



Plant community response to the East Amarillo Complex wildfires in the Southern High Plains, USA

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Abstract: Severe wildfires are increasing in extent in the western US. We used a matched-pairs design with plots in burned and non-burned areas to study effects of the East Amarillo Complex (EAC) wildfires on mixed grass prairie mean community composition and variability in composition. Species composition and ground cover data were collected at 5 study sites each year for three years following the EAC. Fire effects on mean species composition were analyzed with permutational analyses of variance; temporal patterns were analyzed with permutational anova and nonmetric multidimensional scaling; and an index of multivariate dispersion was used to assess variability in plant community composition. We found weak immediate impacts (year 1) of wildfire on mean species composition, but strong impacts by year three. Two general patterns of changes in mean species composition emerged: at 3 study sites, there was a progressive divergence in similarity between burned and non-burned areas following wildfire whereas at 2 study sites, wildfire effects lessened over time. In contrast, a trend of increased homogeneity in burned vegetation relative to non-burned vegetation was apparent at all 5 study sites 2 to 3 years post-fire; burned areas also had higher species diversity, higher evenness but similar species richness 3 years post-fire. Ground cover composition, which was immediately impacted by wildfire through removal of residual dry matter, was fully recovered to non-burned conditions 3 years after wildfire. We observed little seedling recruitment either of native or exotic species following wildfire. Community composition changes in burned areas were likely the result of changing dominance relationships among plants that survived the wildfires rather than the result of recruitment of new individuals in gaps created by dead plants. Given the growth form of perennial C₄ grasses and the fact that these grasslands evolved in the context of repeated fire, it is likely that changes in mean species composition and compositional variability are short-term responses.

Abbreviations: EAC—East Amarillo Complex; IMD—Index of Multidimensional Dispersion; MDS—Multidimensional Scaling.

Introduction

Ecological literature is rich in information about wildfire and prescribed fire effects on individual plant species where plant responses are typically measured with estimates of cover, biomass (Ansley and Castellano 2007) or individual mortality [the latter is particularly common with woody species (Wright et al. 1976) and cacti (Vermeire and Roth 2011)]. At the plant community level in grasslands, fire impacts are usually measured by effects on forage production (Wright and Bailey 1982 and references therein)—that is, biomass is either harvested en masse (e.g., Scheintaub et al. 2009) or by individual plants (e.g. Augustine and Milchunas 2009) and then analyzed by growth form (e.g., forb, grass, and shrubs; Bidwell and Engle 1992, Scheintaub et al. 2009, Vermeire et al. 2011, 2014) or total standing crop (Rideout-Hanzak et al. 2011, Vermeire et al. 2011). In this context, biomass is best considered the *collective* response of the many species and individuals that comprise a plant community rather than the multivariate, or compositional, response of the community.

When fire effects are measured by these collective responses, it commonly has been found that plant response is strongly affected by season of burning (Wright and Bailey 1982 and citations therein) and plant morphology/location of perennating tissues (Bond and Medgley 2001, Bidwell et al. 2005); further, even when short-term effects on plant mortality are negative, longer-term responses of standing crop are minimal (Rideout-Hanzak et al. 2011, Vermeire et al. 2011, 2014).

Unlike biomass data, plant community species composition is multivariate in nature. Community-level analyses based on species composition are potentially powerful (Orloci 1978, Manjarres-Matrinez et al. 2012) for detecting vegetation responses to fire (Bidwell and Engle 1992, Spaeth et al. 2007, Duff et al. 2013) that may be obscured by analyses based on individual- or collective-plant responses. First, univariate analyses fail to capitalize on the correlated responses of individual species to wildfire. Second, an analysis based on a collective response (e.g., biomass) can be misleading if individual species respond differently to wildfire without,

however, affecting their collective response. For example, we (Rideout-Hanzak et al. 2011) found an initially small effect of the EAC wildfires on biomass that further diminished 2 to 3 years post-fire; in contrast, in the current paper we detect wildfire effects on species composition that become more pronounced 2 and 3 years post-fire.

There are a number of multivariate tools available to study compositional changes between treatments and over time. Ordination techniques have a rich history in ecological studies: the ability to summarize multivariate patterns in 2- or 3-dimensional diagrams is a powerful tool to display and communicate results. Ordination analyses, however, typically do not lead to inferential conclusions, and visual inspection of ordination diagrams has an element of subjectivity that can affect one's judgment. In contrast, permutational analysis of variance allows for tests of hypotheses that address mean species composition as well as variability in species composition in a multivariate sense and that are (provisionally) nonparametric (Anderson 2001).

