Crown fires remove a fire-sensitive canopy dominant from oak-juniper woodlands

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Research Article

Keywords: Ashe juniper, Edwards Plateau, Juniperus ashei, oak-juniper woodlands, oak regeneration, repeated fires

Posted Date: January 22nd, 2024

DOI: https://doi.org/10.21203/rs.3.rs-3861143/v1

Version of Record: A version of this preprint was published at Fire Ecology on August 22nd, 2024. See the published version at https://doi.org/10.1186/s42408-024-00311-w.

Abstract

Background

In central Texas, re-sprouting oaks (*Quercus* spp.) co-occur with the non-resprouting Ashe juniper (*Juniperus ashei*). The region's mature oak-juniper woodlands are the only nesting habitat for the endangered golden-cheeked warbler (*Setophaga chrysoparia*). We studied long-term recovery of woodland structure and species composition after single and repeated crown fires on three site types (mesas and slopes with shallow soils and deeper savanna soils).

Results

Understory density of non-juniper species, including oaks, was up to four times higher after the second fire compared to the first fire for the first 2–3 years. On once-burned sites, non-juniper tree density exceeded unburned levels after 14–24 years, indicating successful replacement of hardwood trees (24 years vs unburned, mesa: 481 ± 254 vs 155 ± 137 stems ha^{-1}; slope: 910 ± 330 vs 251 ± 103 stems ha^{-1}; deep: 679 ± 250 vs 251 ± 103 stems ha^{-1}). Non-juniper tree basal area recovered more slowly on slopes and deep soils than on mesas but reached unburned levels by 14–24 years (24 years vs unburned, mesa: 2 ± 1 vs 1 ± 2 m^2 ha^{-1}; slope: 5 ± 2 vs 3 ± 2 m^2 ha^{-1}; deep: 6 ± 2 vs 8 ± 9 m^2 ha^{-1}). Ashe juniper, however, remained almost completely absent from burned woodlands. After 24 years, juniper tree density on once-burned sites was much lower compared to unburned sites (mesa: 6 ± 10 vs 691 ± 410 stems ha^{-1}; slope: 20 ± 17 vs 731 ± 183 stems ha^{-1}; deep: 50 ± 71 vs 317 ± 297 stems ha^{-1}). Juniper trees were still absent from twice-burned sites in year 11 and understory density was recovering more slowly, at least on slopes (one fire: 224 ± 206 stems ha^{-1}; two fires: 26 ± 47 stems ha^{-1}). Juniper recovery was explained in part by distance to the wildfire perimeter, suggesting that regeneration is limited by dispersal.

Conclusions

Oaks and other species successfully recruited after one and two fires, likely due to low deer densities. Ashe juniper recovered very slowly, especially after the second fire, and juniper recovery was limited by dispersal. Our data show that mixed woodlands in the Edwards Plateau can only exist in areas with very long intervals between crown fires. Given the long-term consequences of crown fires for golden-cheeked warbler habitat, maintenance of mature oak-juniper woodlands will require protection from extreme fire.

BACKGROUND

Fire shapes the distribution of ecosystems as well as the structure and species composition of plant communities (He et al. 2019; Hanberry et al. 2020). Species in fire-prone systems are usually adapted to the historical fire regime, which can range from frequent, low-severity surface fires to infrequent, high-

severity crown fires (Keeley et al. 2011). Common adaptations to fire include the ability to resprout after fire, a persistent seedbank, or morphological adaptations that prevent fire damage, such as thick bark (Keeley 2006; Hmielowski et al. 2014; Varner et al. 2016).

In central Texas, re-sprouting oaks (*Quercus* spp.) co-occur with the non-resprouting Ashe juniper (*Juniperus ashei* J. Buchholz). The pre-settlement fire regime of central Texas is debated but likely differed among ecological communities (Fowler and Carden 2024). Grasslands, savannas, and open woodlands had relatively frequent fire (e.g., Murray et al. 2013) but co-dominance by Ashe juniper in dense woodlands requires long fire-free intervals (Diamond 1997; Reemts and Hansen 2008). Endangered or rare species in the region include the woodland-obligate golden-cheeked warbler (*Setophaga chrysoparia* Sclater & Salvin), the shrubland-obligate black-capped vireo (*Vireo atricapilla* Woodhouse), and the light-loving bracted twistflower (*Streptanthus bracteatus* A. Gray). The differing habitat requirements of these (and other) species suggest that the region was a mosaic of fire-maintained and fire-sheltered habitats (Baccus et al. 2007; Fowler et al. 2012; Leonard and Auken 2013; Vázquez-Miranda et al. 2015; Fowler and Carden 2024).

Managers of oak-juniper woodlands must balance the habitat requirements of golden-cheeked warblers with a lack of oak recruitment and high fire risk. High deer densities limit recruitment of oaks and other hardwoods to the canopy (Russell and Fowler 2004; Andruk et al. 2014; Van Auken et al. 2023). Low- to moderate-severity prescribed fires in woodlands can reduce understory density and increase oak regeneration (primarily from resprouting), but do not reduce fuel loads (Yao et al. 2012; Reidy et al. 2016, 2021). However, any mortality of canopy trees reduces habitat quality for golden-cheeked warblers (Reidy et al. 2016, 2021).

In contrast to relatively low-severity prescribed fires, crown fires cause major changes in woodland structure and composition. We have previously shown that Ashe juniper was largely absent for the first 10 years after crown fire (Reemts and Hansen 2008) and that repeated crown fires slowed juniper recovery even more (Reemts and Hansen 2013). Here we provide a long-term follow up to our original studies (24 years after the first fire and 11 years after the second fire) to examine the long-term consequences of crown fires in oak-juniper woodlands. Specifically, we are interested in comparing woodland structure and composition, especially the abundance of Ashe juniper, in once-burned and twice-burned sites with unburned woodlands.

METHODS

Study Area

Fort Cavazos Military Reservation is an ~ 86,000 ha Army installation in Bell and Coryell Counties, Texas. Common plant communities include oak-Ashe juniper woodlands and oak shrublands on slopes and mesa tops. Grasslands are found in the valleys, on rolling lowlands, and on slopes with very high (~ annual) fire frequency. Savannas dominated by Texas live oak (*Quercus fusiformis* Small) and post oak

(*Q. stellata* Wagnenh.) occur in the lowlands and on deeper soils on the mesas. Fort Cavazos includes breeding habitat for a federally endangered songbird (the golden-cheeked warbler) and a recently delisted songbird (the black-capped vireo).

Fire descriptions

On 21 February 1996, military training activities started three grassland fires. Due to hot, dry, and windy conditions, the fires moved into adjacent woodlands, where they burned mostly as crown fires. By the time the fires were controlled on 7 March, they had burned more than 4000 ha of woodlands. The second fire, which burned from 3–12 April 2009, was smaller (608 ha; 360 ha overlapping with first fire). The Palmer Z-index was extreme in February 1996 and mid-range in April 2009. Burn severity in the 2009 fire was lower than in the same areas during the 1996 fire, perhaps due to a combination of less extreme drought and lower fuel loads (Reemts and Hansen 2013).

