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Extreme prescribed fire during drought reduces survival and density of woody resprouters

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Summary

1. Management intervention in ecosystems with degraded environmental services requires innovative resource management strategies that go beyond conventional restoration and conservation practices. We established a unique study that experimentally targeted extreme fire conditions during drought in humid subtropical and semi-arid ecoregions.

2. In the southern Great Plains of North America, conventional restoration and conservation practices have been either historically ineffective or economically cost-prohibitive at restoring grass-dominated ecosystems following conversion to resprouting shrublands. Our aim was to assess the potential for extreme fire during drought to force the system along an alternate ecological trajectory from its current progression towards closed-canopy resprouting shrubland, something that conventional fire prescriptions have been unable to accomplish.

3. We first tested the potential for high-intensity fires exhibiting extreme behaviour to disrupt the progression from grassland to shrubland. In both ecoregions, significant levels of mortality were observed for mature woody resprouters. As a result, densities were either maintained or reduced 3 years following extreme fire treatments, whereas resprouter densities continued to increase in areas that were not burned.

4. A second interventionist approach involving extreme fire and herbicide treatment combinations was not supported. Interactions between prescribed extreme fire and herbicide did not significantly reduce resprouter densities more than using herbicide alone at either site.

5. *Synthesis and applications*. Extreme fires during drought resulted in exceptionally high levels of mortality across all sizes of woody resprouters and limited recruitment, resulting in 35–55% lower densities of resprouters than in areas not burned. These findings counter prevailing scientific and management expectations, which are based largely on studies that impose tight controls over prescribed fire conditions and avoid extreme fire behaviour. Future interventions for controlling woody resprouters with fire may require rethinking the present ideology that extreme fire behaviour has no place in modern social–ecological landscapes.

Key-words: alternative state, drought, ecological restoration, extreme fire, fire intensity, fire regime, intervention ecology, novel ecosystem, regime shift

Introduction

Intervention in an era of global change requires the creation and application of novel resource management strategies that push the boundaries of conventional management practices. Today, many plant communities are compositionally, structurally and functionally different than those that occurred previously (Williams & Jackson 2007). Climate change, invasive species, alterations in disturbance regimes, and human-transformed local and global dispersal pathways have altered the functioning of biophysical processes and their controls over plant community dynamics (Hobbs *et al.* 2006). As a result, conventional approaches to ecosystem restoration and conservation have often failed to meet the expectations of managers (Hobbs *et al.* 2011). An alternative approach,

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and a central tenet of intervention ecology, is to focus on conserving ecosystem services with the expectation for future environmental change rather than seeking to restore potentially unattainable past ecological states (Hobbs & Cramer 2008). This approach challenges scientists and managers to recognize and move beyond conventional management practices that often do not meet the expectations of applied ecologists.

Our understanding of how fire can be used to shape vegetation dynamics in biomes experiencing shifts from grassy to resprouting woody ecosystems may benefit from an interventionist approach. Extensive transformations of the world's grasslands and savannas to woody dominance have occurred over the last century as a result of a global-trend towards less frequent fire occurrences (Bond, Woodward & Midgley 2005). Unlike obligate seeding species, which can be killed by high-intensity fires (Williams, Gill & Moore 1998; Russell-Smith, Edwards & Price 2012; Twidwell *et al.* 2013b; Bowman *et al.* 2014; Brando *et al.* 2014), resprouters persist through fire events by protecting buds below ground and remobilizing subsurface non-structural carbohydrates to foster new stem growth following fire (Clarke *et al.* 2013). As a result, numerous scientific experiments have shown the following effects of fire (e.g. Ansley *et al.* 1998; Enslin *et al.* 2000; Drewa 2003; Higgins *et al.* 2007; Hoffmann *et al.* 2009): (i) fire does not spread into shrub clusters, due to the lack of fine fuel underneath them, and therefore does not damage shrubs; (ii) for shrubs that do experience thermal damage, fire intensity is insufficient to reduce apical dominance; (iii) when fire intensity is sufficient to reduce apical dominance, vigorous resprouting ensues, resulting in greater cover compared with individuals not burned. All of these observations are indicative of a regime shift with strong hysteresis effects (Scheffer *et al.* 2001), making this particular grassland to woody regime shift more difficult to reverse than many others (e.g. obligate seeders transforming grassland to *Juniperus* woodland; Twidwell *et al.* 2013b).

The prevailing consensus then is that fire alters only the structure, but does not reduce density, of mature resprouting woody species compared with areas not burned (e.g. Higgins *et al.* 2007). However, our understanding of resprouting dynamics and expansion are primarily constrained to experimental manipulations that (i) limit the theoretical range of variability of fire behaviour to 'milder' conditions that ensure safety and containment and (ii) avoid drought and instead target optimal rainfall and soil moisture conditions to limit plant stress and foster plant regrowth. Considering that higher levels of mortality of adult resprouting plants have been observed for some species when exposed to high-intensity fires (Bradstock & Myerscough 1988; Adie *et al.* 2011), anthropogenic constraints on fire behaviour may be masking the theoretical potential of fire as an agent of vegetation change (Twidwell *et al.* 2016a).

This study is unique in that it was designed from the start to experimentally target extreme fire conditions in order to better assess the theoretical effect of fire on resprouting capacity. Extreme fire is a technical term that has been used commonly in the US wildland fire community since the 1950s (Potter & Werth 2011) to describe atypical behaviour in high-intensity fires that lead to blow-ups, fire storms, fire whirls and other forms of erratic fire behaviour. Extreme fire is defined, and its technical usage is discussed, in Appendix S1 in Supporting Information. Given the difficulties of conducting and controlling extreme fires, little is known about their contribution to vegetation dynamics. Most of our knowledge on ecological responses to extreme fire results from post-wildfire surveys with little control, replication or *a priori* sampling capable of determining actual rates of mortality.

Two novel interventionist approaches featuring extreme prescribed fires during drought were used in this study. First, we determine whether extreme fire during drought can be a useful intervention response to the woody encroachment problem. For extreme prescribed fire to be considered a useful intervention practice, it needs to be more effective than conventional applications of prescribed fire and reduce both the density and structure of the resprouting community compared with not burning. We then followed up initial extreme fires with a second low-intensity fire conducted during drought, testing the hypothesis that density and structure will be further reduced compared with a single extreme fire. As a second intervention approach, we use herbicide in combination with extreme fire to determine whether their combined use will result in greater shrub density reductions than when herbicides are applied without fire, which is the most common management strategy for controlling resprouting woody plants in the southern Great Plains (Kreuter *et al.* 2001).