Many traditional statistical tests of hypotheses in ecological research address equality of means among groups: the focus on 'central tendency' has a long tradition. It is also true that some have argued that "variation is the hard reality, not a set of imperfect measures for central tendency" (Gould 1985, 1996). We believe that understanding wildfire effects on *variation* in species composition can be as informative as understanding wildfire effects on *mean* composition (e.g., Landres et al. 1999).

In this study, we investigated mixed grass prairie plant community responses to the East Amarillo Complex wildfires of 2006. We focus on two community-level responses: *mean* species composition and *variability* in species composition measured 1, 2 and 3 years post-fire using multivariate analyses that are inferential (with permutational analyses of variance) as well as pattern-seeking (with an index of multivariate dispersion and nonmetric multidimensional scaling ordination).

Methods

The East Amarillo complex wildfires

On 12 March 2006, two separate wildfires were ignited and reported within minutes of each other in the Texas Panhandle. Together these fires became known as the East Amarillo Complex (EAC). They were contained within 4 days, burning over 367 000 hectares during that time. The EAC was the culmination of weather conditions beginning with surplus rainfall during the fall of 2004 and ending with 8 months of drought preceding the fires. The rate of spread (ROS) of these "classic, cigar-shaped, wind-driven wildfires" (R. Mutch, pers comm) in the first 24 hours was unprecedented; the northernmost fire traveled approximately 72 km in the first 9 hours (Zane et al. 2006). This ROS was the result of extreme weather conditions (prolonged drought, low relative humidity, high winds). Effects on the human scale were unsurpassed in Texas history: 12 human lives were lost, over

4 000 head of livestock perished, and over 89 structures and 2 000 miles of fence were destroyed (Zane et al. 2006). This wildfire complex was the largest in the contiguous 48 states since the 1988 Yellowstone fires (NIFC 2013). Its occurrence appears to extend to western grasslands the prediction (Westerling et al. 2006, also see Marlon et al. 2009) that size and severity of forest wildfires in western states will increase as a result of anticipated global climate change.

Study sites

Study sites were located on Mixedland Slopes (R077EY061TX; USDA 2008) ecological sites in Gray, Donley and Roberts counties in the northern Panhandle of Texas. Study sites were located on privately-owned ranches and were selected in August and September 2006 after the fires. Based on field reconnaissance, we selected burned areas that represented the general landscape and that could be paired with similar non-burned areas. We could not control for differences in past or current land management practices. Mixedland Slopes are characterized by Mobeetie fine sandy loams (Coarse-loamy, mixed, superactive, thermic Aridic Haplustepts). Polar very gravelly sandy loams (Loamy-skeletal, mixed, superactive, thermic Ustic Haplocalcids) and Potter gravelly loams (Loamy-skeletal, carbonatic, thermic petronodic Ustic Haplocalcids) and slopes >5% are also present. Many of these sites are mapped as soil complexes that also include heavier-textured soils. Common species include little bluestem (*Schizachyrium scoparium* [Michx.] Nash), sideoats grama (*Bouteloua curtipendula* [Michx.] Torr.), hairy grama (*B. hirsuta* Lag.), sand dropseed (*Sporobolus cryptandrus* [Torr.] A. Gray), Indiangrass (*Sorghastrum nutans* [L.] Nash) and sand bluestem (*Andropogon gerardii* var. *paucipilus* [Nash] Fern.); many areas support scattered sand sagebrush (*Artemisia filifolia* Torr.) (USDA 2008). These sites have species composition and structural features typical of mixed-grass prairies.

Field methods

Because we were studying wildfires, pre-burn data were not available. Our assessment of wildfire effects was therefore based on a comparison of burned areas and nearby non-burned areas that represented controls (see Wiens and Parker 1995, Rideout-Hanzak et al. 2011). We established five pairs of study plots in fall 2006 that were re-measured in late summer 2007 and 2008. We used a "matched-pairs" (Wiens and Parker 1995) design: plots in burned areas that were representative of the surrounding landscape and which could be paired with plots in non-burned areas with similar slope and aspect within the same management unit were selected. Study areas averaged about 5 ha in area and were marked with posts so that they could be re-located for future sampling. It is also important to note that these wildfires were elliptically shaped because of high wind speeds (Pyne 1984). Thus, non-burned plots outside the fires' flanks were located in areas that did not burn because the fire could not flank well against such high winds, rather than because of differences in vegetation,

fuels or prior management. At each study site we established three 100-m step-point transects (Evans and Love, 1957); starting points and directions were randomly chosen and re-randomized each year of sampling. We recorded the identity of the nearest plant at each of 50 points along each transect; at each point, ground cover was described as bare ground, vegetative basal cover, litter or cow (*Bos* spp.) feces. This sampling method allows us to estimate both species composition and ground cover composition.