Vegetation sampling

Following the first fire, we randomly located 101 permanent transects in moderately to severely burned oak-juniper woodlands. We sampled most of these “once-burned” transects annually from 1996 to 2002 and again in 2005, 2010, and 2020; a few transects were first sampled in 1997 (Table 1). After the second fire, we sampled all “twice-burned” transects annually from 2009–2011 and again in 2020. We sampled “unburned” transects in mature woodlands located adjacent to the burned areas on similar slopes and soils in 2001, 2005, 2010, and 2020. While the fire history of these unburned woodlands is not known, all are present in aerial imagery taken in 1938 and appear similar in maturity to the woodlands subsequently burned in 1996. Tree skeletons in the burned areas were also of similar size to trees in the unburned areas.

Table 1
Sample timing and time since fire for the first fire (February 1996) and the second fire (April 2009) at Fort Cavazos, Texas, USA. Num. transects provides total number of transects; transects by soil type are in parentheses (mesa, slope, and deep). – indicates that transects were not sampled in that year. No deep soil transects were burned in the second fire.

Sample year	Time since first fire	Num. transects	Time since second fire	Num. transects
1996	0	58 (23, 23, 12)	–	–
1997	1	65 (30, 23, 12)	–	–
1998	2	65 (30, 23, 12)	–	–
1999	3	65 (30, 23, 12)	–	–
2000	4	65 (30, 23, 12)	–	–
2001	5	65 (30, 23, 12)	–	–
2002	6	65 (30, 23, 12)	–	–
2005	9	65 (30, 23, 12)	–	–
2009	–	–	0	19 (8, 11)
2010	14	46 (22, 12, 12)	1	19 (8, 11)
2011	–	–	2	19 (8, 11)
2020	24	46 (22, 12, 12)	11	19 (8, 11)
2020	unburned	36 (20, 11, 5)		

Transects were classified into three groups based on topographic position and soil type, which influence the dominant plant communities. “Mesa” transects, found on flat-topped hills, were on Eckrant cobbly silty clay soils with shallow slopes (< 8º slope, Low Stony Hill ecological site). On Fort Cavazos, the vegetation on this soil type includes shin oak (*Quercus sinuata* Walter var. *breviloba* [Torr.] C.H. Mull) shrublands and shin oak-Ashe juniper woodlands. “Slope” transects were on sloped Real gravelly clay loam soils (5–30º slope, Steep Adobe ecological site) and were slightly more mesic. This soil series supports a more diverse woodland, co-dominated by Buckley oak (*Q. buckleyi* Nixon & Dorr) and Ashe juniper, that also includes shin oak, Texas ash (*Fraxinus albicans* Buckley), and Texas live oak in the canopy. In mesic canyons on the same soils, Ashe juniper dominance decreases and additional species, such as bigtooth maple (*Acer grandidentatum* Nutt.) and chinkapin oak (*Q. muehlenbergii* Engelm.), are added. Finally, “deep” soil transects were on flat sites with Evant silty clay (1–3º slope, Redland ecological site). These soils are slightly deeper than mesa soils (15–33 cm to bedrock vs 10–30 cm for mesa soils) and have fewer bedrock outcrops. Savannas on these soils are dominated by post oak and blackjack oak (*Q. marilandica* Muencch.); woodlands are created by juniper encroachment.

Transects were 110 m long and followed either a random bearing (for level sites) or were perpendicular to the slope (i.e., followed contour lines). Plots were located at 10 m intervals along the transects and 7

of the 11 possible plots were randomly selected for sampling. From 1996 to 2002, we re-randomized plot selection every year. Starting in 2005, we used the plot locations from the first sampling year on each transect.

Within the plots, we recorded stem density of all woody species in four categories: “seedlings” (< 0.3 m tall), “shrubs” (between 0.3 and 1.8 m tall), “saplings” (≥ 1.8 m tall, < 5 cm diameter at breast height, dbh) and “trees” (≥ 5 cm dbh). We did not distinguish between resprouts from top-killed individuals and regeneration from seed. We counted the stem density of seedlings, shrubs, and saplings in 5 m x 5 m plots (Figure S1). Stems that split above the root crown were counted as one. Saplings were counted in five dbh classes: 0–0.9, 1.0–1.9, 2.0–2.9, 3.0–3.9 and 4.0–4.9 cm.

We sampled trees in 10 m x 10 m plots. From 1996 to 2002, we recorded the stem density of trees in 5- or 10-cm dbh classes. Starting in 2005, we recorded dbh to the nearest 0.1 cm for each tree. If saplings or trees branched above the root crown, only the largest stem was measured and counted. In our study site, Ashe juniper is the only species that usually has multiple branches rather than multiple stems; Ashe juniper is therefore under-represented when density is converted to basal area.

Statistical analyses

While we sampled multiple transects in the burned areas, these transects represent subsamples of the two wildfire events and we lack true replication (Wester 1992). However, our data are still useful to document vegetation responses for comparison with future studies elsewhere in the region.

Analyses were conducted in R 4.3.2 (R Core Team 2024). Graphs were produced using the ggplot2 and ggpubr packages (Wickham 2016; Kassambara 2023).

To analyze woodland structure, we calculated averages by transect for stem density of the understory (seedlings, shrubs, and saplings; all stems < 5 cm dbh or < 1.8 m tall) and overstory (trees, all stems ≥ 5 cm dbh), as well as tree basal area. For data before 2005, tree basal area calculations used the mid-point of the size class; later data used the measured dbh. Calculations were done for Ashe juniper and for all other species (referred to as “non-juniper” species).

Data were analyzed using linear mixed-effects models (lmerTest package, Kuznetsova et al. 2017) with a Gaussian distribution. The model for each response variable differed (see descriptions below and Table 2). Potential fixed effects included soil type (mesa, slope, and deep), number of fires (one, two, and unburned), and time since fire. Because of the long gaps in sampling times, time since fire was always treated as a categorical variable with each time/year as a separate value (Table 1). To account for repeated sampling, we included a random intercept for transect. Following analysis, visual inspection confirmed that all models’ residuals were normally distributed.

Table 2

Linear models tested for each response variable (with data averaged by transect). All models included a random intercept for transect and used data from unburned sites in 2020. Non-juniper species include all woody plants except Ashe juniper. Soil = soil type/topographic position (mesa, slope, and deep). TSF = time since fire; categorical variable that includes "unburned" as a category. Number of fires = one, two, or unburned. Analyses with twice-burned sites include only mesa and slope soils (no deep soil transects burned in the second fire) and compare year 9 for once-burned sites with year 11 in twice-burned sites ("year ~ 10"). Exact contrasts are given in Supplement tables.