Materials and methods

STUDY SITES AND EXPERIMENTAL DESIGN

Identical experimental designs were established in two different ecological regions heavily encroached by woody plants to determine the potential for broader application of the proposed intervention strategies. The first site was the Rob and Bessie Welder Wildlife Refuge (28°06′44″N 97°25′01″W), a humid subtropical site (mean annual precipitation = 900 mm) located approximately 11 km north of Sinton, Texas, in the Coastal Bend ecoregion. The second site is the Texas A&M Agrilife Research Center (30°15′60″N 100°33′55″W), a semi-arid site (mean annual precipitation = 572 mm) located 56 km south of Sonora, Texas, in the Edwards Plateau ecoregion. Additional site descriptions are available in Appendix S2.

Prescribed fire and herbicide treatments were applied in experimental plots, each 30 × 20 m, using a split-plot experimental design (Fig. S1). Eighteen plots were located at each site. Fire treatments were randomly assigned at the whole plot scale. Six plots were burned once with a single extreme fire during drought, six were burned during drought with a single extreme fire and followed by a low-intensity fire, and six served as a control (not burned). At both sites, a 15-m-wide bare ground firebreak

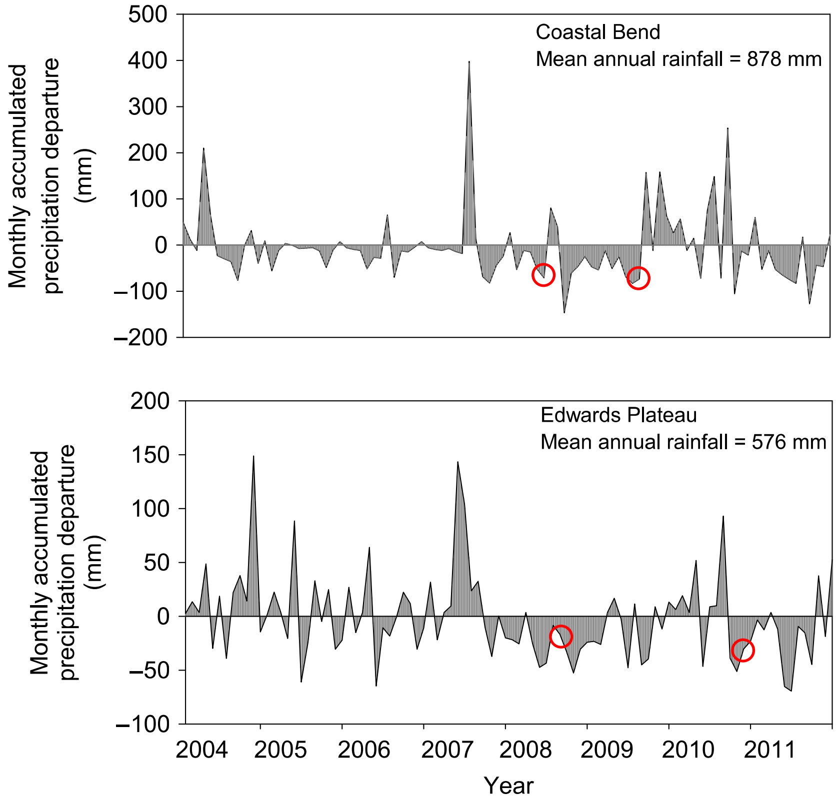

Fig. 1. Monthly departures in accumulated precipitation that coincided with fire treatments. A value of 0 represents the mean long-term precipitation accumulation for a given month, based on 55-year and 94-year weather records at the Coastal Bend (top panel) and Edwards Plateau (bottom panel), respectively. Red circles show when fire treatments were conducted.

surrounded each whole plot to allow each to be burned independently of other experimental plots and to serve as true replicates (Fig. S1). Within each whole plot, three herbicide treatments were randomly assigned at the subplot level (each 20 × 10 m). Herbicide treatments included: (i) herbicide applied in 2007, which was timed to occur 1 year prior to conducting the initial fire treatment, (ii) herbicide applied in 2009, which was timed to occur after the initial fire treatment when resprouting stems from burned *P. glandulosa* trees were approximately 0·5 m in length, and (iii) no herbicide, which served as a control. Domestic livestock (cattle and goats) were removed prior to initiation of this experiment and were excluded for its duration.

All fires were conducted in this study during months when precipitation was well below the historical average (Fig. 1). On the Coastal Bend, total precipitation in June 2008 was 96% below the historical monthly mean (based on nearby weather station records from Sinton, TX; 1958–2011) and was less than the long-term monthly average for eight of the 9 months preceding initial fire treatment (Fig. 1). Low precipitation conditions continued when the second fire treatment was conducted in July 2009. Precipitation was less than the historical mean for 11 months before the second fire treatment. The site then received above-average precipitation for the remainder of the growing season (Fig. 1). On the Edwards Plateau, both fire treatments were conducted in the middle of yearlong droughts (Fig. 1). The 5 months preceding, as well as following, the fire treatment in August 2008 were both well below typical rainfall amounts (based on experimental station records, 1919–2011). In November 2010, when low intensity fires were conducted (Fig. 1), rainfall was 99% below the long-term monthly mean of 310 mm. These fires occurred 3 months into one of the worst droughts the region had experienced during the last 100 years (Twidwell *et al.* 2014). These rainfall conditions correspond to some of the most severe droughts observed on modern record (PDSI < −4 in both ecoregions, NOAA Historical Palmer Drought Indices).

The first set of fire treatments was conducted in June 2008 on the Coastal Bend and August 2008 on the Edwards Plateau. Twelve plots were burned at each site at those times. At both sites, fire behaviour was not typical of other experimental field studies conducted in similar vegetation types. Maximum fireline intensities were considerably higher on the Edwards Plateau in 2008 (Table 1) than have been reported in resprouting shrublands of the south-central USA and elsewhere (Table 2); however, mean fire intensities were within the range of values observed in Texas for ecosystems with greater herbaceous fuel continuity and higher fine fuel loading (Tables 1 and 2). We also observed numerous examples of extreme fire behaviour at both study sites. Sudden blow-ups and fire whirls were observed in multiple experimental plots within these high-density mixed shrub communities. When the first fires were conducted on the Edwards Plateau, plots with scattered *Juniperus pinchotti* Sudw. within a nearly closed-canopy mixed shrub fuel matrix led to a switch in fire type from surface fires to localized active crown fires (defined as a sustained and continuous flaming front actively burning throughout the surface and canopy layers, Alexander & Cruz 2011). In comparison, all fire treatments on the Coastal Bend were surface fires with isolated combustion of the crowns of individual shrubs, which is more typical of fires in savanna and shrub-dominated vegetation (Govender, Trollope & van Wilgen 2006).