Data analysis

We used PERMANOVA+ and PERMDISP (version 1.0.3 in PRIMER-E, Ltd., version 6.1.13, Plymouth, UK) to test for differences in mean species composition and variability (or dispersion) in species composition, respectively, among study areas in non-burned sites in 2006; the Bray-Curtis coefficient (without transformation or standardization) was used for a similarity measure. In this analysis each study site represented a population of interest that was sampled with 3 transects (Wester 1992). Results from this analysis indicated that species composition differed among study sites prior to the wildfires (likely because of inherent site effects and land owner practices) and confirmed the appropriateness of our matched-pairs study design. Because of different initial species composition among sites, subsequent analyses tested for fire effects as well as time effects on species composition on a within-site basis. In these analyses, each pair of two study sites (i.e., a burned site and its paired non-burned site) represented populations of inference. In each year, these study sites were sampled with 3 transects (which were randomly relocated each year). Thus, analyses were based on data from burned and non-burned sites (see Littell et al. 2006 for a discussion of “multi-location” analyses) over 3 years, leading to a 2-way analysis of variance (e.g., Kempthorne 1952) that provided tests of wildfire effects, year effects, and their interaction. When wildfire and year of sampling interacted, we tested simple main effects of each factor prior to examining simple effects (Kirk 1995).

Following Jost (2010), we partitioned species richness (S) into independent measures of species diversity ($\exp H'$, where H' is Shannon's index) and species evenness ($\exp H'/S$). Because these diversity indices are not normally distributed, (Fritsch and Hsu 1999, Rogers and Hsu 2001), we used permutational analysis of variance with Euclidean distance as a resemblance measure to test effects of wildfire, time of sampling and their interaction.

We used nonmetric multidimensional scaling in meta-MDS in R (version 1.17-5. <http://CRAN.R-project.org/package=vegan>) for plant community and ground cover ordination; the Bray-Curtis coefficient (without transformation or standardization) was used as a similarity measure. Scree plots (McCune and Grace 2002) were used to determine the number of ordination axes.

We used an index of multidimensional dispersion (IMD; Warwick and Clarke 1993) to compare relative variability in species composition among transects between non-burned

and burned sites at each study area. A value of IMD near zero indicates little difference between burned and non-burned sites; a value of IMD that increases from 0 toward +1 indicates that burned vegetation is more heterogeneous than non-burned vegetation (or, equivalently, that non-burned vegetation is more homogeneous than burned vegetation); an IMD value decreasing from 0 toward -1 indicates that non-burned vegetation is more heterogeneous than burned vegetation. As an index, IMD is descriptive rather than inferential.

Weather records

Closest weather stations to our study sites are McLean, TX (Gray Co.) and Pampa, TX (Gray Co.). Because rainfall data can be spatially variable, we averaged monthly and seasonal precipitation data from NOAA (www.ncdc.noaa.gov/oa/ncdc) and West Texas Mesonet (www.mesonet.ttu.edu) sites.

Results

Precipitation

Seasonal rainfall at Pampa, TX (Fig. 1) and McLean, TX (data not shown) was generally at or above average in 2004 (2 years before the fire); at or below average in 2005 and 2006; and at or above average in 2007 and 2008.

First-year species composition analyses—Non-burned sites

Mean 2006 species composition differed among our 5 non-burned study sites in 2006 (PERMANOVA $F_{4,10} = 26.9$, $P = 0.0001$, Table 1). There was no evidence (PERMDISP $F_{4,10} = 2.9$, $P = 0.189$), however, that variability in species composition differed among non-burned study areas in 2006.

Wildfire and time effects on mean species composition

Wildfire and year of sampling interacted ($P < 0.05$, $df = 2, 12$) in their effects on mean species composition at 4 of 5 study sites. Subsequent analyses therefore examined wildfire effects in each year of sampling and time effects in each burn treatment.

Wildfire effects. Immediate (2006) effects of wildfire on mean species composition were strong ($F_{2,12} = 10.96$, $P = 0.0003$) only at one site (Flowers 1; Table 2). In contrast, there were no immediate effects ($F_{1,4} = 2.54$, $P = 0.1060$) of wildfire on mean species composition at Burger and weak effects ($0.0468 < P < 0.0584$, $df = 4$) at the remaining sites. Wildfire effects on mean species composition were stronger in 2007 (affecting 4 of 5 study sites) and even stronger in 2008 (affecting all 5 study sites) than they were in 2006.