Variable	Data included	Model Terms	Contrasts
Understory stem density (non-juniper species)	Once-burned	Soil, TSF, interaction	Burned vs unburned by soil Soil by TSF
Understory stem density (non-juniper species)	Once-burned and twice-burned (years 0–2, and ~ 10)	Soil, TSF, number of fires, all interactions	Soil by TSF and number of fires Number of fires by soil
Tree stem density; tree basal area (non-juniper species)	Once-burned (years 4–24)	Soil, TSF, interaction	Burned vs unburned by soil Soil by TSF
Tree stem density; tree basal area (non-juniper species)	Once-burned and twice-burned (year ~ 10 and unburned)	Soil, number of fires, interaction	Soil by TSF and number of fires Number of fires by soil
Ashe juniper understory stem density	Once-burned (years 3+)	Soil, TSF, interaction	Burned vs unburned by soil Soil by TSF
Ashe juniper understory stem density	Once-burned and twice-burned (year ~ 10 and unburned)	Soil, number of fires, interaction	Soil by TSF and number of fires Number of fires by soil
Ashe juniper tree density; tree basal area	Once-burned (years 14+)	Soil, TSF, interaction	Burned vs unburned by soil Soil by TSF

Because the maximum time since fire and number of repeated samples for once- and twice-burned sites was very different (24 years vs 11 years; 10 samples vs 4 samples), we compared the full once-burned dataset to unburned data and, separately, compared once-, twice- and unburned sites for only years 0–11. In the analyses with twice-burned data, we defined year "10" as year 9 for once-burned transects and year 11 for twice-burned transects (Table 1). Analyses with twice-burned data only include mesa and slope transects, because no deep soil transects were burned in the second fire. For comparisons with unburned sites, we always used the data from 2020.

We also used contrasts (defined *a priori*, see Table 2 and Supplement Tables) to examine differences among soils, number of fires, and burned/unburned sites using the multcomp package (Hothorn et al. 2008). P values were adjusted in a single step for each set of contrasts based on the joint *t*-distribution of the linear function.

For non-juniper understory stem density in once-burned transects, fixed effects were soil, time since fire, and their interaction (Table 2). Contrasts compared each time since fire sample with unburned data on the same soil (e.g., mesa year 0 vs mesa unburned, slope year 0 vs slope unburned) and compared soils at the same time since fire (e.g., mesa year 0 vs slope year 0, Table S2). A separate analysis compared non-juniper understory stem density in once-, twice- and unburned transects in years 0, 1, 2, and "10" using soil type, time since fire, number of fires, and all two-way and three-way interactions. Contrasts compared soils at each time since fire with separate comparisons for once- and twice-burned sites (e.g., twice-burned mesa year 0 vs twice-burned slope year 0); once- and twice-burned transects on the same soil at each time since fire (e.g., once-burned mesa year 0 vs twice-burned mesa year 0); and each time since fire for twice-burned sites to unburned sites on the same soil (e.g., twice-burned mesa year 0 vs unburned mesas, Table S4).

For non-juniper tree stem density and basal area in once-burned transects, we used data starting in year 4, because fewer than 8% of transects had trees in years 0–3 (mean: 2.3 stems ha^{-1}; median: 0 stems ha^{-1}). Model fixed effects were soil, time since fire, and their interaction. Contrasts compared each burned time since fire with unburned data on the same soil and soils at each time since fire (Table S6, Table S10). A separate analysis compared non-juniper tree stem density and basal area in once-, twice- and unburned transects in year "10" and unburned transects. Earlier years were not included because trees were very uncommon. Model fixed effects were soil, number of fires, and their interaction. Contrasts compared burned once- and twice-burned transects on the same soil, twice-burned transects on different soils, and twice-burned transects with unburned transects on the same soil (Table S8, Table S12).

For Ashe juniper understory stem density in once-burned transects, we used data beginning in year 3, because junipers were uncommon in years 0–2 (< 14% of transects had any juniper; mean: 5.8 stems ha^{-1}; median = 0 stems ha^{-1}). Model fixed effects included soil, time since fire, and their interaction. Contrasts compared each burned time since fire sample with unburned data on the same soil and soils at each time since fire (Table S14). A separate analysis with twice-burned sites used data from year "10" and unburned sites. Model fixed effects were soil, number of fires, and their interaction. Contrasts compared burned once- and twice-burned transects on the same soil, twice-burned transects on different soils, and twice-burned transects with unburned transects on the same soil (Table S16).

For Ashe juniper tree density and basal area on once-burned transects, we used data beginning in year 14, because trees were absent in earlier samples. Model fixed effects were soil, time since fire, and their interaction. Contrasts compared each burned time since fire sample with unburned data on the same

soil and soils at each time since fire (Table S18, Table S20). We did not analyze data from twice-burned sites because trees were still absent in year 11.

Finally, we examined the relationship between understory Ashe juniper stem density and distance to the wildfire perimeter for once-burned transects. We used data from all years (1996–2020) in a linear mixed model with soil, distance to fire edge, and their interaction as fixed effects. We also included a random intercept effect for transect. Only 6 transects in twice-burned areas had understory juniper, so the analysis could not be repeated for the second fire.

RESULTS

In once-burned transects, understory stem density of all species except Ashe juniper ("non-juniper" species) was similar to unburned transects in most years (Fig. 1, Table S1, Table S2). On mesas, density in once-burned transects was higher compared to unburned transects in years 5–9 (~ 69,000–76,000 vs ~ 37,000 stems ha^{-1}; $p < 0.01$). On slopes, density in burned transects was higher only in year 9 (~ 63,000 vs ~ 34,000 stems ha^{-1}, $p = 0.04$). On deep soils, density in burned transects was higher compared to unburned transects in years 6 and 9 (~ 79,000–82,000 vs ~ 26,000 stems ha^{-1}; $p < 0.01$). Density did not differ among soils at the same time since fire.

After the second fire, non-juniper understory density was up to 4 times higher compared to the first fire for the first few growing seasons (Fig. 1, Table S3). On mesas, density was significantly higher for years 0–2 ($p < 0.01$); on slopes, it was higher for years 0–1 ($p < 0.01$, Table S4). Approximately a decade later, there was no difference between once- and twice-burned sites (mesa, $p = 0.45$; slope, $p = 0.97$). When compared to unburned transects, twice-burned density was similarly higher for the first few years ($p < 0.01$, Table S4). Density was not different between mesas and slopes at the same time since fire.

Tree density of non-juniper species in once-burned transects was initially low but exceeded unburned density in later years (Fig. 1, Table S5, Table S6). On mesas, tree density was higher than unburned sites in year 24 (481 ± 254 vs 155 ± 137 stems ha^{-1}, $p < 0.01$). On slopes, tree density was higher in years 14 and 24 (733 ± 363–910 ± 330 vs 251 ± 103 stems ha^{-1}, $p < 0.01$). On deep soils, tree density did not differ from unburned sites in years 4–24 (45 ± 41–679 ± 250 vs 334 ± 411 stems ha^{-1}, $p \geq 0.26$). Tree density on mesas was lower compared to density on both slopes and deep soil in years 9 and 14 (year 9, mesa: 55 ± 98; slope: 275 ± 239; deep: 275 ± 235; year 14, mesa: 277 ± 289; slope: 733 ± 363; deep: 570 ± 410 stems ha^{-1}, $p \leq 0.03$), and lower compared to slopes in year 24 (mesa: 481 ± 254; slope: 910 ± 330 stems ha^{-1}, $p < 0.01$).