A second low-intensity fire was conducted after the initial extreme fire to establish the second fire treatment. Six plots were burned again in July 2009 on the Coastal Bend, and six were burned again in November 2010 on the Edwards Plateau. As expected *a priori*, follow-up fires were indeed of lower intensity than initial fires and no extreme fire behaviour was observed, constituting an 'extreme fire followed by low-intensity fire'

Table 1. Fireline intensity, peak fire temperatures and percentage of area burned for fire treatments conducted during extended periods of drought on the Coastal Bend and Edwards Plateau of Texas, USA

				Fireline intensity ($kW m^{-1}$)		Peak fire temperature (°C)				
						0 cm height		150 cm height		Area burned (%)
Site	Year	Fire trt.*	Herb. trt.	Mean ± SE	Max	Mean ± SE	Max	Mean ± SE	Max	Mean ± SE
Coastal Bend	2008	EF	2007	725 ± 255	5291	869 ± 58	1038	526 ± 95	1038	97 ± 2
			2009	811 ± 296	5291	825 ± 104	1038	458 ± 110	927	96 ± 2
			None	589 ± 283	8595	907 ± 94	1038	542 ± 82	1038	93 ± 4
		EF+LI	2007	1101 ± 356	8595	905 ± 35	1038	399 ± 83	816	97 ± 2
			2009	929 ± 288	5291	901 ± 61	1038	407 ± 84	927	98 ± 1
			None	1229 ± 383	8595	992 ± 32	1038	432 ± 56	927	98 ± 1
	2009	EF+LI	2007	28 ± 9	58	163 ± 38	621	38 ± 21	399	50 ± 9
			2009	28 ± 9	58	219 ± 82	760	48 ± 33	371	53 ± 10
			None	20 ± 7	58	162 ± 55	677	60 ± 32	593	58 ± 5
Edwards Plateau	2008	EF	2007	1569 ± 505	68 613	1007 ± 15	1038	395 ± 52	1038	100 ± 0
			2009	1233 ± 346	38 788	982 ± 27	1038	341 ± 65	816	100 ± 0
			None	1103 ± 285	23 879	1004 ± 34	1038	513 ± 87	1038	100 ± 0
		EF+LI	2007	824 ± 155	38 788	1003 ± 36	1038	398 ± 51	649	100 ± 0
			2009	1525 ± 564	47 718	996 ± 27	1038	477 ± 99	1038	98 ± 2
			None	1462 ± 568	23 879	994 ± 44	1038	394 ± 64	816	99 ± 1
	2010	EF+LI	2007	377 ± 113	877	798 ± 88	1038	206 ± 92	538	100 ± 0
			2009	436 ± 67	627	690 ± 131	1038	65 ± 34	288	100 ± 0
			None	446 ± 152	1173	996 ± 44	1038	156 ± 69	454	100 ± 0

*Abbreviations stand for the following treatments: EF+LI, extreme fire +low intensity; EF, single extreme fire.

Table 2. Fireline intensities and fire temperatures reported from (i) experiments in ecological regions within or nearby the ecosystems featured in this study and (ii) high-intensity experimental fires conducted in grass-tree codominated plant communities on other continents

Ecosystem	Fireline intensity ($kW m^{-1}$)*	Fire temperature (°C)[†]	Reference
1. Experiments in/near southern Great Plains resprouting shrublands			
Prosopis-Acacia shrubland, Gulf Coastal Bend, Texas, USA	15–8595	0–1038	This study
Prosopis-Juniperus pinchotti woodland, Edwards Plateau, Texas, USA	139–68 613	253–1038	This study
Shrub-encroached Gulf Coastal Prairie, USA	–	110–820	Scifres *et al.* (1988); Grace *et al.* (2005); Owens, Proffitt & Grace (2007); Hartley *et al.* (2007)
Prosopis savanna, Texas Rolling Plains, USA	165–7731	150–700	Ansley & Jacoby (1998); Ansley *et al.* (1998)
Prosopis-Acacia shrubland, South Texas Plains, USA	54–314	106–700	Streeks, Owens & Whisenant (2005)
Prosopis desert grassland, Chihuahuan Desert, USA	26–782	586–1392	Drewa (2003)
2. High-intensity fire experiments on other continents			
Wooded savanna, Kruger National Park, South Africa	28–17 905	–	Govender, Trollope & van Wilgen (2006)
Open savanna, Kruger National Park, South Africa	4048–10 906	–	Stocks *et al.* (1996)
Dry *Eucalyptus* savanna, Northern Territory, Australia	500–18 000	–	Williams, Gill & Moore (1998)
Dry *Eucalyptus* forest, south-western Australia	0–10 573[‡]	–	McCaw *et al.* (2012)
Cerrado grassland-savanna continuum, Brazil	2842–16 394	–	Kauffman, Cummings & Ward (1994)

*Fireline intensity estimates can differ widely among studies as a result of the methodology used to make the estimate and should be considered when making interstudy comparisons (see text for further explanation).
[†]Only fire temperature measurements taken at ground level are reported for these studies.
[‡]Based on maximum value reported in the study and derived from observations of fuel loading (w) and rate of fire spread (R) input into the equation: $I = hwR$ (Byram 1959); the maximum flame length observed in McCaw *et al.* (2012) was 14·2 m, which was one metre more than observed in this study.

treatment. In 2009, herbaceous fuels had only started to recover from the previous year's fires on the Coastal Bend, so no examples of extreme fire behaviour were observed. Fireline intensities averaged 25 ± 3 $kW m^{-1}$ in 2009 burned plots compared with 897 ± 62 $kW m^{-1}$ the year prior on the Coastal Bend. Fire temperatures in burned plots were 80% lower than in the first fire, and surface fire spread was highly discontinuous leading to nearly half the plots remaining unburned following fire treatment (Table 1). Fires were delayed for an additional year on the Edwards Plateau because herbaceous biomass in 2009 was below the amount required to sustain surface fire spread in mixed grass fuels. The extra year of recovery provided sufficient surface fuels to completely burn treatment plots (Table 1). Fireline intensities were lower in 2010, averaging 420 ± 45 kW m^{-1} compared with 1286 ± 84 kW m^{-1} in 2008. Maximum flame length observed was 4 m (compared with 14 m in 2008). Fire temperatures were also 15% lower for surface measurements and 67% lower at 1·5 m. Fire behaviour and area burned statistics are summarized at the subplot level in Table 1.

