated wildfires where oaks and other resprouters are present may convert previously mixed woodlands into oak shrublands (Diamond 1997; Reemts and Hansen 2013). If a stand with few resprouting hardwoods experiences repeated crown fire, a savanna or grassland might result. Soil erosion after a crown fire may slow or alter post-fire community trajectories, especially on steep slopes; an increase in exposed bedrock is a possible effect.

Roles of fire in eastern Edwards Plateau savannas

The importance of fire in the savannas (C in Fig. 2) in this region is much less controversial. Like all the other savannas in North America (Fowler and Beckage 2019), eastern Edwards Plateau savannas are assumed to have been created and maintained by some mix of lightning-started and anthropogenic fire that slowed or reversed woody plant encroachment (Smeins 1980; solid circular arrow under C in Fig. 2). Parallel to the process of juniperization observed in local woodlands, without fire or mechanical clearing these savannas are on trajectories towards low-diversity stands of nearly pure Ashe juniper (Fuhlendorf et al. 1996; Fowler and Simmons 2009). Mechanical removal of woody plants, not fire, remains the primary method of maintaining savannas on private land.

Despite general agreement that fires once maintained these savannas, we lack important knowledge about the effects of fire season, frequency, and intensity on woody plant encroachment. We also lack a good understanding of the effects of fire characteristics on the herbaceous components of the savanna communities. Finally, we know very little about the effects of fire on woody savanna species.

Savanna fire—effects on woody encroachment

In the absence of fire, Fuhlendorf et al. (1996) estimated that an open savanna would be converted into cedar brake in approximately 75 years (Fig. 2). Ashe juniper does not resprout after top-kill, so top-kill, even if only by scorch, is sufficient to kill an individual. However, the mortality rate of Ashe juniper drops off quickly with plant size in low-intensity savanna fires (Noel and Fowler 2007). Because fire severity is affected by fuel load (Wink and Wright 1973), as well as weather, land managers may have to forego grazing for a period of time to allow fine fuels to accumulate. They may also need to postpone a fire until after a period of relatively high precipitation has caused sufficient grass biomass to be produced.

The reintroduction of surface fires into these savannas has had mixed success in slowing or reversing woody encroachment. Repeated burns conducted on Austin Water Quality Protection lands near Austin have resulted in control of encroachment but reversal in only a subset of sites (Kreuter et al. 2022; D. Grobert, City of Austin, TX, USA, personal communication). On the western Edwards Plateau, both winter and summer fires were effective in reducing Ashe juniper abundance (Taylor et al. 2012). In the same site there were high shrub mortality rates and low resprouting rates following a high-intensity fire (Twidwell et al. 2016). Interestingly, mortality was apparently unrelated to shrub height. The authors noted that shrub mortality was likely especially high because the plants were already stressed by drought. More studies of the effects of high-intensity fires on woody plant encroachment in the savannas of the eastern Edwards Plateau are needed, separately and in combination with different drought conditions. Because Ashe juniper might not be the primary woody encroacher if deer densities were not so high, studies of high-intensity fires under different deer densities are also needed.

Savanna fire—effects on herbaceous species

As it does elsewhere, woody encroachment reduces native biodiversity in central Texas (Ratajczak et al. 2012; Fuhlendorf et al. 1997; Alofs et al. 2014). In addition to its role in slowing woody plant encroachment, fire affects the composition of savanna plant communities. Differences among fires in season, frequency, and intensity likely affect different savanna species differently. Most research in this region on fire and herbaceous species in savannas has been motivated by the goal of using fire to control King Ranch bluestem. This species is a non-native invasive perennial grass that is very common in savannas of the eastern Edwards Plateau. It is highly grazing-tolerant, is found in a wide range of soils and topographical positions, and often forms near-monocultures that greatly reduce native biodiversity (Gabbard and Fowler 2007).

Evidence is accumulating that under the right circumstances fire can favor native grasses and forbs over King Ranch bluestem. Low-intensity fires, especially in November–February, have little direct effect on King Ranch bluestem, presumably because it is dormant then (Gabbard and Fowler 2007; Simmons et al. 2007; Havill et al. 2015; Novak et al. 2021). Some relatively high-intensity fires in May–October have successfully reduced the abundance of King Ranch bluestem, although the conditions (season, weather, plant condition, etc.) necessary to achieve this outcome reliably are still unclear (Simmons et al. 2007; Ruckman et al. 2011; Reemts et al. 2019, 2021; Novak et al. 2021; Whiting 2022; Behr et al. in press). It is also important to determine whether a fire has a greater deleterious effect on King Ranch bluestem than on co-occurring native species. Several studies indicate that this outcome is possible, although the conditions for achieving it are also not yet clear (Havill et al. 2015; Novak et al. 2021; Reemts et al. 2021; Whiting 2022; Behr et al. in press).

Like most savanna species in this region, King Ranch bluestem does not persist in the shade of most woody plants (Gabbard and Fowler 2007). Therefore control of King Ranch bluestem is not sufficient to maintain native savanna biodiversity; it must be paired with control of woody plant encroachment. Without effective fires or mechanical clearing, not only King Ranch bluestem but almost all native savanna species are eventually lost from a site due to woody plant encroachment (Fuhlendorf et al. 1997; Alofs and Fowler 2010; Alofs et al. 2014).