Changes over time. Mean species composition was stable ($0.0664 < P < 0.7583$) over time at 3 non-burned sites (Burger, Flowers 2 and Shaw 2); on burned areas at these sites, however, mean composition changed over time but followed site-specific patterns that were difficult to generalize

(Table 2). For example, mean species composition on burned Burger differed each year. At Shaw 2, mean composition at the burned site in 2006 differed from mean composition in 2007 and 2008; species composition was similar, however, in these latter two years. At Flowers 2, mean burned composition changed from 2006 to 2007 but recovered in 2008. Fire and year of sampling interacted ($F_{2,12} = 2.09, P = 0.0463$) at Shaw 1 and in contrast to the other study sites, we detected changes in mean composition on non-burned areas as well as on burned areas. Finally, in contrast to the foregoing 4 sites, wildfire and year of sampling did not interact ($F_{2,12} = 1.63, P = 0.1084$) at Flowers 1 although both main effects were significant ($P < 0.0002, df = 2,12$): mean composition differed each year on both burn and non-burned sites and composition differed between burned and non-burned sites.

Effects on species richness, diversity and evenness

Wildfire and year of sampling acted independently ($P > 0.5069$) in their effects on species richness at each study site (Table 3). Species richness was higher ($F_{1,12} = 17.8, P < 0.0014$) on the burned site at Shaw 2; at the other 4 study sites, however, wildfire did not affect ($P > 0.2216$) richness. Additionally, richness remained constant ($P > 0.1544$) over time at 4 of 5 study sites; at Shaw 1, richness was lower ($t_{1,8} = 2.5, P < 0.0387$) in 2006 than in 2007 or 2008.

Wildfire increased ($P < 0.0291$) species diversity at 4 of 5 study sites, and this effect was independent ($P > 0.0881$) of year of sampling (Table 4). In addition, diversity did not differ ($P > 0.1055$) across years at 3 of these sites; at Shaw 1, however, diversity progressively increased from 2006 through 2008. Wildfire and sampling year interacted ($F_{2,12} = 1.88, P < 0.0366$) only at Flowers 1: at this study site, diversity was not affected ($P > 0.0769$) by wildfire during any sampling year; diversity was similar across years in burned areas ($P > 0.0855$); and diversity was lower in 2007 than in 2008.

Table 1. Average Bray-Curtis similarity in species composition within and between sites on non-burned study sites in 2006. Study sites differed with respect to average species composition (PERMANOVA $F_{4,10} = 26.9, P = 0.0001$); within-site dispersions did not differ (PERMDISP $F_{4,10} = 2.9, P = 0.188$).

Study site	Study site				
	Burger	Flowers 1	Flowers 2	Shaw 1	Shaw 2
Burger	74.7 ¹⁾	16.0 ²⁾ 0.0004 ³⁾	24.8 0.0010	10.1 0.0008	11.7 0.0008
Flowers 1		83.4	44.1 0.0022	60.8 0.0034	67.6 0.0210
Flowers 2			76.6	26.8 0.0004	35.4 0.0012
Shaw 1				83.9	76.8 0.1482
Shaw 2					77.1

¹⁾ Diagonal entries are within-site Bray-Curtis similarities.
²⁾ Off-diagonal entries are between-site Bray-Curtis similarities
³⁾ Monte-Carlo *P*-values associated with between-site pairwise comparisons.

Wildfire and year of sampling acted independently ($P > 0.0881$) in their effects on species evenness at 4 of 5 study sites; at 3 of these sites evenness was higher ($P < 0.0013$) in burned areas than in non-burned areas (Table 5). Wildfire and sampling year interacted ($F_{2,12} = 7.1, P < 0.0106$) in their effects on evenness at Flowers 1, where evenness was similar ($P > 0.1365$) between burned and non-burned areas in 2006 and 2008 but higher ($P < 0.0118$) in burned areas in 2007.

Wildfire effects on variability in species composition

The index of multivariate dispersion (IMD) quantifies variability in species composition. As originally used