For subplots that were randomly selected for herbicide treatments, herbicide was basally applied to all shrubs in those subplots by spraying a 75% diesel – 25% Remedy Ultra mix (triclopyr, Dow Agrosciences). When this experiment was established, basal application of this herbicide was regarded as the best approach for killing *Prosopis glandulosa* Torr. and other problematic shrub species and has been widely adopted by Texas landowners as a preferred management practice for killing established shrubs (Kreuter *et al.* 2001).

EXTREME PRESCRIBED FIRE DESIGN

All fire treatments were conducted with special exemptions during periods of government-imposed burning restrictions. To ensure containment of extreme prescribed fires and to prevent wildfires, a large 'buffer area' with little-to-no surface fuel was established at each site to provide sufficient space to prevent the ignition of spot fires and eliminate the potential for 'prescribed fire turned wildfire'. Surface fuels were removed in the buffer area prior to conducting extreme fire treatments by burning it in mild fire weather conditions (i.e. high fine fuel moisture, low temperature, high relative humidity, low wind speed). The buffer area was established downwind of the plots in the direction of the prevailing wind. Plots were oriented upwind of the buffer area in a horizontal configuration so that each experimental plot could be burned with a headfire (Fig. S1). The size of the buffer area was determined using quantitative predictions of spot fire distance in flat terrain (Albini 1981).

FIRE MEASUREMENTS

Flame lengths and fire temperatures were recorded in each subplot. Mean flame lengths were estimated visually along a 10-m transect that bisected the length of each 20 × 10 m subplot to calculate the mean fireline intensity of a given area. Peak fire temperatures were recorded using ceramic tile pyrometers, which were painted with 25 temperature-indicating lacquers that melted from 79 to 1038 °C (OMEGALAQ® Liquid Temperature Lacquers). Tile pyrometers were located on the downwind side of three randomly selected large shrubs (>1·5 m) in each subplot. The same shrubs were used to measure peak fire temperatures with tile pyrometers for those plots that were burned a second time in 2009 on the Coastal Bend and 2010 on the Edwards Plateau. A total of 648 tile pyrometers were used [2 tiles per tree location (1 tile at 0 cm + 1 tile at 150 cm) × 3 locations per subplot × 3 subplots per plot × 18 burned plots per site (12 in 2008 + 6 in 2009/2010) × 2 sites]. Details of how flame lengths and fire temperatures were measured are expanded on in Appendix S3.

WOODY VEGETATION MEASUREMENTS

Prior to applying fire and herbicide treatments, every individual shrub ≥100 cm tall was identified, measured and tagged to track individual responses to treatments. A total of 4203 shrubs were sampled in 2006 ($n = 1634$ at Coastal Bend; $n = 2569$ at Edwards Plateau). Because fires were designed to maximize fire severity and consume above-ground portions of the plant, shrubs in burned treatments were tagged by placing a metal flag with an aluminium tag hanging from it next to each individual. Tags were used to relocate each individual in 2011 to assess mortality.

Tagging individual shrubs in 2006 and tracking them for mortality enabled us to identify and record the recruitment of new juvenile individuals in 2011. Juvenile recruits were those individuals that were ≥100 cm tall in 2011 but were not measured in 2006 because they were either too small (i.e. <100 cm) or were not present.

DATA ANALYSIS

To determine how the density of shrubs changed in response to the treatments, percentage of change was calculated by comparing the number of individuals in 2006 (denoted by the number of tagged individuals) to the number of individuals in 2011 (denoted by the number of tagged individuals plus new recruits) for each subplot. Percentage of mortality was calculated by dividing the number of tagged shrubs that died in 2011 to the number of tagged shrubs that were alive at the beginning of the study in 2006. Values for each subplot were used to test for differences in the percentage of change in the density of shrubs using split plot analysis of variance. Pairwise comparisons were made for each treatment combination using Student's t-test. The hypotheses associated with this test were established prior to the initiation of the study, so pairwise comparisons between treatments were made using Tukey's HSD. Logistic regression was used to test whether the relationship between the probability of mortality and tree height differed among treatments for each of the study sites, as indicated by the likelihood ratio chi-square statistic for treatment.

Results

POTENTIAL OF EXTREME FIRE IN DROUGHT FOR INTERVENTION

Extreme fires in droughts produced consistent changes to the density and structure of the woody plant communities in both ecological regions. A single extreme fire in drought resulted in shrub densities that were 35–55% lower than shrub densities in control treatments (not burned, no herbicide) also subject to drought conditions, and the magnitudes of change were remarkably consistent at both sites (Fig. 2). Densities of resprouters were lower 3 years after applying extreme fire because mortality of established individuals exceeded recruitment of new individuals for multiple species, whereas recruitment exceeded mortality in control plots, despite drought conditions (Table 3). Changes (%) in shrub height and crown area