Savanna biodiversity

One of the pieces of evidence for the substantial extent of savannas on the eastern Edwards Plateau before non-Indigenous settlement is that herbaceous savanna species make up a large proportion of the plant species richness of the region. In the list of 71 plants endemic to the eastern Edwards Plateau, 39% grow only in unshaded sites, and hence are obligate savanna species (Carr 2022). The well-known Texas roadside wildflowers such as Texas bluebonnet (*Lupinus texensis* Hook.), evening primrose (*Oenothera speciosa* Nutt.), and other species adapted to sites with high disturbance frequency and intensity also occur in savannas. Regional savanna species also include large perennial species adapted to fire but not to frequent roadside mowing, such as Maximilian sunflower (*Helianthus maximiliani* Schrad.) and Lindheimer's muhly grass (*Muhlenbergia lindheimeri* Hitchc.). While many native wildflowers in this region need full or nearly full sun, very few can tolerate full shade (Carr 2022). The same is true of native grasses, almost all of which do not grow in present woodlands outside of glades. In contrast, the understory herbaceous vegetation in cedar brakes may consist of little but cedar sedge (*Carex planostachys* Kunze) (Wayne and Van Auken 2010).

Roles of fire in eastern Edwards Plateau shrublands

Fire also plays a well-recognized and critical role in the creation and maintenance of the shrublands of the eastern Edwards Plateau (D in Figs. 2 and 3). These shrublands have been studied primarily as breeding habitat for the black-capped vireo. Suitable nesting habitat consists of irregular clusters of shin oak and other thicket-forming shrubs and trees, interspersed with grasses, with approximately 30–60% woody cover 1–3 m in height (Grzybowski et al. 1994; Bailey and Thompson 2007). These communities are maintained by frequent fires: after a fire, the shrubs resprout and clusters reform after 1–5 years. Twenty to 25 years after the fire, woodlands form (Diamond 1997), which are unsuitable for the vireo. The best vireo habitat in central Texas is at Fort Cavazos due to repeated wildfires from military activity there (Cimprich and Kostecke 2006).

Plateau live oak and fire

Plateau live oak is one of the few species, other than Ashe juniper, that is common in woodlands, savannas, and shrublands. As mentioned above, its regeneration is failing. Live oak leaves, which are sclerophyllous, entire, and relatively flat, form a shallow, dense leaf litter that is less flammable than red oak litter (Kane et al. 2008). Varner et al. (2016) proposed that a closely related species, southern live oak (*Q. virginiana* Mill.), is a "fire avoider" that persists in fire-prone environments but does not contribute to vegetation-fire positive feedback loops. Instead, it produces low-flammability litter that reduces local fire effects in its immediate vicinity, thereby protecting it (Varner et al. 2016). In eastern Edwards Plateau savannas, Plateau live oak forms clusters (mottes) with low surface light levels and cool microclimates (Gass and Barnes 1998). However, fire apparently burns these clusters at temperatures similar to burns in nearby grasslands (Fonteyn et al. 1988). Close proximity to a mature Plateau live oak did not reduce fire effects on Ashe juniper seedling mortality (Noel and Fowler 2007). Varner et al.'s hypothesis may therefore not apply to Plateau live oak. Furthermore, Plateau live oak resprouts after being burned and can become common following fire (Reemts and Hansen 2008). Deer herbivory, rather than fire suppression, remains the most likely explanation for the failure of Plateau live oak regeneration in open savannas, but this needs study.

Management goals and methods

The communities discussed above provide a set of possible targets for land managers on the eastern Edwards Plateau. The choice of target community will depend, at least in part, on land management goals. Sometimes the goal is straightforward. If cattle forage is the primary consideration, a savanna with some large trees but almost no small woody plants is probably the target community. However, if deer hunting is also a ranch goal, a mix of savanna and woodland may be a more appropriate target (Armstrong and Young 2000).

Reduction of fire danger, especially in the wildland-urban interface, is another possible land management goal. Reduction of wildfire smoke is a related goal. The use of prescribed fire to achieve these goals, however, may be controversial if it is seen as degrading green belts and other natural areas.

When biodiversity restoration and preservation is the management goal, selecting a target community is complex. Golden-cheeked warblers require dense canopy cover and mature junipers for nest construction but also mature oaks for foraging (Pulich 1976; Marshall et al. 2013). However, maintaining these dense woodlands does not address the widespread failure of oak regeneration in this region, as discussed above, and will therefore ultimately make woodland sites unsuitable for this bird. Perhaps a period of surface fire to open the canopy to allow oak regeneration, followed by a fire-free period to allow the canopy to close, would be best for this bird. Reidy et al. (2021) found that after a surface fire, warbler usage of burned plots was reduced, but 6 years after burning, differences between control and treated plots were no longer detectable. The same fires also increased relative hardwood sapling abundance after 6 years.

No single community supports all the species of conservation concern. Golden-cheeked warblers require closed-canopy oak–juniper woodlands. Black-capped vireos require recently burned shrubland. Grassland birds require savannas. Bracted twistflower requires open-canopy woodland. Thus the greatest native biodiversity will be preserved by maintaining a mosaic landscape that includes all of these communities, each in sufficient quantity. When native biodiversity is the goal, a common target in North America is a landscape that includes the full set of communities and disturbance regimes present prior to colonization by non-Indigenous peoples (Hayward 2009). Unfortunately, as discussed above, the composition, patch sizes, and spatial arrangements of plant communities on the eastern Edwards Plateau at that time are uncertain.

Other management goals, beyond the scope of this paper, include a range of recreational uses, including hunting. They also may include improving water quantity and quality for runoff, infiltration, and aquifer recharge. Each of these may call for a different mix of plant communities.

As argued above, fires once created and maintained most of the potential target plant communities in this region. Prescribed fire is therefore a potential management tool for restoring and managing woodland, savanna, and shrubland communities in this region. The choice of fire frequency, fire season, and fire intensity will depend on the target community. For example, high-severity summer burns may be necessary to control King Ranch bluestem, while mixed severity surface fires with limited canopy torching may be adequate to maintain open mixed woodlands.