In twice-burned transects, non-juniper tree stem density was similar to once-burned transects and unburned transects (Fig. 1, Table S7, Table S8). In year 11, density was lower on twice-burned mesas compared to slopes (mesa: 34 ± 58; slope: 251 ± 202 stems ha^{-1}, $p < 0.01$).

Recovery of non-juniper tree basal area in once-burned transects varied by soil type (Fig. 1, Table S9, Table S10). On mesas, basal area on once-burned transects did not differ from unburned transects in years 4–24 (0 ± 0.01–2 ± 1.24 vs 1.41 ± 1.78 m^2 ha^{-1}). On slopes, basal area was lower through year 9 (0.06 ± 0.09–0.83 ± 0.77 vs 3.31 ± 2.11 m^2 ha^{-1}, $p \leq 0.02$), while on deep soils, basal area was lower through year 14 (0.12 ± 0.17–3.38 ± 1.83 vs 8.03 ± 8.65 m^2 ha^{-1}, $p < 0.01$). Basal area on mesas was lower than on deep soil in year 14 (mesa: 0.92 ± 1.06; deep: 3.38 ± 1.84 m^2 ha^{-1}, $p < 0.01$) and lower than both deep soil and slopes in year 24 (mesa: 2.00 ± 1.24; slope: 5.04 ± 1.79; deep: 6.02 ± 1.83 m^2 ha^{-1}; $p < 0.01$). Unburned basal area was higher on deep soils compared to mesas and slopes (slope: 3.31 ± 2.11; mesa: 1.41 ± 1.78; deep: 8.03 ± 8.65 m^2 ha^{-1}; $p < 0.01$).

In twice-burned transects, tree basal area was similar to once-burned transects a decade after fire (Fig. 2, Table S11, Table S12). On both mesas and slopes, twice-burned tree basal area in year 11 was lower compared to unburned transects (year 11 vs unburned, mesa: 0.10 ± 0.17 vs 1.41 ± 1.78 m^2 ha^{-1}, $p = 0.01$; slope: 0.69 ± 0.58 vs 3.31 ± 2.11 m^2 ha^{-1}, $p < 0.01$).

Ashe juniper understory density was lower in once-burned transects compared to unburned transects in all years sampled (Fig. 2, Table S13, Table S14; year 24 vs unburned, mesa: 101 ± 93 vs 2157 ± 1929; slope: 143 ± 139 vs 4732 ± 2768; deep: 152 ± 153 vs 2811 ± 2671 stems ha^{-1}; $p < 0.01$ for all). Density was not different among soils at the same time since fire, except that density was higher on unburned slope transects compared to unburned mesa transects (slope: 4732 ± 2768; mesa: 2157 ± 1929 stems ha^{-1}, $p < 0.01$). In twice-burned transects, Ashe juniper understory stem density was very low in year 0–2 and remained lower than in unburned transects in year 11 (mesa: 14 ± 26 vs 2157 ± 1929; slope: 26 ± 47 vs 4732 ± 2768 stems ha^{-1}; $p < 0.01$ for both). Approximately a decade after fire, density in mesa transects was similar in once- and twice-burned transects (one fire: 30 ± 51; two fires: 14 ± 26 stems ha^{-1}, $p = 1.00$), while density in slope transects was lower in twice-burned transects (one fire: 224 ± 306; two fires: 26 ± 47 stems ha^{-1}, $p = 0.01$; Fig. 2, Table S15, Table S16).

Ashe juniper tree density was lower in once-burned transects compared to unburned transects in most years and soils (Fig. 2, Table S17, Table S18). On deep soils, tree density was lower but not significantly different in years 14 and 24 (year 14: 5 ± 9 stems ha^{-1}; year 24: 50 ± 71 stems ha^{-1}; unburned: 317 ± 297 stems ha^{-1}; $p \geq 0.08$). Juniper tree density on unburned deep soil transects was lower compared to slopes and mesas (deep: 317 ± 297 stems ha^{-1}; mesa: 690 ± 410 stems ha^{-1}; slope: 731 ± 183 stems ha^{-1}; $p < 0.01$) but did not differ in any burned transects at the same time since fire. Ashe juniper tree basal area followed a similar pattern (Fig. 2, Table S19, Table S20). Basal area on unburned deep soils was much lower compared to slope and mesa transects (deep: 3.95 ± 3.78; mesa: 14.54 ± 8.37; slope: 16.47 ± 4.14 m^2 ha^{-1}; $p < 0.01$). Ashe juniper trees were completely absent from twice-burned transects for the duration of the study.

In once-burned transects, Ashe juniper understory density increased closer to the wildfire edge (Fig. 3, Table S21). The increase was steepest in deep soils, although these soils also had the lowest maximum distance to the wildfire perimeter (deep: 344 m; slope: 438 m; mesa: 575 m for mesas).

DISCUSSION

Single or repeated crown fires changed oak-juniper woodland structure and removed one of the co-dominants (Ashe juniper) for at least 24 years after fire at Fort Cavazos (central Texas). A single fire had little effect on understory stem density of non-juniper species (stems < 5 cm dbh or < 1.8 m tall), but increased tree density above unburned values on some soils a decade after fire. Basal area of non-juniper species took longer to recover but was similar to unburned areas by year 24 in all soils. After the second fire, understory stem density of non-juniper species was initially much higher but quickly became similar to once-burned areas; tree density and basal area did not differ in the first decade. Importantly, Ashe juniper remained essentially absent from the woodlands 24 years after one crown fire and recovered even more slowly after a second fire.

Unlike elsewhere in central Texas and in other oak-dominated forests (e.g., Andruk et al. 2014; Alexander et al. 2021; Van Auken et al. 2023), oaks and other hardwood trees recruited successfully after one and two crown fires. In 2020, oaks made up 71% of trees in once-burned areas and 84% of trees in twice-burned areas, compared with 21% of trees in unburned areas. We observed that the vast majority of this recruitment came from resprouting and not from seed. In most oak forests, recruitment is limited by deer herbivory and by lack of fire, which allows fire-sensitive mesophytic species to crowd out shade-intolerant oaks (Habeck and Schultz 2015; Hanberry et al. 2020). Fire clearly played a role in stimulating resprouting at Fort Cavazos, but in other sites, deer browsing can negate the effects of prescribed fire (e.g., Andruk et al. 2014; Cory and Leland Russell 2022). However, sustained hunting pressure at Fort Cavazos had reduced deer density to ~ 6 deer/100 ha at the time of the first crown fire (Wolverton et al. 2009), reducing browsing pressure on recruiting stems. The presence of saplings in unburned areas, where there has been no fire, also supports the importance of low deer numbers. Our data support the current approach of managing deer density or excluding deer to promote recruitment of oaks and other hardwoods.