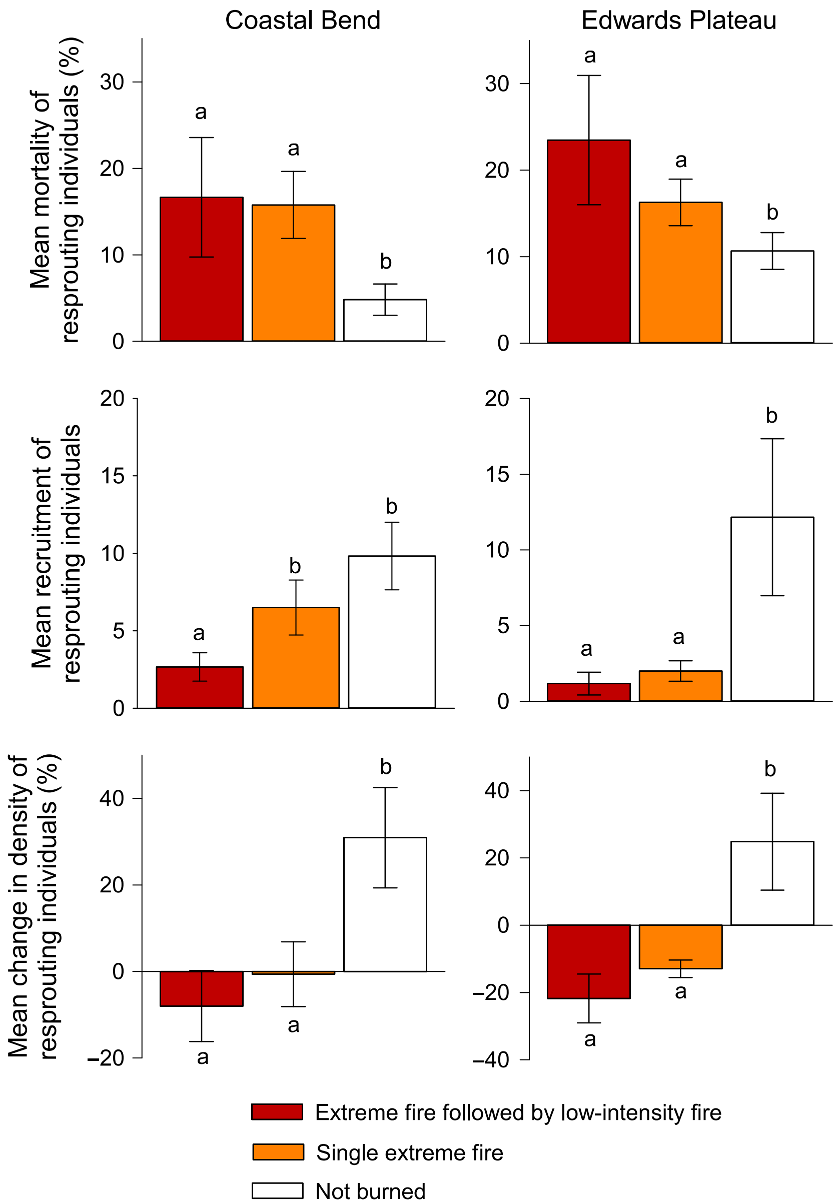

Fig. 2. Resprouter densities following extreme prescribed fire treatments (extreme fire followed by a low-intensity fire and single extreme fire) relative to the control (not burned) in subhumid (Coastal Bend) and semi-arid (Edwards Plateau) ecoregions. Data are presented as the mean (± SE) mortality and recruitment resulting in the percentage of change in the density of resprouting woody plants 3 years after conducting initial treatments. Different letters denote significantly different treatment means ($P < 0{\cdot}05$). Note the scale of the *y*-axis differs between experimental sites.

per individual were significantly lower at both sites following a single extreme fire treatment compared with not burning (Fig. 3), whereas percentage of change in the number of stems per individual increased (Fig. 3). Relative differences in the contribution of the most common species to the population metrics height, crown area and stem number did not differ among treatments (Table S1), indicating that species are not having a major effect on treatment response.

Following an extreme fire with a low intensity fire did not significantly increase mortality or reduce densities beyond the initial extreme fire event (Fig. 2). Shrub mortality was therefore interpreted to primarily be a result of the first burn. Mortality was defined as shrubs that were without foliage for 3 years after initial treatment. For plots where extreme fire was followed by a low-intensity fire, this definition of mortality assumes shrubs without foliage were killed 1 year after the second fire on the Edwards Plateau and 2 years after the second fire on the Coastal Bend. Because we observed many shrubs resprout after 2 years of no foliage in the single extreme fire treatment (whereas no shrubs were observed to resprout after 3 years without foliage), this assumption could have led to an overestimation of mortality in plots burned twice; however, mortality did not differ between burn treatments, making this assumption reasonable for the objectives of this study.

Following extreme fire with a low intensity fire decreased the height and crown area of shrub individuals relative to pre-treatment more than a single extreme fire on the Edwards Plateau, while percentage change in number of stems did not differ (Fig. 3). Changes (%) in shrub height, crown area and number of stems did not differ between the two burn treatments on the Coastal Bend (Fig. 3).

The relationship between probability of mortality and shrub height differed among experimental treatments (Table 4). On both the Coastal Bend and Edwards

Table 3. Summary of common woody resprouter species present in the experiment and their responses across fire treatments. Data are for the total number of resprouting individuals sampled prior to treatment in areas that were part of burn treatments but were not sprayed with herbicide (total in 2006 across all treatments, n_o), total number of new recruits (new individuals in 2011, n_r) and the relative rates of mortality in 2011 (percentage of mortality, $\%_m$) observed for each shrub species*

		Extreme fire + low-intensity fire						Single extreme fire					
Shrub species	Ecological region	n_o	$\%_m$	n_r	ΔHt	ΔCA	Δn_s	n_o	$\%_m$	n_r	ΔHt	ΔCA	Δn_s
Larger shrubs													
Acacia farnesiana (L.) Willd.	Coastal Bend	38	53	5	−70	−33	57	29	41	9	−34	19	74
Prosopis glandulosa Torr.	Coastal Bend	38	8	1	−46	−23	168	25	8	3	−21	−3	140
	Edwards Plateau	121	17	2	−75	−79	217	118	16	1	−82	−49	161
Juniperus pinchotii Sudw.	Edwards Plateau	12	67	0	−74	−84	−100	4	25	1	−72	−80	−100
Diospyros texana Scheele	Coastal Bend	25	16	2	−20	−39	53	18	6	8	−51	−41	107
	Edwards Plateau	33	21	2	−84	−91	280	26	20	0	−67	−61	534
Acacia rigidula Benth.	Coastal Bend	17	5	2	−25	−51	143	14	10	4	4	−7	34
Acacia greggii A. Gray	Coastal Bend	16	6	2	−18	−22	182	13	0	4	−26	−36	134
Celtis ehrenbergiana (Klotzsch) Liebm.	Coastal Bend	12	0	1	13	35	108	11	0	1	3	−1	96
Smaller shrubs													
Mahonia trifoliolata (Moric.) Fedde	Coastal Bend	22	18	0	−51	−77	−31	26	15	1	−29	−55	31
	Edwards Plateau	33	39	0	−87	−94	−56	26	15	0	−82	−95	−61
Aloysia gratissima (Gillies & Hook.) Troncoso	Edwards Plateau	60	18	3	−81	−58	371	83	16	10	−54	0	231

		Not burned					
Shrub species	Ecological region	n_o	$\%_m$	n_r	ΔHt	ΔCA	Δn_s
Larger shrubs							
Acacia farnesiana (L.) Willd.	Coastal Bend	55	4	16	44	213	6
Prosopis glandulosa Torr.	Coastal Bend	37	14	5	−24	0	47
	Edwards Plateau	76	12	1	−43	−43	111
Juniperus pinchotii Sudw.	Edwards Plateau	8	0	1	19	73	0
Diospyros texana Scheele	Coastal Bend	25	0	2	15	49	−3
	Edwards Plateau	42	0	26	16	44	68
Acacia rigidula Benth.	Coastal Bend	8	0	7	7	78	35
Acacia greggii A. Gray	Coastal Bend	20	5	10	10	46	75
Celtis ehrenbergiana (Klotzsch) Liebm.	Coastal Bend	13	0	2	20	59	16
Smaller shrubs							
Mahonia trifoliolata (Moric.) Fedde	Coastal Bend	15	0	1	−11	5	9
	Edwards Plateau	30	20	3	−46	−75	73
Aloysia gratissima (Gillies & Hook.) Troncoso	Edwards Plateau	18	6	39	26	188	160

*A total of 1297 individual shrubs were sampled in 2006 across the burned treatments that did not experience herbicide across the two sites and were relocated again in 2011 to assess mortality (a total of 4203 individual shrubs occurred in both the fire and herbicide treatments; data for shrubs in areas where herbicide was applied are not provided here).