Safety, cost, logistics, intermittent county burn bans, and public opinion also factor into developing prescribed burn plans. It may be necessary to precede prescribed fire with thinning of woody fuels, especially Ashe juniper. Pre-fire removal of understory Ashe juniper can be an effective way to reduce ladder fuels and avoid a crown fire in a mixed woodland (e.g., Andruk et al. 2014). Pre-fire Ashe juniper removal in areas being restored to savanna has also been found to be effective (e.g., Kreuter et al. 2022).

Ranchers in the region commonly use mechanical removal of woody plants to maintain savannas, but some ranchers are beginning to use prescribed fire for the same purpose. Safety and liability issues, plus county-imposed burn bans are concerns, especially for the use of relatively intense prescribed fires. However, burn associations exist in the region (e.g., the Prescribed Burn Alliance of Texas: https://www.pbatexas.org/) and the use of fire as a management tool on private land may become more common.

Conclusion

Whatever the characteristics of past landscapes on the eastern Edwards Plateau, maximum native biodiversity will be supported by landscapes that include substantial amounts of mixed woodlands, savannas, and shrublands. We argue that fires are important for the maintenance of all these communities and that prescribed fire can be an effective tool in re-creating and managing each of them. Furthermore, surface fires are an essential part of what we argue is the lost open woodland community that is essential to support a significant part of native plant diversity. However, under present conditions of fire suppression combined with high deer populations, evidence indicates that both mixed woodlands and savannas are on trajectories to become low-diversity stands of Ashe juniper (cedar brakes). The future of these stands of Ashe juniper is unclear, but crown fires are one likely eventuality.

The optimum management of any given tract of land, including the choice of target communities, will depend on the particular goals of its managers and the constraints they face, as discussed above. However, in many cases there is insufficient knowledge to provide adequate guidance to them. We need to know much more about optimum fire frequencies, seasons, intensities, and spatial patterns in all of these communities—woodlands, savannas, and shrublands. We also need to better communicate this knowledge to the public, to land managers, and to everyone else concerned with land management of the eastern Edwards Plateau.

Acknowledgements
The eastern Edwards Plateau, including Austin, is part of the traditional homelands of the Tonkawa, Apache, and Comanche peoples. We thank the organizers of the 7th Fire in Eastern Oak Forests Conference for the invitation to deliver the talk that led to this paper. We thank B. Carr, Acme Botanical Services, botanist extraordinaire, for allowing us to use his data. For supporting the research of Fowler and her lab members over many years, we thank the US Fish and Wildlife Service, Texas Parks and Wildlife Department, the National Science Foundation, and the US Department of Agriculture. For providing access, information and in some cases material support over the same time period, we thank the managers and staff of many publicly owned sites and the owners of several private ranches. We thank C. Reemts, D. Grobert, José Panero, three anonymous reviewers, and the Associate Editor for comments on earlier versions of the manuscript.

Authors' contributions
NLF contributed the general structure and major hypotheses of the paper. NLF and REC jointly reviewed the literature and wrote the manuscript.

Funding
Preparation of this paper was in part supported by a grant from the U.S. Fish and Wildlife Service.

Availability of data and material
Not applicable.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Bill Carr gave NLF permission to use his data (Carr 2022). Charlotte Reemts gave REC permission to include a photograph (Fig. 3D).

Competing interests
The authors declare that they have no competing interests.

Author details
[1]Department of Integrative Biology, University of Texas at Austin, 2415 Speedway #C0930, Austin, TX, USA.

Received: 15 December 2023 Accepted: 26 May 2024
Published online: 24 June 2024

References

Abrams, M.D. 1992. Fire and the development of oak forests. *BioScience* 42: 346–353.

Alexander, H.D., C. Siegert, J.S. Brewer, J. Kreye, M.A. Lashley, J.K. McDaniel, A.K. Paulson, H.J. Renninger, and J.M. Varner. 2021. Mesophication of oak landscapes: Evidence, knowledge gaps, and future research. *BioScience* 71: 531–542.

Alofs, K.M., and N.L. Fowler. 2010. Habitat fragmentation caused by woody plant encroachment inhibits the spread of an invasive grass. *Journal of Applied Ecology* 47: 338–347.

Alofs, K.M., A.V. González, and N.L. Fowler. 2014. Local native plant diversity responds to habitat loss and fragmentation over different time spans and spatial scales. *Plant Ecology* 215: 1139–1151.

Amos, B.B., and F.R. Gehlbach, eds. 1988. *Edwards Plateau vegetation: Plant ecological studies in central Texas*. Waco: Baylor University Press.

Andruk, C.M., C. Schwope, and N.L. Fowler. 2014. The joint effects of fire and herbivory on hardwood regeneration in central Texas woodlands. *Forest Ecology and Management* 334: 193–200.

Armstrong, W.E., and E.L. Young. 2000. *White-tailed deer management in the Texas Hill Country*. Austin: Texas Parks and Wildlife Department.

Armstrong, W.E., D.E. Harmel, M.J. Anderegg, and M.S. Traweek. 1991. In *A checklist. Vegetation of the Kerr Wildlife Management Area and its preference by white-tailed deer*. Austin: Texas Parks and Wildlife Department, Fisheries and Wildlife Division, Wildlife Section.

Arthur, M.A., H.D. Alexander, D.C. Dey, C.J. Schweitzer, and D.L. Loftis. 2012. Refining the oak-fire hypothesis for management of oak-dominated forests of the eastern United States. *Journal of Forestry* 110: 257–266.

Bahre, C.J. 1991. *A legacy of change: Historic human impact on vegetation in the Arizona borderlands*. Tucson: University of Arizona Press.

Bailey, J.W., and F.R. Thompson III. 2007. Multiscale nest-site selection by black-capped vireos. *Journal of Wildlife Management* 71: 828–836.