The virtual elimination of a reseeding canopy dominant after crown fire has been noted in other studies. In the pine-oak forests of the southwestern United States and Mexico, for example, crown fires can eliminate ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) from large areas, shifting the community from pine forest to oak shrubland (e.g., Barton and Poulos 2018; Coop 2022). Regeneration of pines depends on distance to unburned sites and topography, and is hampered by competition from resprouting oaks and unfavorable weather (Haffey et al. 2018; Rodman et al. 2020; Stevens et al. 2021). In central Texas, loblolly (*Pinus taeda* L.) regeneration was lower in high-severity burn patches than in moderate-severity patches (Cooper et al. 2018). As with ponderosa pine, loblolly regeneration seems to be limited by dispersal, competition with resprouting oaks, and xeric conditions in burned sites.

In our study, Ashe juniper regeneration was influenced by distance to wildfire perimeter, suggesting dispersal limitation. Ashe juniper is dispersed by birds and mammals (Chavez-Ramirez and Slack 1993, 1994). Birds can potentially disperse seeds very long distances into burned areas, but the lack of other food sources in the burned area may limit the use of burned habitat. Furthermore, dispersal distribution varies by species, with flocking birds and mammals create highly clumped distributions (Chavez-Ramirez and Slack 1993, 1994). Studies of other juniper species have found variable dispersal efficiencies, ranging from 3 m per year for Utah juniper (*Juniperus osteosperma* (Torr.) Little) to more than 12 m for eastern redcedar (*Juniperus virginiana* L., (Holthuijzen and Sharik 1985; Neupane and Powell 2015). Our data suggests that common dispersers of Ashe juniper do not efficiently disperse seeds into burned areas, slowing woodland recovery.

On deep soils after a single fire, average juniper tree density and basal area abundance remained lower than unburned sites but were no longer statistically different by year 14 (Fig. 3, Tables S18 and S20). Before the fire, the woodlands on these soils were juniper-encroached post oak savannas with the lowest basal area of juniper and the highest basal area of other species. The sites also had the greatest variability in density, which is characteristic of savannas with an uneven distribution of trees. Fonteyn et al. (1988) suggested that a single crown fire could restore a juniper-encroached savanna; our data suggest repeated treatments would be needed to prevent re-encroachment and reduce density of resprouting stems. The benefits of repeated treatments have been shown in oak savannas elsewhere in the United States, but low-intensity fire must usually be combined with mechanical thinning or brush control in long-unburned sites (e.g., Glennemeier et al. 2020; Vander Yacht et al. 2020). Follow-up treatments after crown fire, such as prescribed fire or mechanical thinning, would be needed to create and maintain a savanna on our sites.

After the second fire, recovery of Ashe juniper may be proceeding even more slowly than after the first fire. On slopes, understory stem density was lower a decade after the second fire compared to a similar period after the first fire. In other systems such as Mediterranean pine forests, Australian eucalyptus forests, and California chaparral, repeated wildfires can reduce or eliminate obligate reseeders if fires recur before plants mature enough to produce more seed (e.g., Zedler et al. 1983; Fairman et al. 2015; Taboada et al. 2017). In our sites, the slower recovery must be due to other factors, because juniper did not reseed successfully after even one fire. One potential reason is the smaller sample size of twice-burned transects (19 vs 65 once-burned at the equivalent time), which makes it less likely that widely dispersed seedlings fall in a transect. Another reason may be the initial higher density of resprouters after the second fire that provided stronger competition with juniper seedlings. Previous studies have found that Ashe juniper seedling establishment and survival are highest in shaded conditions but growth is highest at canopy edges and in open grasslands (Jackson and Van Auken 1997; Van Auken et al. 2004). Longer monitoring will be needed to confirm that juniper recovery remains slower after repeated fires.

Ashe juniper is a critical habitat component for the endangered golden-cheeked warbler, which nests only in central Texas. Warblers used shredding bark from mature junipers for nest building and forage in

juniper crowns (Pulich 1976). The presence of junipers also increases fledgling survival (Trumbo et al. 2021). Kroll (1980) estimated that juniper bark begins shredding at the tree base after ~ 20 years and most studies find that warblers prefer woodlands where juniper makes up around half of the canopy (e.g., DeBoer and Diamond 2006; Peak and Thompson 2013). Given these requirements, oak-juniper woodlands burned by crown fires will remain unsuitable as habitat for many decades.

CONCLUSIONS

Oaks and other species successfully recruited after one and two fires, likely due to low deer densities. Crown fires removed the fire-sensitive Ashe juniper from canopy co-dominance for decades. While the pre-settlement fire regime and vegetation distribution in the Edwards Plateau is debated, our data show that mixed woodlands would only exist in areas with very long intervals between crown fires. Given the long-term consequences of crown fires, especially for golden-cheeked warbler habitat, maintenance of mature oak-juniper woodlands will require protection from extreme fire.

Declarations

Availability of data

The datasets used during the current study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

Funding

This project was funded by the U.S. Army through cooperative agreements DPW-ENV-97-A-0001, DPW-ENV-02-A-0001, and DPW-ENV-07-A-0001 with The Nature Conservancy of Texas, as well as the Department of Defense Legacy Resource Management Program. The content of this manuscript does not necessarily reflect the position or policy of the government and no official endorsement should be inferred.

Authors' contributions

CR helped to collect some of the data, analyzed the data, and wrote the manuscript. CP helped to collect some of the data and organized the 2020 data collection. JS organized the 2020 data collection. All authors read and approved the final manuscript.

ACKNOWLEDGEMENTS

We would like to thank the many seasonals and staff who helped collect data, especially L. Hansen who initiated the project.

References

1. Alexander, H. D., C. Siegert, and J. S. Brewer et al. 2021. Mesophication of Oak Landscapes: Evidence, Knowledge Gaps, and Future Research. *BioScience* 71: 531–542. https://doi.org/10.1093/biosci/biaa169.
2. 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. https://doi.org/10.1016/j.foreco.2014.08.037.
3. Baccus, J. T., J. D. Cornelius, M. E. Tollé, and J. D. Cornelius. 2007. *Response of golden-cheeked warblers (Dendroica chrysoparia) to wildfires at Fort Hood, Texas*. Houston, Texas, USA: Texas Ornithological Society.
4. Barton, A. M., and H. M. Poulos. 2018. Pine vs. oaks revisited: Conversion of Madrean pine-oak forest to oak shrubland after high-severity wildfire in the Sky Islands of Arizona. *Forest Ecology and Management* 414: 28–40. https://doi.org/10.1016/j.foreco.2018.02.011.
5. Chavez-Ramirez, F., and R. D. Slack. 1993. Carnivore Fruit-Use and Seed Dispersal of Two Selected Plant Species of the Edwards Plateau, Texas. *The Southwestern Naturalist* 38: 141. https://doi.org/10.2307/3672066.
6. Chavez-Ramirez, F., and R. D. Slack. 1994. Effects of Avian Foraging and Post-Foraging Behavior on Seed Dispersal Patterns of Ashe Juniper. *Oikos* 71: 40. https://doi.org/10.2307/3546170.
7. Coop, J. D. 2022. Post-fire futures in southwestern forests: Climate and landscape influences on trajectories of recovery and conversion. *Ecological Applications n/a* e2725. https://doi.org/10.1002/eap.2725.
8. Cooper, C. E., J. P. Muir, C. L. S. Morgan, and G. W. Moore. 2018. Tortoise or hare: Will resprouting oaks or reseeding pines dominate following severe wildfire? *Forest Ecology and Management* 408: 54–66. https://doi.org/10.1016/j.foreco.2017.10.044.
9. Cory, B. J., and F. Leland Russell. 2022. Deer browsing and light availability limit post oak (Quercus stellata) sapling growth and post-fire recovery in a xeric woodland. *Forest Ecology and Management* 519: 120346. https://doi.org/10.1016/j.foreco.2022.120346.
10. DeBoer, T. S., and D. D. Diamond. 2006. Predicting presence-absence of the endangered golden-cheeked warbler (Dendroica chrysoparia). *Southwestern Naturalist* 51: 181–190. https://doi.org/10.1894/0038-4909(2006.)51[181:PPOTEG]2.0.CO;2.
11. Diamond, D. D. 1997. *An old-growth definition for western juniper woodlands: Texas Ashe juniper dominated or codominated communities*. Asheville, North Carolina, USA: USDA Forest Service, Southern Research Station.
12. Fairman, T. A., C. R. Nitschke, and L. T. Bennett. 2015. Too much, too soon? A review of the effects of increasing wildfire frequency on tree mortality and regeneration in temperate eucalypt forests. *Int J Wildland Fire* 25: 831–848. https://doi.org/10.1071/WF15010.