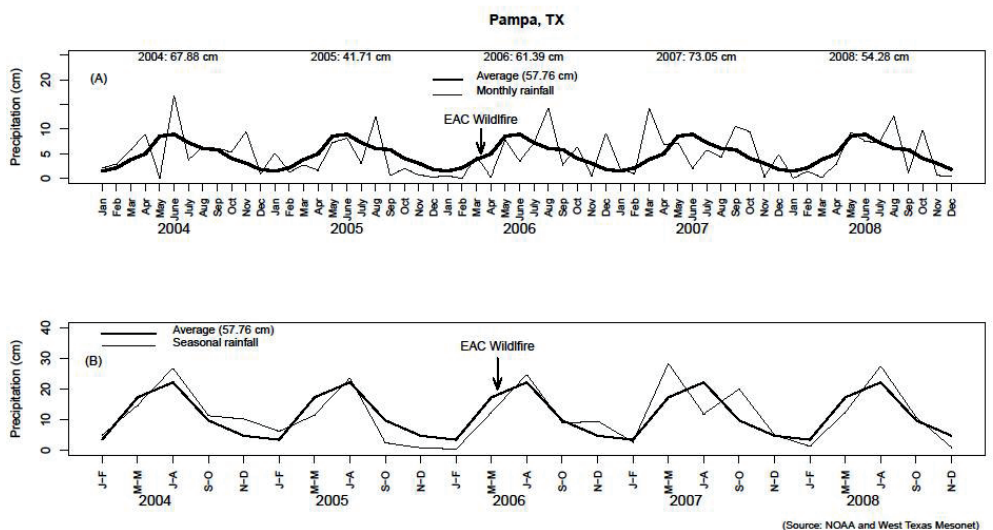


Figure 1. Monthly (top) and seasonal (bottom) precipitation from 2004 through 2008 in Pampa, TX. Data are averages from NOAA and West Texas Mesonet. Long-term average precipitation is shown by dark line. EAC wildfires occurred in mid March, 2006 (Rideout-Hanzak et al. 2011).

Table 2. Average Bray-Curtis similarity in species composition sampled in 2006, 2007 and 2008 for 5 study sites burned by the EAC wildfires and paired non-burned sites. For each study site, diagonal entries display within treatment/year similarities and off-diagonal entries display between treatment-year group similarities.

Study site	Year	Year		
		2006	2007	2008
Burger	2006 <i>a¹</i>	<i>2006 a¹</i>	<i>2007 a</i>	<i>2008 a</i>
		77.2 ² ; 74.7; [71.3]	<i>77.3</i> ³	75.2
		(0.1060)	(0.5641)	(0.7583)
	2007 b	70.0 ³	78.9 ; 77.5; [61.3]	75.3
		(0.0486)	(0.0129)	<i>(0.6716)</i>
	2008 c	65.2	66.1	77.5 ; 69; [55.4]
	(0.0320)	(0.0251)	(0.0226)	
Flowers 1	2006 <i>a</i>	<i>2006 a</i>	<i>2007 b</i>	<i>2008 c</i>
		74.7 ; 83.4; [65.2]	<i>43.1</i>	77.3
		(0.0003)	(0.0002)	<i>(0.0206)</i>
	2007 b	58.7	64.2 ; 80.9; [50.2]	48.2
		(0.0002)	(0.0003)	(0.0007)
	2008 c	69.1	67.8	79.5 ; 78.8; [68.8]
	(0.0206)	(0.0007)	(0.0003)	
Flowers 2	2006 <i>a</i>	<i>2006 a</i>	<i>2007 a</i>	<i>2008 a</i>
		83.3 ; 76.6; [72.6]	<i>69.4</i>	66.7
		(0.0584)	<i>(0.1519)</i>	(0.0664)
	2007 b	56.2	73.1 ; 71.0; [40.2]	72.4
		(0.0095)	(0.0068)	<i>(0.3579)</i>
	2008 a	75.8	58.6	76.7 ; 75.0; [61.2]
	(0.1157)	(0.0194)	(0.0287)	
Shaw 1	2006 <i>a</i>	<i>2006 a</i>	<i>2007 a</i>	<i>2008 b</i>
		73.3 ; 83.9; [66.9]	<i>77.4</i>	69.0
		(0.0490)	<i>(0.0889)</i>	<i>(0.0150)</i>
	2007 a	67.8	68.4 ; 81.1; [67.6]	73.6
		(0.3000)	(0.1320)	<i>(0.0458)</i>
	2008 b	54.9	52.3	75.3 ; 82.9; [53.4]
	(0.0228)	(0.0247)	(0.0085)	
Shaw 2	2006 <i>a</i>	<i>2006 a</i>	<i>2007 a</i>	<i>2008 a</i>
		68.6 ; 77.1; [63.2]	<i>73.7</i>	68.3
		(0.0468)	<i>(0.1633)</i>	<i>(0.2391)</i>
	2007 b	51.3	65.5 ; 77.6; [37.4]	69.0
		(0.0382)	(0.0081)	<i>(0.3701)</i>
	2008 b	40.4	54.4	51.8 ; 64.6; [32.4]
	(0.0364)	(0.2679)	(0.0223)	

¹) For each site, years within burned areas followed by the same bold-faced lower case letters (a,b) are not significantly different ($P > 0.05$); years within non-burned areas followed by the same italicized lower case letters (a,b) are not significantly different ($P > 0.05$)

²) For each site, diagonal entries are: (i) within-site similarities on burned areas (bold face), (ii) within-site similarities on non-burned areas (italics), and (iii) between treatment similarities within a year (bracketed diagonal values). Parenthetical values on diagonals are Monte Carlo P values associated with a comparison between burned areas and non-burned areas within a site. At Flowers 1, wildfire and year of sampling did not interact and so the P value shown is for a comparison between burned and non-burned sites (i.e., the main effect test); however, within-year similarities are shown.