Barnes, P.W., S.-Y. Liang, K.E. Jessup, P.A. Ramirez, L.E. D'Souza, K.G. Elliott, and P.L. Phillips. 2008. Ecological impacts of Ashe juniper on subtropical savanna parklands and woodlands. In *Western North American Juniperus communities: A dynamic vegetation type*, ed. O.W. Van Auken, 133–155. New York: Springer.

Behr, W.L., C. Andruk, C. Schwope, and N.L. Fowler. Benefits to native grasses from a summer fire still present 12 years later. *Natural Areas Journal*. In press

Bradley, B.A., and E. Fleishman. 2008. Relationships between expanding pinyon–juniper cover and topography in the central Great Basin, Nevada. *Journal of Biogeography* 35: 951–964.

Bray, W.L. 1904a. *Forest resources of Texas. Bulletin No. 47*. Washington: US Department of Agriculture, Bureau of Forestry.

Bray, W.L. 1904b. *The timber of the Edwards Plateau of Texas; its relations to climate, water supply, and soil. Bulletin No. 49*. Washington: US Department of Agriculture, Bureau of Forestry.

Briggs, J.M., G.A. Hoch, and L.C. Johnson. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. *Ecosystems* 5: 578–586.

Brockway, D.G., R.G. Gatewood, and R.B. Paris. 2002. Restoring grassland savannas from degraded pinyon-juniper woodlands: Effects of mechanical overstory reduction and slash treatment alternatives. *Journal of Environmental Management* 64: 179–197.

Brose, P.H., D.C. Dey, R.J. Phillips, and T.A. Waldrop. 2013. A meta-analysis of the fire-oak hypothesis: Does prescribed burning promote oak reproduction in eastern North America? *Forest Science* 59: 322–334.

Bryant, F.C., G.K. Launchbaugh, and B.H. Koerth. 1983. Controlling mature Ashe juniper in Texas with crown fires. *Journal of Range Management* 36: 165–168.

Buechner, H.K. 1944. The range vegetation of Kerr County, Texas, in relation to livestock and white-tailed deer. *The American Midland Naturalist* 31: 697–743.

Burton, J.A., S.W. Hallgren, and M.W. Palmer. 2010. Fire frequency affects structure and composition of xeric forests of eastern Oklahoma. *Natural Areas Journal* 30: 370–379.