13. Fonteyn, P. J., M. W. Stone, and M. A. Yancy et al. 1988. Determination of community structure by fire. In *Edwards Plateau vegetation: plant ecological studies in central Texas*, eds. B. B. Amos, and F. R. Gehlbach. 79–90. Waco, Texas, USA: Baylor University Press.
14. Fowler, N., A. Center, and E. Ramsey. 2012. Streptanthus bracteatus (Brassicaceae), a rare annual woodland forb, thrives in less cover: evidence of a vanished habitat? *Plant Ecology* 213: 1511–1523. https://doi.org/10.1007/s11258-012-0109-2.
15. Fowler, N. L., and R. Carden. 2024. Roles of fire in the plant communities of the eastern Edwards Plateau. Fire Ecology: in review.
16. Glennemeier, K., S. Packard, and G. Spyreas. 2020. Dramatic long-term restoration of an oak woodland due to multiple, sustained management treatments. *Plos One* 15: 1–19. https://doi.org/10.1371/journal.pone.0241061.
17. Habeck, C. W., and A. K. Schultz. 2015. Community-level impacts of white-tailed deer on understorey plants in North American forests: a meta-analysis. *AoB PLANTS* 7: plv119. https://doi.org/10.1093/aobpla/plv119.
18. Haffey, C., T. D. Sisk, and C. D. Allen et al. 2018. Limits to Ponderosa Pine Regeneration following Large High-Severity Forest Fires in the United States Southwest. *Fire Ecology* 14: 143–163. https://doi.org/10.4996/fireecology.140114316.
19. Hanberry, B. B., M. D. Abrams, M. A. Arthur, and J. M. Varner. 2020. Reviewing Fire, Climate, Deer, and Foundation Species as Drivers of Historically Open Oak and Pine Forests and Transition to Closed Forests. *Frontiers in Forests and Global Change* 3.
20. He, T., B. B. Lamont, and J. G. Pausas. 2019. Fire as a key driver of Earth's biodiversity. *Biological Reviews* 94: 1983–2010. https://doi.org/10.1111/brv.12544.
21. Hmielowski, T. L., K. M. Robertson, and W. J. Platt. 2014. Influence of season and method of topkill on resprouting characteristics and biomass of Quercus nigra saplings from a southeastern U.S. pine-grassland ecosystem. *Plant Ecology* 215: 1221–1231. https://doi.org/10.1007/s11258-014-0380-5.
22. Holthuijzen, A. M. A., and T. L. Sharik. 1985. The avian seed dispersal system of eastern red cedar (Juniperus virginiana). *Canadian Journal Of Botany* 63: 1508–1515. https://doi.org/10.1139/b85-208.
23. Hothorn, T., F. Bretz, and P. Westfall. 2008. *Simultaneous Inference in General Parametric Models*. Munich, Germany: University of Munich.
24. Jackson, J. T., and O. W. Van Auken. 1997. Seedling survival, growth and mortality of *Juniperus ashei* (Cupressaceae) in the Edwards Plateau region of central Texas. *The Texas Journal of Science* 49: 267–278.
25. Kassambara, A. 2023. *ggpubr: ggplot2*. Based Publication Ready Plots.
26. Keeley, J. E. 2006. Fire severity and plant age in postfire resprouting of woody plants in sage scrub and chaparral. *Madrono* 53: 373–379. https://doi.org/10.3120/0024-9637(2006)53[373:fsapai]2.0.co;2.

27. Keeley, J. E., J. G. Pausas, and P. W. Rundel et al. 2011. Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science* 16: 406–411.
28. Kroll, J. C. 1980. Habitat requirements of the golden-cheeked warbler: management implications. *Journal of Range Management* 33: 60–65.
29. Kuznetsova, A., P. Brockhoff, and R. Christensen. 2017. lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software* 82: 1–26. https://doi.org/doi: 10.18637/jss.v082.i13.
30. Leonard, W. J., and O. W. V. 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. https://doi.org/10.3375/043.033.0306.
31. 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. *American Midland Naturalist* 170: 348–369. https://doi.org/10.1674/0003-0031-170.2.348.
32. Neupane, R. C., and J. A. Powell. 2015. Mathematical Model of Seed Dispersal by Frugivorous Birds and Migration Potential of Pinyon and Juniper in Utah. *Applied Mathematics* 06: 1506. https://doi.org/10.4236/am.2015.69135.
33. Peak, R. G., and F. R. Thompson. 2013. Amount and type of forest cover and edge are important predictors of golden-cheeked warbler density. *Condor* 115: 659–668. https://doi.org/10.1525/cond.2013.120043.
34. Pulich, W. M. 1976. *The golden-cheeked warbler, a bioecological study*. Austin, Texas, USA: Texas Parks and Wildlife Department.
35. R Core Team. 2024. R: a language and environment for statistical computing.
36. 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.
37. Reemts, C. M., and L. L. Hansen. 2013. Short-Term Effects of Repeated Wildfires in Oak-Juniper Woodlands. *Fire Ecology* 9: 64–79.
38. Reidy, J. L., F. R. Thompson, and S. Rowin et al. 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. https://doi.org/10.1016/j.foreco.2021.119191.
39. Reidy, J. L., F. R. Thompson III, and C. Schwope et al. 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. http://dx.doi.org/10.1016/j.foreco.2016.06.005.
40. Rodman, K. C., T. T. Veblen, and T. B. Chapman et al. 2020. Limitations to recovery following wildfire in dry forests of southern Colorado and northern New Mexico, USA. *Ecological Applications* 30: 1–20. https://doi.org/10.1002/eap.2001.