³) For each site, off-diagonal entries are between-year similarities within burned areas (bold face) and non-burned areas (italics). Parenthetical values are Monte Carlo P values associated with pairwise comparisons between years within a burn treatment. At Flowers 1, wildfire and year of sampling did not interact and so the P value shown is for a comparison between years (i.e., the main effect comparisons).

(Warwick and Clarke 1993), this index is descriptive in nature and in this context the index (Fig. 2) leads to the following observations: (1) burned sites were more homogeneous in species composition than their corresponding non-burned sites at 2 study areas (Burger and Flowers 2) in 2006; the converse applied to the remaining 3 sites; (2) the immediate effect of wildfire depended on study site: at 3 sites (Flowers 1 and 2, and Burger), burned areas became more heterogeneous than non-burned areas; Shaw 2 showed the converse; and

Shaw 1 showed no apparent change; and (3) at all 5 study areas, IMD values decreased from 2007 to 2008 (towards zero at Flowers 1, Shaw 1 and Shaw 2, and towards -1 at Burger and Flowers 2). In other words, regardless of initial (2006) differences in relative variability between burned and non-burned areas at each study site, vegetation at all study sites showed a similar pattern of change from 2007 to 2008 toward increased homogeneity at burned sites relative to non-burned sites. This trend is also apparent in the similarity values in Table 2.

Table 3. Average species richness (S) (standard error) for 5 study sites sampled in 2006, 2007 and 2008.

Site	Treatment	Sampling year			Mean
		2006	2007	2008	
Burger	Burned	8.3 (0.88)	9.0 (1.15)	8.0 (0.58)	8.4 a ¹⁾ (0.47)
	Non-burned	8.7 (0.88)	7.7 (1.20)	8.3 (0.88)	8.2 a (0.52)
	Mean	8.5 x ²⁾ (0.56)	8.3 x (0.80)	8.2 x (0.48)	
Flowers 1	Burned	7.3 (0.33)	7.0 (0.58)	7.3 (0.33)	7.2 a (0.22)
	Non-burned	7.3 (0.33)	7.0 (1.53)	9.0 (1.0)	7.8 a (0.62)
	Mean	7.3 x (0.21)	7.0 x (0.73)	8.2 x (0.60)	
Flowers 2	Burned	8.7 (0.88)	9.3 (0.33)	9.7 (0.88)	9.2 a (0.40)
	Non-burned	8.7 (0.33)	11.3 (0.88)	10.3 (1.33)	10.1 a (0.61)
	Mean	8.6 x (0.42)	10.3 x (0.61)	10.0 x (0.73)	
Shaw 1	Burned	7.3 (0.88)	10.0 (0.0)	10.7 (1.20)	9.3 a (0.7)
	Non-burned	6.0 (1.15)	9.7 (2.03)	9.0 (1.00)	8.2 a (0.92)
	Mean	6.7 x (0.71)	9.8 y (0.91)	9.8 y (0.79)	
Shaw 2	Burned	11.3 (0.67)	10.3 (0.33)	12.3 (0.88)	11.33 a (0.44)
	Non-burned	8.7 (1.45)	8.0 (0.58)	8.7 (0.67)	8.4 b (0.50)
	Mean	10.0 x (0.93)	9.2 x (0.60)	10.5 x (0.96)	

¹⁾ For a given study site, treatment means followed by the same lower case letter (a, b) are not significantly different ($P > 0.05$)

²⁾ For a given study site, year means followed by the same lower case letter (x, y) are not significantly different ($P > 0.05$)

Table 4. Average diversity [$\exp H'$] index (standard error) for 5 study sites sampled in 2006, 2007 and 2008.