Burton, J.A., S.W. Hallgren, S.D. Fuhlendorf, and D.M. Leslie Jr. 2011. Understory response to varying fire frequencies after 20 years of prescribed burning in an upland oak forest. *Plant Ecology* 212: 1513–1525.
Carlisle, J.D. 2020. *Apache Indians*. In *Handbook of Texas*, ed. Texas State Historical Association. Austin: Texas State Historical Association. https://www.tshaonline.org/handbook/entries/apache-indians. Accessed 14 Dec 2023.
Carr, W.R. 2022. Appendix 2: distribution of endemic plants in the Eastern Edwards Plateau relative to three categories of shading. In *2022 recommended land management for the Water Quality Protection Lands, Austin, Texas*, ed. U.P. Kreuter, B.P. Wilcox, J.W. Veldman, and N.L. May, A8-A9. Austin: City of Austin, Austin Water, Wildland Conservation Division, Water Quality Protection Lands.
Cartwright, W.J. 1966. The cedar chopper. *Southwestern Historical Quarterly* 70: 247–255.
Chapman, R.A., E. Heitzman, and M.G. Shelton. 2006. Long-term changes in forest structure and species composition of an upland oak forest in Arkansas. *Forest Ecology and Management* 236: 85–92.
Cimprich, D.A., and R.M. Kostecke. 2006. Distribution of black-capped vireo at Fort Hood, Texas. *The Southwestern Naturalist* 51: 99–102.
Clark, S.L., and S.W. Hallgren. 2003. Dynamics of oak (*Quercus marilandica* and *Q. stellata*) reproduction in an old-growth Cross Timbers forest. *Southeastern Naturalist* 2: 559–574.
Cordova, C.E., and W.C. Johnson. 2019. An 18 ka to present pollen- and phytolith-based vegetation reconstruction from Hall's Cave, south-central Texas, USA. *Quaternary Research* 92: 497–518.
Cory, B.J., F.L. Russell, and N. Keoshkerian. 2019. Canopy gap regime as a function of woodland age in the Kansas Cross Timbers. *Plant Ecology* 220: 887–900.
Cutter, B.E., and R.P. Guyette. 1994. Fire frequency on an oak-hickory ridgetop in the Missouri Ozarks. *American Midland Naturalist* 132: 393–398.
Denevan, W.M. 1992. The pristine myth: The landscape of the Americas in 1492. *Annals of the Association of American Geographers* 82: 369–385.
DeSantis, R.D., and S.W. Hallgren. 2011. Prescribed burning frequency affects post oak and blackjack oak regeneration. *Southern Journal of Applied Forestry* 35: 193–198.
DeSantis, R.D., S.W. Hallgren, T.B. Lynch, J.A. Burton, and M.W. Palmer. 2010. Long-term directional changes in upland *Quercus* forests throughout Oklahoma, USA. *Journal of Vegetation Science* 21: 606–615.
DeSantis, R.D., S.W. Hallgren, and D.W. Stahle. 2011. Drought and fire suppression lead to rapid forest composition change in a forest-prairie ecotone. *Forest Ecology and Management* 261: 1833–1840.
Dey, D.C., and G. Hartman. 2005. Returning fire to Ozark Highland forest ecosystems: Effects on advance regeneration. *Forest Ecology and Management* 217: 37–53.
Diamond, D.D., and C.D. True. 2008. Distribution of Juniperus woodlands in central Texas in relation to general abiotic site type. In *Western North American Juniperus communities: A dynamic vegetation type*, ed. O.W. Van Auken, 48–57. New York: Springer.
Diamond, D.D. 1997. *An old-growth definition for western juniper woodlands: Texas Ashe juniper dominated or codominated communities. GTR SRS-15*. Asheville: US Department of Agriculture, Forest Service, Southern Research Station.
Fan, Z., Z. Ma, D.C. Dey, and S.D. Roberts. 2012. Response of advance reproduction of oaks and associated species to repeated prescribed fires in upland oak-hickory forests, Missouri. *Forest Ecology and Management* 266: 160–169.
Fonteyn, P.J., M.W. Stone, M.A. Yancy, J.T. Baccus, and N.M. Nadkarni. 1988. Determination of community structure by fire. In *Edwards Plateau vegetation: Plant ecological studies in central Texas*, ed. B.B. Amos and F.R. Gehlbach, 79–90. Waco: Baylor University Press.
Foster, J.H. 1917. The spread of timbered areas in central Texas. *Journal of Forestry* 15: 442–445.
Fowler, N.L. 1988. Grasslands, nurse trees, and coexistence: Three views of community structure. In *Edwards Plateau vegetation: Plant ecological studies in central Texas*, ed. B.B. Amos and F.R. Gehlbach, 91–100. Waco: Baylor University Press.
Fowler, N.L., and B. Beckage. 2019. Savannas of North America. In *Savanna woody plants and large herbivores*, ed. P.F. Scogings and M. Sankaran, 123–150. Hoboken: John Wiley & Sons Ltd.
Fowler, N.L., and K. Clay. 1995. Environmental heterogeneity, fungal parasitism and the demography of the grass *Stipa leucotricha*. *Oecologia* 103: 55–62.
Fowler, N.L., and D.W. Dunlap. 1986. Grassland vegetation of the eastern Edwards Plateau. *The American Midland Naturalist* 115: 146–155.
Fowler, N.L., and M.T. Simmons. 2009. Savanna dynamics in central Texas: Just succession? *Applied Vegetation Science* 12: 23–31.
Fowler, N.L., A. Center, and E.A. Ramsey. 2012. *Streptanthus bracteatus* (Brassicaceae), a rare annual woodland forb, thrives in less cover: Evidence of a vanished habitat? *Plant Ecology* 213: 1511–1523.
Fuhlendorf, S.D., and F.E. Smeins. 1997. Long-term vegetation dynamics mediated by herbivores, weather and fire in a *Juniperus-Quercus* savanna. *Journal of Vegetation Science* 8: 819–828.
Fuhlendorf, S.D., F.E. Smeins, and W.E. Grant. 1996. Simulation of a fire-sensitive ecological threshold: A case study of Ashe juniper on the Edwards Plateau of Texas, USA. *Ecological Modelling* 90: 245–255.
Fuhlendorf, S.D., F.E. Smeins, and C.A. Taylor. 1997. Browsing and tree size influences on Ashe juniper understory. *Journal of Range Management* 50: 507–512.
Gabbard, B.L., and N.L. Fowler. 2007. Wide ecological amplitude of a diversity-reducing invasive grass. *Biological Invasions* 9: 149–160.
Gao, P., A.J. Terando, J.A. Kupfer, J.M. Varner, M.C. Stambaugh, T.L. Lei, and J.K. Hiers. 2021. Robust projections of future fire probability for the conterminous United States. *Science of the Total Environment* 789: 147872.
Gass, L., and P.W. Barnes. 1998. Microclimate and understory structure of live oak (*Quercus fusiformis*) clusters in central Texas, USA. *The Southwestern Naturalist* 43: 183–194.
González, A.V. 2010. *Dynamics of woody plant encroachment in Texas savannas: density dependence, environmental heterogeneity, and spatial patterns*. Ph.D. dissertation. University of Texas at Austin.
Goyne, M.A. 1991. *A life among the Texas flora: Ferdinand Linheimer's letters to George Engelmann*. College Station: Texas A&M University Press.
Griffith, G.E., S.A. Bryce, J.M. Omernik, J.A. Comstock, A.C. Rogers, B. Harrison, S.L. Hatch, and D. Bezanson. 2004. *Ecoregions of Texas*. US Environmental Protection Agency. https://gaftp.epa.gov/EPADataCommons/ORD/Ecoregions/tx/tx_eco_lg.pdf. Accessed 14 Dec 2023.
Groce, J.E., H.A. Mathewson, M.L. Morrison, and N. Wilkins. 2010. *Scientific evaluation for the 5-year status review of the golden-cheeked warbler. Prepared for the US Fish and Wildlife Service*. College Station: Texas A&M University, Institute of Renewable Natural Resources and Department of Wildlife and Fisheries Science.
Grzybowski, J.A., D.J. Tazik, and G.D. Schnell. 1994. Regional analysis of black-capped vireo breeding habitats. *The Condor* 96: 512–544.
Hamilton, H., R.L. Smyth, B.E. Young, T.G. Howard, C. Tracey, S. Breyer, D.R. Cameron, A. Chazal, A.K. Conley, C. Frye, and C. Schloss. 2022. Increasing taxonomic diversity and spatial resolution clarifies opportunities for protecting US imperiled species. *Ecological Applications* 32: e2534.
Hanberry, B.B., J.M. Kabrick, and H.S. He. 2014. Densification and state transition across the Missouri Ozarks landscape. *Ecosystems* 17: 66–81.
Havill, S., S. Schwinning, and K.G. Lyons. 2015. Fire effects on invasive and native warm-season grass species in a North American grassland at a time of extreme drought. *Applied Vegetation Science* 18: 637–649.
Hayward, M.W. 2009. Conservation management for the past, present and future. *Biodiversity and Conservation* 18: 765–775.
Hicks, R.A., and W.A. Dugas. 1998. Estimating Ashe juniper leaf area from tree and stem characteristics. *Journal of Range Management* 51: 633–637.
Johnson, D.D., and R.F. Miller. 2006. Structure and development of expanding western juniper woodlands as influenced by two topographic variables. *Forest Ecology and Management* 229: 7–15.
Kane, J.M., J.M. Varner, and J.K. Hiers. 2008. The burning characteristics of southeastern oaks: Discriminating fire facilitators from fire impeders. *Forest Ecology and Management* 256: 2039–2045.
Knapp, B.O., K. Stephan, and J.A. Hubbart. 2015. Structure and composition of an oak-hickory forest after over 60 years of repeated prescribed burning in Missouri, USA. *Forest Ecology and Management* 344: 95–109.
Kreuter, U.P., B.P. Wilcox, J.W. Veldman, and N.L. May. 2022. *2022 recommended land management for the Water Quality Protection Lands, Austin, Texas. Submitted by the Department of Ecology and Conservation Biology, Texas A&M University*. Austin: City of Austin, Austin Water, Wildland Conservation Division, Water Quality Protection Lands.