41. 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.
42. Stevens, J. T., C. M. Haffey, and J. D. Coop et al. 2021. Tamm Review: Postfire landscape management in frequent-fire conifer forests of the southwestern United States. *Forest Ecology and Management* 502: 119678. https://doi.org/10.1016/j.foreco.2021.119678.
43. Taboada, A., R. Tárrega, and E. Marcos et al. 2017. Fire recurrence and emergency post-fire management influence seedling recruitment and growth by altering plant interactions in fire-prone ecosystems. *Forest Ecology and Management* 402: 63–75. https://doi.org/10.1016/j.foreco.2017.07.029.
44. Trumbo, E. M., M. P. Ward, and J. N. Macey et al. 2021. Post-fledging ecology of endangered Golden-cheeked Warblers. *Journal of Field Ornithology n/a*. https://doi.org/10.1111/jofo.12382.
45. 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, USA1. *The Journal of the Torrey Botanical Society*. https://doi.org/10.3159/TORREY-D-23-00009.1.
46. 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.
47. Vander Yacht, A. L., P. D. Keyser, and S. A. Barrioz et al. 2020. Litter to glitter: promoting herbaceous groundcover and diversity in mid-southern USA oak forests using canopy disturbance and fire. *Fire Ecology* 16: 17. https://doi.org/10.1186/s42408-020-00072-2.
48. Varner, J. M., J. M. Kane, and J. K. Hiers et al. 2016. Suites of fire-adapted traits of oaks in the southeastern USA: multiple strategies for persistence. *Fire Ecology* 12: 48–64. https://doi.org/10.4996/fireecogly.1202048.
49. Vázquez-Miranda, H., K. R. Barr, C. C. Farquhar, and R. M. Zink. 2015. Fluctuating fire regimes and their historical effects on genetic variation in an endangered shrubland specialist. *Ecology and Evolution* 5: 5487–5498. https://doi.org/10.1002/ece3.1811.
50. Wester, D. B. 1992. Viewpoint: replication, randomization, and statistics in range research. *Journal of Range Management* 45: 285–290.
51. Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag.
52. Wolverton, S., M. A. Huston, and J. H. Kennedy et al. 2009. Conformation to Bergmann's Rule in White-tailed Deer can be Explained by Food Availability. amid 162:403–417. https://doi.org/10.1674/0003-0031-162.2.403.
53. 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. http://dx.doi.org/10.1016/j.foreco.2012.05.042.
54. Zedler, P. H., C. R. Gautier, and G. S. McMaster. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. *Ecology* 64: 809–818.

Figures

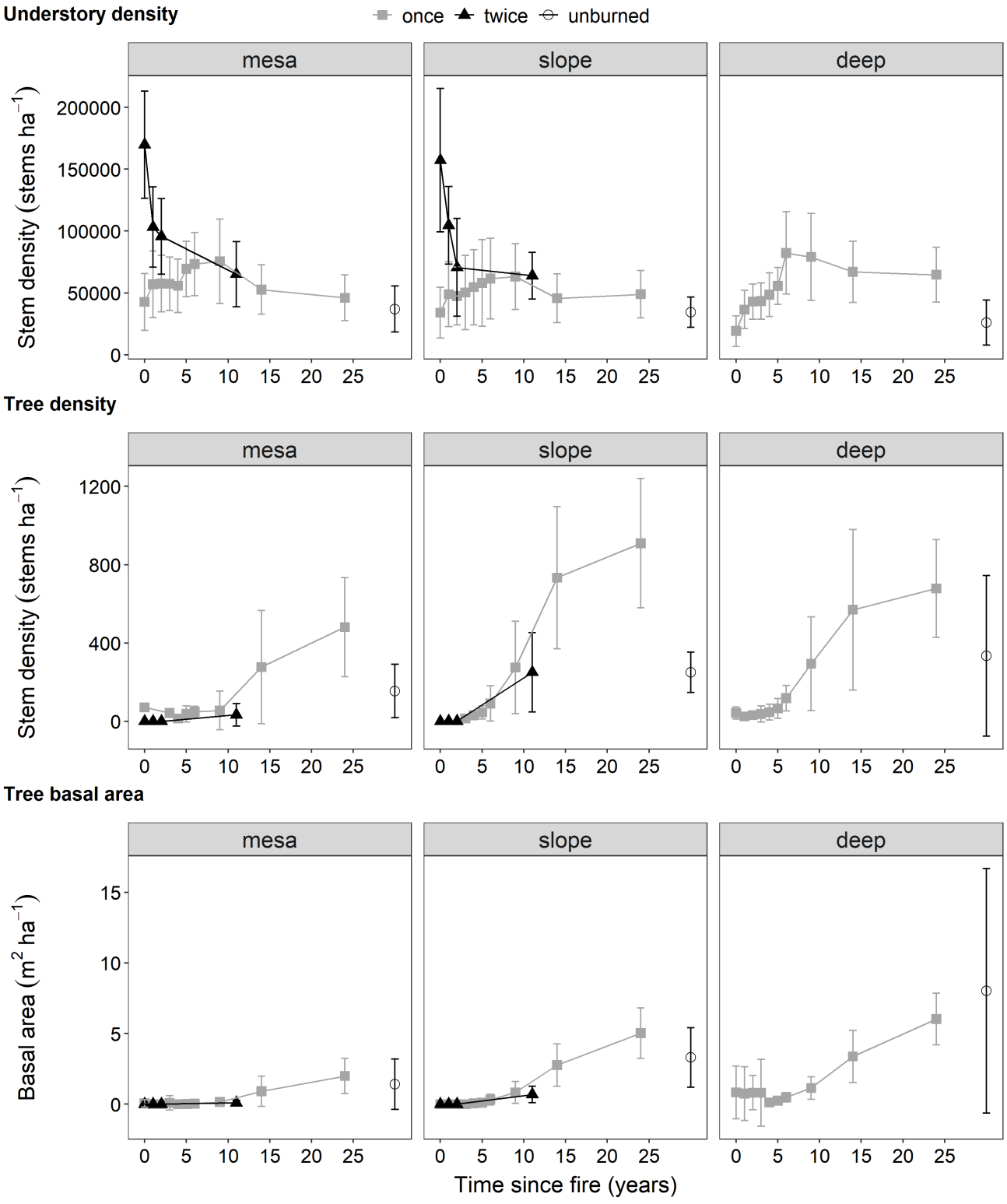

Figure 1

Oak-juniper woodland response to one or two crown fires compared to unburned woodlands at Fort Cavazos, Texas, USA for all woody species except Ashe juniper. Top—understory stem density (stems < 5 cm dbh or <1.8 m tall). Middle—tree stem density (stems ≥ 5 cm dbh). Bottom—tree basal area (stems ≥

5 cm dbh). Mesas are dominated by shin oak; slopes are dominated by Buckley oak; deep soils are dominated by post oak.