Plateau, probability of mortality increased with increasing shrub height in the extreme fire followed by low-intensity fire treatment (Fig. 4). In the single extreme fire treatment, probability of mortality remained constant with increasing shrub height on the Edwards Plateau, whereas it declined with increasing shrub height on the Coastal Bend. In contrast, probability of mortality decreased with shrub height in the control at both sites (Fig. 4).

POTENTIAL OF EXTREME FIRE AND HERBICIDE FOR INTERVENTION

We observed significant fire and herbicide interaction effects on resprouter densities for both ecological regions ($F_{4,30} = 2{\cdot}76$, $P = 0{\cdot}046$ at Coastal Bend; $F_{4,30} = 3.15$, $P = 0.028$ at Edwards Plateau); however, this effect was driven by the herbicide treatment alone, not its interaction with fire, and therefore does not reflect a statistical interaction that is relevant to the second hypothesis tested in this experiment. Fire and herbicide combinations did not significantly reduce densities of shrubs compared with herbicide alone at either site (Fig. 5), and no clear advantage was observed for shrub height, stem number or crown area over herbicide alone (Fig. S2). Our data therefore do not support the combinations of extreme prescribed fire and herbicide featured in this study as potentially novel intervention techniques in resprouting shrublands of the southern Great Plains.

Discussion

Our evaluation of novel interventionist approaches provides new insight into the role of fire in limiting biogeographical distributions and abundances of resprouting

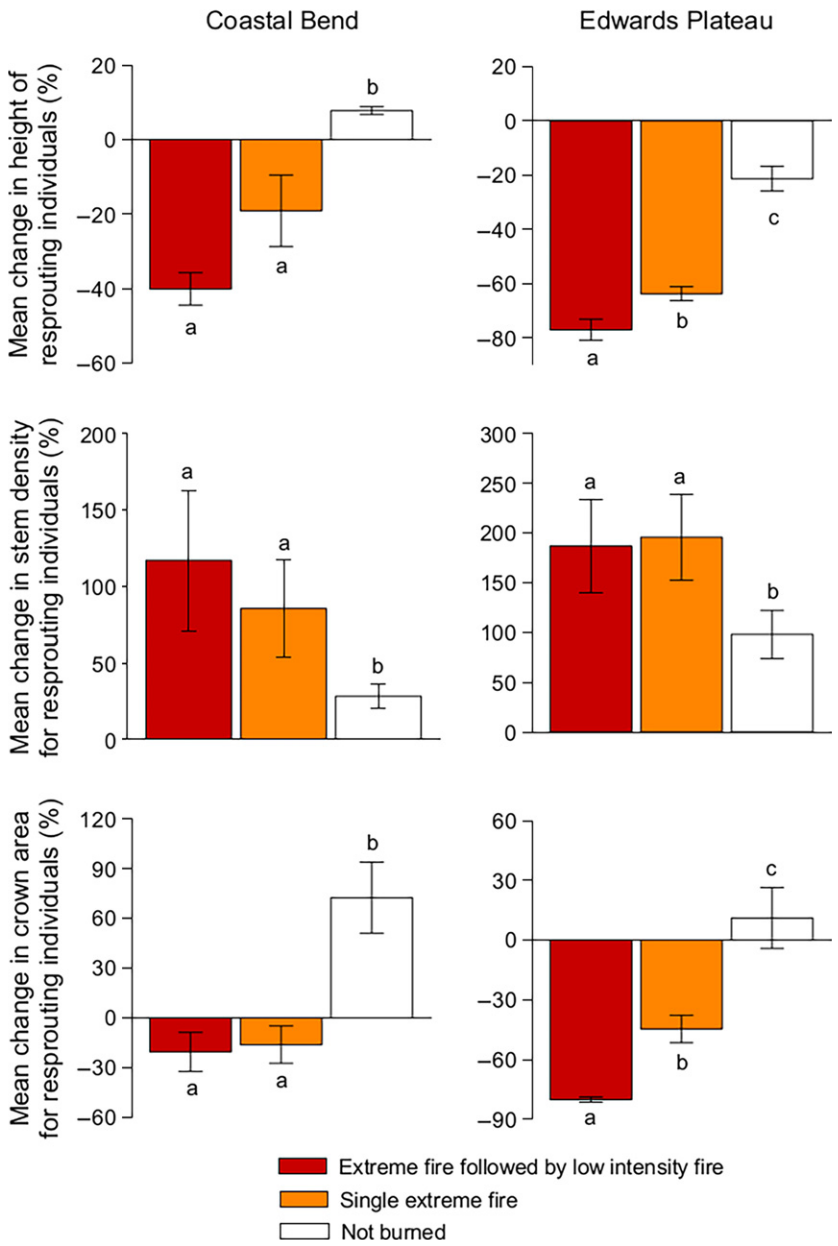

Fig. 3. Changes (percentage of mean ± SE) in height, number of stems and crown area of individual resprouters among treatments 3 years after initial applications of extreme fire treatments. Different letters denote significantly different treatment means ($P < 0{\cdot}05$). Note the scale of the y-axes differ among panels.

woody species. The expansion of woody resprouters occurs as a result of (i) establishment of new individuals into patches of grassland (Archer *et al.* 1988) and (ii) clonal stems extending into grassland patches from existing individuals (Ratajczak *et al.* 2011). In this study, fires exhibiting extreme behaviour and occurring during periods of precipitation deficit have resulted in exceptionally high levels of mortality across all height classes and limited recruitment for both clonal and non-clonal resprouting species, thereby resulting in 35–55% lower densities of resprouters than in areas not burned. This finding counters the prevailing scientific and management purviews that (i) fire is incapable of causing mortality sufficient to decrease densities in resprouting shrublands and (ii) tall resprouting shrubs escape the fire trap and are less likely to be killed than smaller size classes. In addition, fires reduced crown area 43% to 81% on the Edwards Plateau and 18% to 26% on the Coastal Bend, which could be key to the re-establishment and long-term recovery of the herbaceous layer.