Leonard, W.J., and O.W. Van Auken. 2013. Light levels and herbivory partially explain the survival, growth, and niche requirements of *Streptanthus bracteatus* A. Gray (bracted twistflower, Brassicaceae), a rare central Texas endemic. *Natural Areas Journal* 33: 276–285.

Lipscomb, C.A. 2020. Comanche Indians. In *Handbook of Texas*, ed. Texas State Historical Association. Austin: Texas State Historical Association. https://www.tshaonline.org/handbook/entries/comanche-indians. Accessed 14 Dec 2023.

Maginel, C.J., B.O. Knapp, J.M. Kabrick, and R.M. Muzika. 2019. Landscape- and site-level responses of woody structure and ground flora to repeated prescribed fire in the Missouri Ozarks. *Canadian Journal of Forest Research* 49: 1004–1014.

Marshall, M.E., M.L. Morrison, and R.N. Wilkins. 2013. Tree species composition and food availability affect productivity of an endangered species: The golden-cheeked warbler. *The Condor* 115: 882–892.

McCaw, W.M., D.M. Grobert, S.B. Brown, S. Strickland, G.A. Thompson, G. Gillman, L.M. Ball, and C.D. Robinson. 2018. Seasonal patterns and drivers of Ashe juniper foliar live fuel moisture and relevance to fire planning. *Fire Ecology* 14: 50–64.

McEwan, R.W., J.M. Dyer, and N. Pederson. 2011. Multiple interacting ecosystem drivers: Toward an encompassing hypothesis of oak forest dynamics across eastern North America. *Ecography* 34: 244–256.

McGreevy, E. 2021. *Wanted! mountain cedar: Dead and alive*. Austin: Spicewood Publications.

Miller, R.F., and J.A. Rose. 1999. Fire history and western juniper encroachment in sage-brush steppe. *Journal of Range Management* 52: 550–559.

Murray, D.B., J.D. White, and J. Yao. 2013. Loss of neighbors, fire, and climate effects on Texas red oak growth in a juniper-dominated woodland ecosystem. *The American Midland Naturalist* 170: 348–369.

Newcomb, W.W., Jr. 1961. *The Indians of Texas from prehistoric to modern times*. Austin: University of Texas Press.

Nielsen-Gammon, J.W. 2012. The 2011 Texas drought. *Texas Water Journal* 3: 59–95.

Nielsen-Gammon, J., S. Holman, A. Buley, S. Jorgensen, J. Escobedo, C. Ott, J. Dedrick, and A. Van Fleet. 2021. *Assessment of historic and future trends of extreme weather in Texas, 1900–2036: 2021 update. Document OSC-202101*. College Station: Texas A&M University, Office of the Texas State Climatologist.

Noel, J.M., and N.L. Fowler. 2007. Effects of fire and neighboring trees on Ashe juniper. *Rangeland Ecology and Management* 60: 596–603.

Northup, A.P., T.H. Keitt, and C.E. Farrior. 2021. Cavitation-resistant junipers cease transpiration earlier than cavitation vulnerable oaks under summer dry conditions. *Ecohydrology* 15: e2337.

Novak, E.N., M. Bertelsen, D. Davis, D.M. Grobert, K.G. Lyons, J.P. Martina, W.M. McCaw, M. O'Toole, and J.W. Veldman. 2021. Season of prescribed fire determines grassland restoration outcomes after fire exclusion and overgrazing. *Ecosphere* 12: e03730.

Nowacki, G.J., and M.D. Abrams. 2008. The demise of fire and "mesophication" of forests in the eastern United States. *BioScience* 58: 123–138.

O'Donnell, L. 2019. *Historical ecology of the Texas Hill Country*. Austin: City of Austin, Wildland Conservation Division, Balcones Canyonlands Preserve. https://www.researchgate.net/profile/Lisa-Odonnell-4/publication/331582514_HISTORICAL_ECOLOGY_OF_THE_TEXAS_HILL_COUNTRY/links/5f159ebd92851c1eff219878/HISTORICAL-ECOLOGY-OF-THE-TEXAS-HILL-COUNTRY.pdf. Accessed 15 Dec 2023.

Olmsted, F.L. 1857. *A journey through Texas: Or a saddle-trip on the southwestern frontier*. New York: Dix, Edwards, and Co. Prescribed Burn Alliance of Texas. https://www.pbatexas.org/ . Accessed 14 Dec 2023.

Pulich, W.M. 1976. *The golden-cheeked warbler: a bioecological study*. Austin: Texas Parks and Wildlife Department.