Site	Treatment	Sampling year			Mean
		2006	2007	2008	
Burger	Burned	4.2 (0.21)	6.2 (0.56)	4.6 (0.14)	5.0 a ¹⁾ (0.35)
	Non-burned	3.6 (0.45)	3.7 (0.54)	3.8 (0.96)	3.7 b (0.34)
	Mean	3.9 x ²⁾ (0.26)	4.9 x (0.65)	4.2 x (0.46)	
Flowers 1	Burned	3.9 a ³⁾ X ⁴⁾ (0.09)	4.8 a X(0.54)	4.7 a X(0.35)	4.5 (0.24)
	Non-burned	4.0 a XY (0.29)	3.0 a X (0.53)	4.8 a Y (0.24)	4.0 (0.33)
	Mean	4.0 (0.14)	3.9 (0.53)	4.8 (0.19)	
Flowers 2	Burned	5.5 (0.40)	5.5 (0.53)	6.3 (0.18)	5.8 a (0.24)
	Non-burned	6.3 (0.07)	7.2 (0.65)	6.4 (0.49)	6.6 b (0.27)
	Mean	5.9 x (0.26)	6.4 x (0.54)	6.3 x (0.24)	
Shaw 1	Burned	3.8 (0.10)	4.8 (0.37)	7.2 (0.15)	5.3 a (0.52)
	Non-burned	2.2 (0.16)	3.5 (0.89)	4.1 (0.15)	3.3 b (.39)
	Mean	3.0 x (0.37)	4.2 y (0.51)	5.6 z (0.71)	
Shaw 2	Burned	6.0 (0.05)	6.7 (0.51)	8.0 (1.17)	6.9 a (0.48)
	Non-burned	3.5 (0.71)	4.2 (0.30)	4.8 (0.98)	4.2 b (0.41)
	Mean	4.7 x (0.64)	5.4 x (0.62)	6.4 x (1.0)	

¹⁾ For a given study site, treatment means followed by the same lower case letter (a, b) are not significantly different ($P > 0.05$)

²⁾ For a given study site, year means followed by the same lower case letter (x, y) are not significantly different ($P > 0.05$)

³⁾ For a given study site, treatment means within a year followed by the same lower case letter (a, b) are not significantly different ($P > 0.05$)

⁴⁾ For a given study site, year means within a treatment followed by the same upper case letter (X, Y) are not significantly different ($P > 0.05$).

Species composition ordination

Scree analysis (results not shown) indicated that the dissimilarity matrix among sites could be adequately represented along 2 MDS ordination axes. The most obvious source of variation in ordination scores was among sites (Fig. 3a),

suggesting that vegetation differed among sites regardless of wildfire or year of sampling, and supporting a similar conclusion based on PERMANOVA analyses. Subsequent ordination analyses (Fig. 3, b-f) were therefore conducted for each site separately.

Figure 2. Index of multivariate dispersion (Warwick and Clarke 1993) that compares between burned and non-burned vegetation at each study site in 2006, 2007 and 2008. An increasing IMD from 0 towards +1 indicates that burned vegetation is more heterogeneous than non-burned vegetation; a decreasing IMD value from 0 towards -1 indicates that non-burned vegetation is more heterogeneous than burned vegetation.

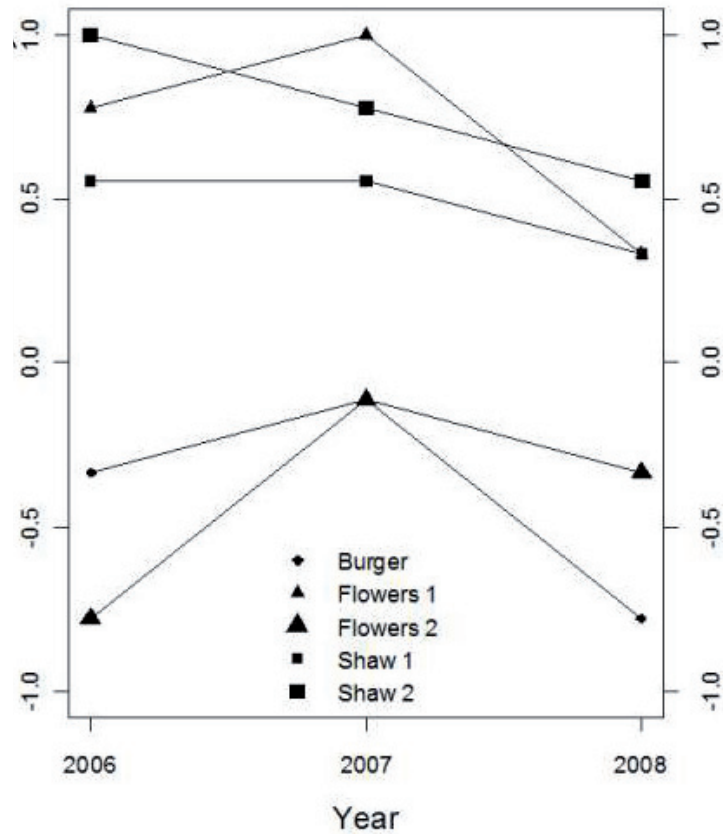


Figure 3. Nonmetric multidimensional scaling ordination diagram of species composition on Mixedland Slopes sites following the East Amarillo Complex wildfires. Differences among five sites are indicated by symbol shape (circles, small squares, large squares, small triangles, large triangles). Non-burned transects are coded with open symbols; burned transects are coded with closed symbols. Data collected 1, 2 and 3 years post-wildfire are coded with red, blue and green symbols, respectively. (a) Transect scores within a site, year and wildfire state were averaged for plotting purposes: each point is the average across 3 transects; (b) – (f) individual transects plotted for each site, year and wildfire state.