Contrary to the fire and weather conditions targeted in this study, both scientific experiments and fire management policies typically minimize fire intensity and avoid drought episodes (Twidwell *et al.* 2016a,b). Limiting fires to times of saturation in soil moisture weakens competitive feedbacks in tallgrass prairie that support C4 dominance over shrubs during periods of soil moisture depletion (Ratajczak *et al.* 2011). Rates of woody plant recruitment and recovery exceed mortality in such conditions, resulting in woody plant expansion (Enslin *et al.* 2000; Higgins *et al.* 2007). In contrast, the spatial boundary of woody islands can be expected to retreat, or islands

Table 4. Results of logistic regression for the Coastal Bend and Edward's Plateau

Site	Variable	d.f.	Coefficient	Standard error	Wald χ^2	*P* value
Coastal Bend	Intercept	1	−0·44	0·593	−0·746	0·455
	Height	1	0·10	0·230	0·434	0·664
	Treatment	1	−0·86	0·207	−4·128	<0·0001
Edwards Plateau	Intercept	1	−0·44	0·309	−1·442	0·149
	Height	1	0·0006	0·113	0·005	0·996
	Treatment	1	−0·63	0·132	−4·786	<0·0001

For the Coastal Bend, the likelihood ratio chi-square statistic for the final model was 20·80 (d.f. = 2, $P < 0{\cdot}001$). The McFadden $R^2 = 0{\cdot}39$, with values in the range of 0·2 to 0·4 indicating excellent fit (McFadden 1974). For the Edwards Plateau, the likelihood ratio chi-square statistic for the final model was 25·29 (d.f. = 2, $P < 0{\cdot}001$). The McFadden $R^2 = 0{\cdot}32$, with values in the range of 0·2 to 0·4 indicating excellent fit (McFadden 1974).

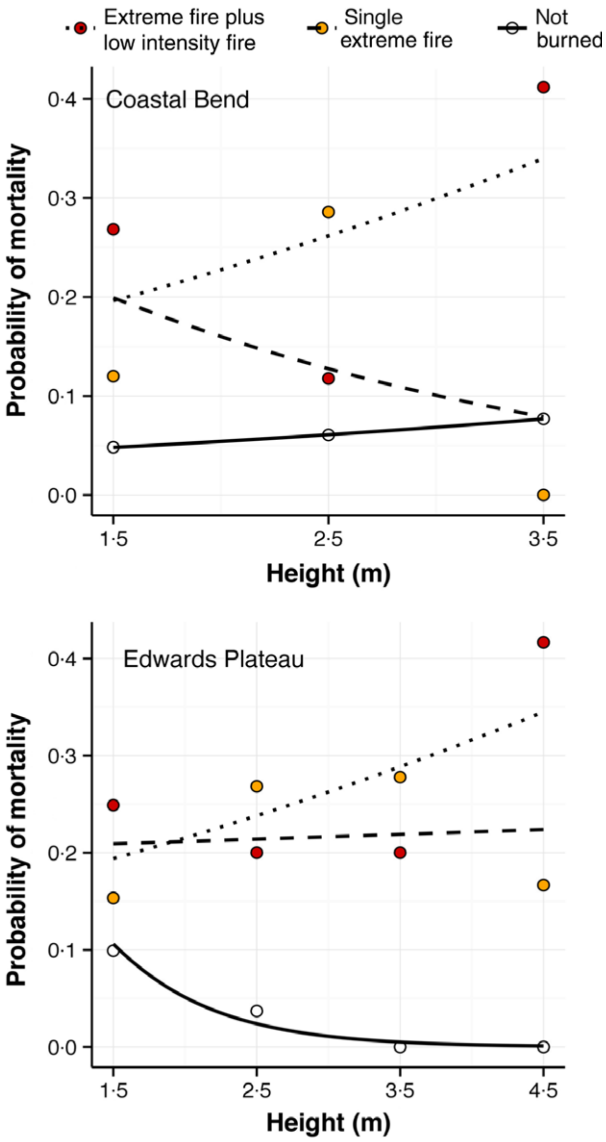

Fig. 4. Relationships between shrub height class (m) and probability of mortality following extreme fire treatments (data for the combination of extreme fire and herbicide are not given here).

can be removed altogether, when fire-induced mortality exceeds recruitment, which occurred in this study following extreme fires during drought.

Resprouting theory and the persistence niche concept establish a mechanism capable of contributing to explanations of spatiotemporal shifts in the boundaries of grass and resprouting woody alternative states. In fire-prone environments, basal resprouters persist by protecting buds below ground and remobilizing subterranean non-structural carbohydrates to foster new stem growth (Clarke *et al.* 2013) and by initiating local feedbacks that reduce herbaceous fuel loading or increase herbaceous fuel moisture near stems, thereby reducing thermal damage (Eldridge *et al.* 2011). Based on these persistence pathways, mortality of basal resprouters can theoretically occur from fire as a result of (i) thermal senescence of buds and subsequent depletion of bud bank availability and (ii) the inability for individuals to remobilize below-ground non-structural carbohydrates for stem development. It is anticipated that most individuals killed in this study did so from the exhaustion of below-ground resources (although glowing combustion and transfer of heat to below-ground buds were observed for a small number of large diameter, single stemmed individuals; data not shown).

Little is currently known, however, about how interactions between variability in the magnitude of fire intensity and deficits in plant-available water contribute to resprouting potential. Additional investigation is needed to determine whether extreme fires in drought are needed to cause the types of mortality observed in this study, or whether low-intensity fires conducted in a drought would cause similar outcomes. We do not consider this to be a likely outcome given the occurrence of dense shrub clusters in both study regions. Fuel gaps occur beneath the canopies of dense shrub clusters and disrupt the propagation of low-intensity fires and the amount of area burned (Twidwell *et al.* 2009; note that approximately 50% of plots remained unburned on the Coastal Bend in the second, low-intensity fire treatment in 2009). In such cases, individual shrubs located in the interior of the cluster are not exposed to the fire and would respond more like our control treatments. We emphasize, though, that different outcomes may manifest in other shrublands, particularly for those that do not create patchy distributions of grassland fuels.