Ratajczak, Z., J.B. Nippert, and S.L. Collins. 2012. Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology* 93: 697–703.

Reemts, C.M., and L.L. Hansen. 2013. Short-term effects of repeated wildfires in oak-juniper woodlands. *Fire Ecology* 9: 64–79.

Reemts, C.M., W.M. McCaw, T.A. Greene, and M.T. Simmons. 2019. Short-term control of an invasive C4 grass with late-summer fire. *Rangeland Ecology and Management* 72: 182–188.

Reemts, C.M., and L.L. Hansen. 2008. Slow recolonization of burned oak–juniper woodlands by Ashe juniper (Juniperus ashei): ten years of succession after crown fire. *Forest Ecology and Management* 255: 1057–1066.

Reemts, C.M., C. Picinich, and T.A. Greene. 2021. Late-summer fire provides long-term control of the invasive Old World bluestem (*Bothriochloa ischaemum*). *Southeastern Naturalist* 20: 589–601.

Reidy, J.L., F.R. Thompson III., C. Schwope, S. Rowin, and J.M. Mueller. 2016. Effects of prescribed fire on fuels, vegetation, and golden-cheeked warbler (*Setophaga chrysoparia*) demographics in Texas juniper-oak woodlands. *Forest Ecology and Management* 376: 96–106.

Reidy, J.L., F.R. Thompson III., S. Rowin, C. Schwope, and J.M. Mueller. 2021. Effects of prescribed fire on fuels, vegetation, and golden-cheeked warbler (*Setophaga chrysoparia*) demographics in Texas juniper-oak woodlands: An update six years post-fire. *Forest Ecology and Management* 492: 119191.

Rice, E.L., and W.T. Penfound. 1959. The upland forests of Oklahoma. *Ecology* 40: 593–608.

Roemer, F. 1935. *Texas, with particular reference to German immigration and the physical appearance of the country. Described through personal observation, by Dr. Ferdinand Roemer; Translated from the German by Oswald Mueller*, 1983rd ed. San Antonio: Standard Printing Company.

Ruckman, E.M., S. Schwinning, and K.G. Lyons. 2011. Effects of phenology at burn time on post-fire recovery in an invasive C4 grass. *Restoration Ecology* 20: 756–763.

Russell, F.L., and N.L. Fowler. 1999. Rarity of oak saplings in savannas and woodlands of the eastern Edwards Plateau, Texas. *The Southwestern Naturalist* 44: 31–41.

Russell, F.L., and N.L. Fowler. 2002. Failure of adult recruitment in *Quercus buckleyi* populations on the eastern Edwards Plateau, Texas. *The American Midland Naturalist* 148: 201–217.

Russell, F.L., and N.L. Fowler. 2004. Effects of white-tailed deer on the population dynamics of acorns, seedlings and small saplings of *Quercus buckleyi*. *Plant Ecology* 173: 59–72.

Ryan, K.C., E.E. Knapp, and J.M. Varner. 2013. Prescribed fire in North American forests and woodlands: History, current practice, and challenges. *Frontiers in Ecology and the Environment* 11: e15–e24.

Scholtz, R., S.D. Fuhlendorf, and S.R. Archer. 2018. Climate-fire interactions constrain potential woody plant cover and stature in North American Great Plains grasslands. *Global Ecology and Biogeography* 27: 936–945.

Short, M.F., M.C. Stambaugh, and D.C. Dey. 2019. Prescribed fire effects on oak woodland advance regeneration at the prairie-forest border in Kansas, USA. *Canadian Journal of Forest Research* 49: 1570–1579.

Simmons, M.T., S. Windhager, P. Power, J. Lott, R.K. Lyons, and C. Schwope. 2007. Selective and non-selective control of invasive plants: The short-term effects of growing-season prescribed fire, herbicide, and mowing in two Texas prairies. *Restoration Ecology* 15: 662–669.

Smeins, F.E., and S.D. Fuhlendorf. 1997. Biology and ecology of Ashe juniper. In *Juniper Symposium 1997. Technical Report 97–1*, ed. C.A. Taylor, 3.33–3.47. College Station: Texas A&M University AgriLife Extension Service.

Smeins, F.E. 1980. Natural role of fire on the Edwards Plateau. In *Proceedings: Prescribed burning of the Edwards Plateau*, ed. L.D. White, 4–16. College Station: Texas A&M University, Texas Agriculture Extension Service.

Snow, D.R. 1995. Microchronology and demographic evidence relating to the size of pre-Columbian North American Indian populations. *Science* 268: 1601–1604.

Sparks, J.C., M.C. Stambaugh, and E.L. Keith. 2012. Restoring fire suppressed Texas oak woodlands to historic conditions using prescribed fire. In *Proceedings of the 4th Fire in Eastern Oak Forests Conference, GTR-NRS-P-102*, ed. D.C. Dey, M.C. Stambaugh, S.L. Clark, and C.J. Schweitzer, 127–141. Newtown Square: US Department of Agriculture, Forest Service, Northern Research Station.

Stambaugh, M.C., J.M. Marschall, and R.P. Guyette. 2014a. Linking fire history to successional changes of xeric oak woodlands. *Forest Ecology and Management* 320: 83–95.

Stambaugh, M.C., J.C. Sparks, and E.R. Abadir. 2014b. Historical pyrogeography of Texas, USA. *Fire Ecology* 10: 72–89.

Sullivan, J. 1993. *Juniperus ashei*. In *Fire Effects Information System*. Fort Collins: US Department of Agriculture Rocky Mountain Research Station, Fire Sciences Laboratory. https://www.fs.usda.gov/database/feis/plants/tree/junash/all.html. Accessed 9 March 2024.