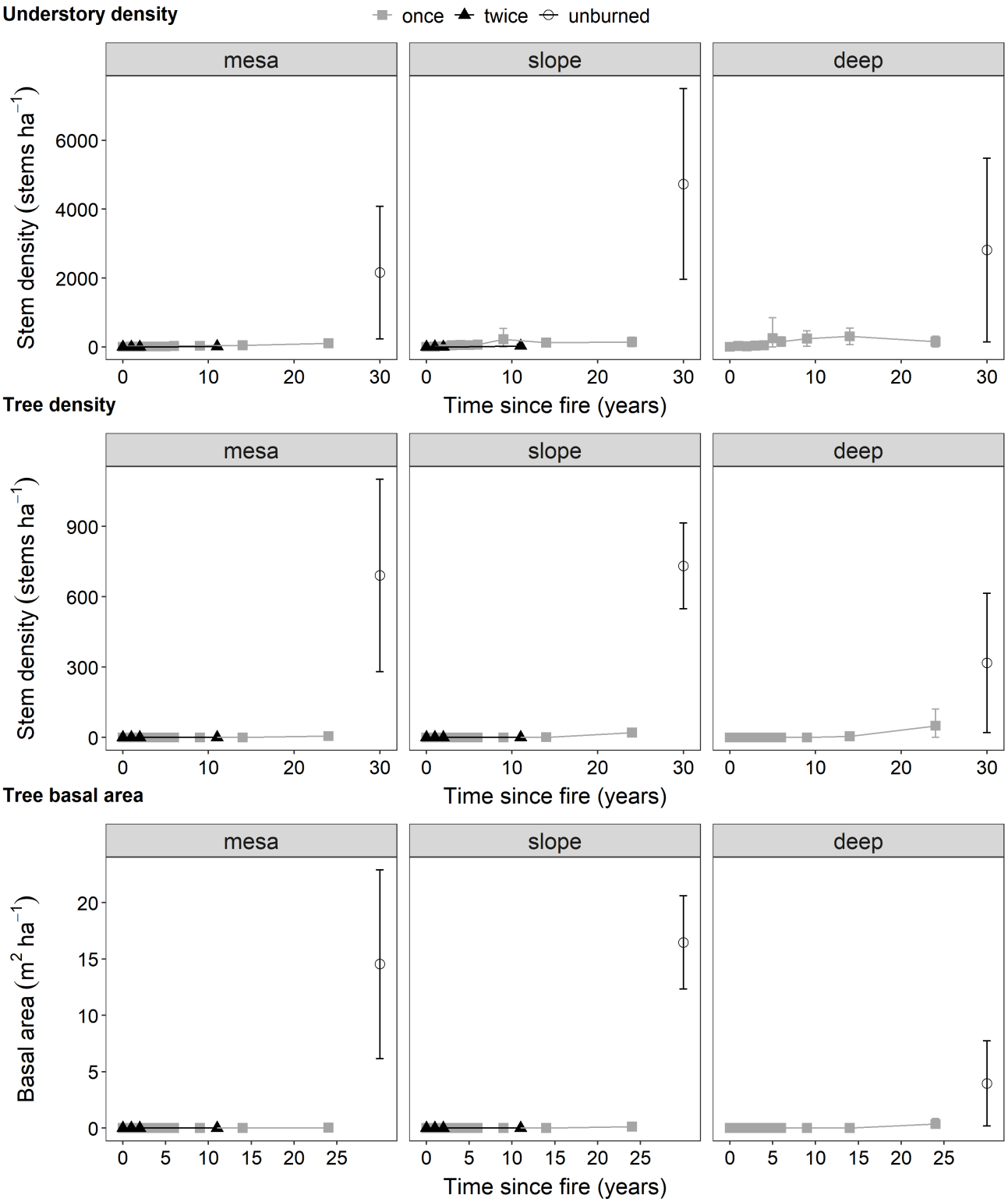

Figure 2

Ashe juniper response to one or two crown fires compared to unburned woodlands at Fort Cavazos, Texas, USA. Top—understory stem density (stems < 5 cm dbh or <1.8 m tall). Middle—tree stem density (stems ≥ 5 cm dbh). Bottom—tree basal area. Juniper trees were absent from once-burned sites until

year 14 and were absent from twice-burned sites in all years. Mesas are dominated by shin oak; slopes are dominated by Buckley oak; deep soils are dominated by post oak.

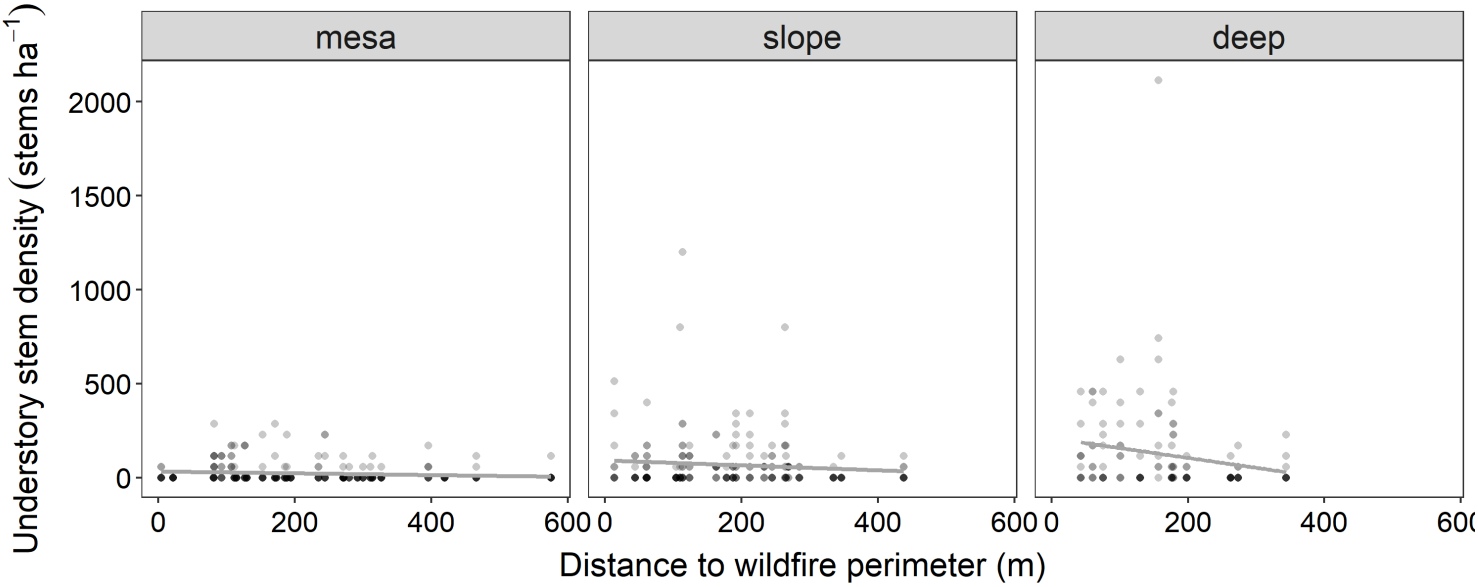

Figure 3

Ashe juniper understory stem density (stems < 5 cm dbh or < 1.8 m tall) in once-burned transects increased closer to the edge of the 1996 wildfire at Fort Cavazos, Texas, USA. Points are slightly transparent to show overlap. Mesas are dominated by shin oak; slopes are dominated by Buckley oak; deep soils are dominated by post oak.

Supplementary Files

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