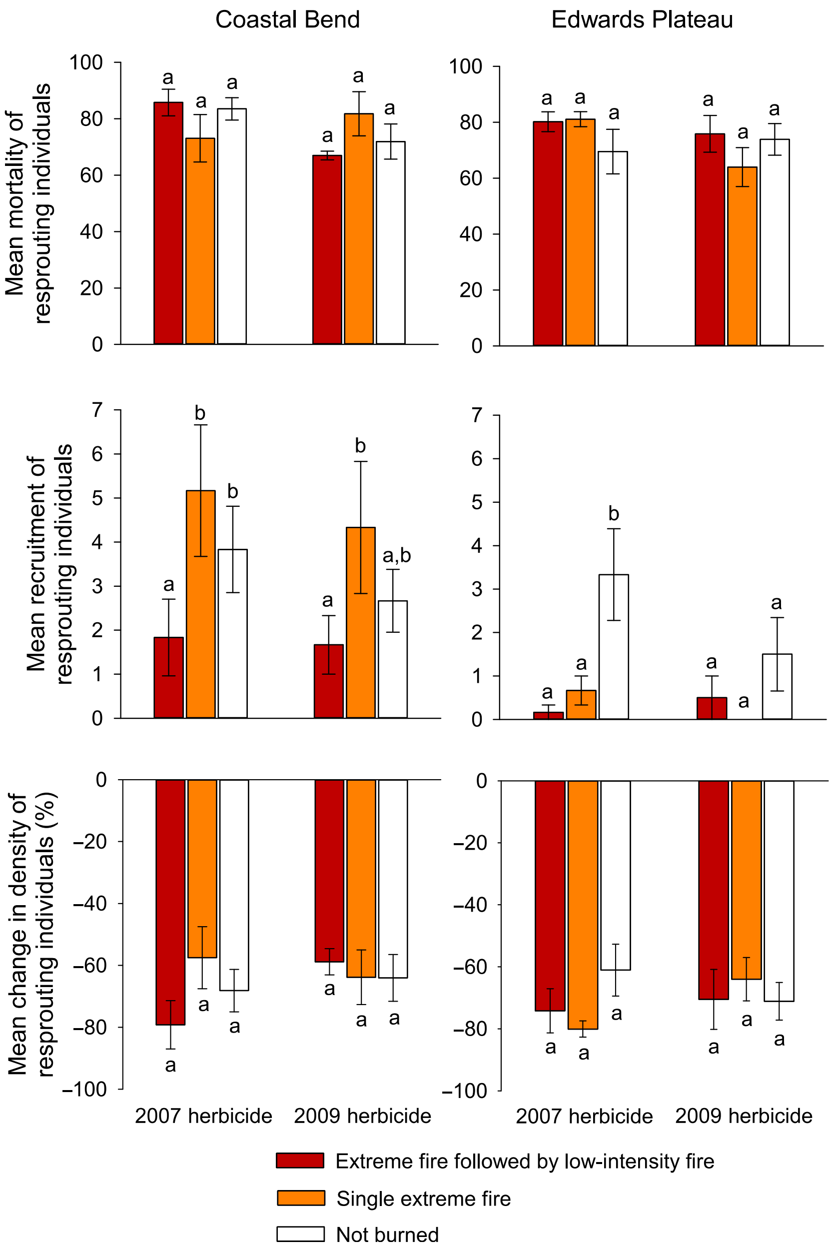

Fig. 5. Resprouter densities among treatments that combined extreme prescribed fire and herbicide compared with plots that were treated only with herbicide (not burned). Data are presented as the mean (± SE) mortality and recruitment driving percentage of change in the density of resprouting woody plants 3 years after conducting initial treatments. Different letters denote significantly different treatment means ($P < 0{\cdot}05$).

A consistent counter to restoring historical fire regimes in grasslands is that herbicides are a modern day surrogate for fire and even better at controlling woody plants (Mitchell, Whisenant & Sosebee 2004). It is well established that herbicide is a very effective technique for killing resprouting woody species (DiTomaso 2000) and its use in this study resulted in considerably higher rates of mortality than extreme fire. Over the last several decades, intensive herbicide programmes have been the prominent approach for attempting to restore grasslands following shrubland encroachment in the southern Great Plains. Yet, dense shrublands dominate the region, despite annual expenditures of tens of millions of dollars by natural resource agencies in the United States (Twidwell, Allred & Fuhlendorf 2013). So while herbicides are effective at killing established individuals and slowing woody plant recruitment, they fail to address the scale of the transformation. Economic constraints limit herbicide use to a relatively small area compared with the spatial extent of woody plant expansion (Twidwell, Allred & Fuhlendorf 2013). Additionally, herbicides are typically applied after woody plants become established and the transformation is already underway, whereas self-reinforcing feedbacks in grasslands and savannas promote more frequent and intense fires prior to woody establishment, reducing the need to react to woody plant expansion with intensive interventions. Finally, herbicides do not create the types and ranges of heterogeneity in grassland structure that are critical to grassland biodiversity of non-plant taxa. For these reasons, it is our view that herbicides should not be used as a replacement for fire regimes and greater recognition is needed of the potential spatiotemporal scale of impact of herbicides relative to fire.

Even with such recognition, restoring the extreme fire and drought interaction as part of modern day fire regimes comes with social–ecological challenges and trade-offs. Strong opinions from the public at large can be expected that question the appropriateness of extreme fire in modern ecosystem management (Toledo, Sorice & Kreuter 2013). Increasingly, however, fire researchers are calling attention to human controls over fire (Trauernicht *et al.* 2012; Valko *et al.* 2014), the critical absence of high-intensity fires in fire management (Twidwell *et al.* 2016a) and their importance in structuring grasslands (Twidwell *et al.* 2013a), savannas (Keeley & Zedler 2009; Taylor *et al.* 2012) and forests (Swanson *et al.* 2010). The prevailing assumption has been that extreme fire cannot be controlled in modern landscapes, but cases do exist for humans to manipulate and control fire on the landscape during conditions that lead to extreme fire behaviour (as done in this study). Furthermore, in localized areas, private citizens are acquiring special exemptions to apply extreme fires during periods of government-mandated burning restrictions (Twidwell *et al.* 2013b). Applied fire ecologists can assess the potential utility and trade-offs of extreme fire for ecological intervention using, for example, spatial fire models to explore new fuel and fire break designs at landscape and ecoregion scales. Such approaches will answer questions on whether opportunities exist, especially in grassland and savanna ecosystems adjacent to agricultural lands or large water bodies, to control extreme prescribed fires at broad spatial extents.

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Data accessibility

Data from this study have been deposited in Dryad Digital Repository doi:10.5061/dryad.7rf84 (Twidwell *et al.* 2016b).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Illustration of experimental design.

Fig. S2. Structural change following combination of fire and herbicide treatments.

Table S1. Test of contribution of species to structural differences among treatments.

Appendix S1. Technical definition for extreme fire.

Appendix S2. Additional study site details.

Appendix S3. Fire behaviour measurements.