Taylor, C.A., Jr., D. Twidwell, N.E. Garza, C. Rosser, J.K. Hoffman, and T.D. Brooks. 2012. Long-term effects of fire, livestock herbivory removal, and weather variability in Texas semiarid savanna. *Rangeland Ecology and Management* 65: 21–30.

Taylor, W.T.T., P. Librado, M. Hunska Tašunke Icu, C. Shield Chief Glover, J. Arterberry, A. Luta Wiŋ, A. Nujipi, T. Omniya, M. Gonzalez, B. Means, S. High Crane, et al. 2023. Early dispersal of domestic horses into the Great Plains and northern Rockies. *Science* 379: 1316–1323.

Thomas, J.A., J.D. White, and D.B. Murray. 2016. Tree species influence woodland canopy characteristics and crown fire potential. *Forest Ecology and Management* 362: 169–176.

TPWD (Texas Parks and Wildlife Department). 2023. *Texas deer population forecasted to rebound from drought conditions*. *News Release October 27, 2023*. Austin: Texas Parks and Wildlife Department. https://tpwd.texas.gov/newsmedia/releases/?req=20231027b. Accessed 14 Dec 2023.

Texas Parks and Wildlife Department. n.d. *Landscape ecology program: by ecoregion (vector)*. Austin: Texas Parks and Wildlife Department. https://tpwd.texas.gov/gis/programs/landscape-ecology/. Accessed 20 Oct 2023.

Twidwell, D., W.E. Rogers, S.D. Fuhlendorf, C.L. Wonkka, D.M. Engle, J.R. Weir, U.P. Kreuter, and C.A. Taylor Jr. 2013. The rising Great Plains fire campaign: Citizens' response to woody plant encroachment. *Frontiers in Ecology and the Environment* 11: e64–e71.

Twidwell, D., W.E. Rogers, C.L. Wonkka, C.A. Taylor Jr., and U.P. Kreuter. 2016. Extreme prescribed fire during drought reduces survival and density of woody resprouters. *Journal of Applied Ecology* 53: 1585–1596.

USDA NRCS (US Department of Agriculture Natural Resources Conservation Service). 2014. *Juniperus ashei* J. Buchholz. https://plants.usda.gov/home/plantProfile?symbol=JUAS. Accessed 8 March 2024.

USFWS (US Fish and Wildlife Service). 2018. Endangered and threatened wildlife and plants; removing the black-capped vireo from the federal list of endangered and threatened wildlife. *Federal Register* 83 (73): 16228–16242.

Van Auken, O.W. 1993. Size distribution patterns and potential population change of some dominant woody species of the Edwards Plateau region of Texas. *The Texas Journal of Science* 45: 199–210.

Van Auken, O.W. 2000. Characteristics of intercanopy bare patches in *Juniperus* woodlands of the southern Edwards Plateau, Texas. *The Southwestern Naturalist* 45: 95–110.

Van Auken, O.W., and D.C. McKinley. 2008. Structure and composition of Juniperus communities and factors that control them. In *Western North American Juniperus communities: A dynamic vegetation type*, ed. O.W. Van Auken, 19–47. New York: Springer.

Van Auken, O.W., A.L. Ford, and A. Stein. 1979. A comparison of some woody upland and riparian plant communities of the southern Edwards Plateau. *The Southwestern Naturalist* 24: 165–180.

Van Auken, O.W., A.L. Ford, and J.L. Allen. 1981. An ecological comparison of upland deciduous and evergreen forests of central Texas. *American Journal of Botany* 68: 1249–1256.

Van Auken, O.W., J.T. Jackson, and P.N. Jurena. 2004. Survival and growth of *Juniperus* seedlings in *Juniperus* woodlands. *Plant Ecology* 175: 245–257.

Van Auken, O.W., J.K. Bush, D.L. Taylor, and J.R. Singhurst. 2023. Lack of woody species recruitment in isolated deep canyon deciduous woodlands in central Texas, USA. *The Journal of the Torrey Botanical Society* 150: 525–537.

Vander Yacht, A.L., P.D. Keyser, S.A. Barrioz, C. Kwit, M.C. Stambaugh, W.K. Clatterbuck, and R. Jacobs. 2020. Litter to glitter: Promoting herbaceous groundcover and diversity in mid-southern USA oak forests using canopy disturbance and fire. *Fire Ecology* 16: 17.

Varner, J.M., J.M. Kane, J.K. Hiers, J.K. Kreye, and J.W. Veldman. 2016. Suites of fire-adapted traits of oaks in the southeastern USA: Multiple strategies for persistence. *Fire Ecology* 12: 48–64.

Wayne, E.R., and O.W. Van Auken. 2010. Herbaceous cover and biomass of *Carex planostachys* in *Juniperus ashei* woodlands of central Texas. *The Southwestern Naturalist* 55: 434–441.

Whiting, C.V. 2022. *Ecological relationships between invasive grasses, native grasses, and wildfire*. Ph.D. dissertation. University of Texas at Austin.

Wink, R.L., and H.A. Wright. 1973. Effects of fire on an Ashe juniper community. *Journal of Range Management* 26: 326–329.

Yager, L.Y., and F.E. Smeins. 1999. Ashe juniper (*Juniperus ashei*: Cupressaceae) canopy and litter effects on understory vegetation in a juniper-oak savanna. *The Southwestern Naturalist* 44: 6–16.

Yao, J., D.B. Murray, A. Adhikari, and J.D. White. 2012. Fire in a sub-humid woodland: The balance of carbon sequestration and habitat conservation. *Forest Ecology and Management* 280: 40–51.

Zippin, D.Z. 1997. *Herbivory and the population biology of a rare annual plant, the bracted twistflower (*Streptanthus bracteatus*)*. Ph.D. dissertation. University of Texas at Austin.

Publisher's Note