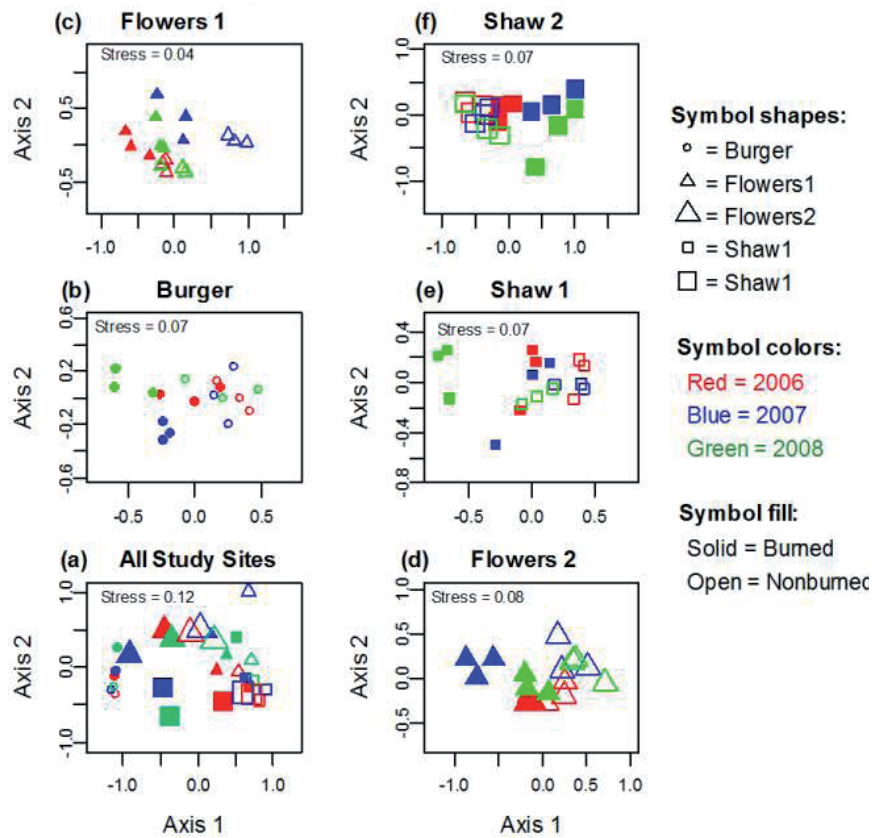


Table 5. Average evenness [$\exp H'/S$] index (standard error) for 5 study sites sampled in 2006, 2007 and 2008.

Site	Treatment	Sampling year			Mean
		2006	2007	2008	
Burger	Burned	0.52 (0.06)	0.69 (0.04)	0.57 (0.03)	0.59 a ¹⁾ (0.03)
	Non-burned	0.41 (0.03)	0.49 (0.01)	0.45 (0.07)	0.45 b (0.02)
	Mean	0.46 x ²⁾ (0.04)	0.59 y (0.05)	0.51 xy (0.04)	
Flowers 1	Burned	0.43 a ³⁾ X ⁴⁾ (0.01)	0.68 a Y(0.04)	0.64 a X (0.2)	0.62 (0.03)
	Non-burned	0.55 a X (0.03)	0.44 a X (0.04)	0.55 a X (0.05)	0.51 (0.03)
	Mean	0.54 (0.02)	0.56 (0.06)	0.59 (0.03)	
Flowers 2	Burned	0.63 (0.02)	0.59 (0.04)	0.66 (0.05)	0.63 a (0.02)
	Non-burned	0.73 (0.03)	0.64 (0.04)	0.63 (0.03)	0.66 a (0.02)
	Mean	0.68 x (0.03)	0.61 x (0.03)	0.64 x (0.03)	
Shaw 1	Burned	0.53 (0.05)	0.48 (0.04)	0.69 (0.06)	0.57 a (0.04)
	Non-burned	0.39 (0.06)	0.36 (0.03)	0.46 (0.03)	0.40 b (0.03)
	Mean	0.46 xy (0.05)	0.42 x (0.03)	0.58 y (0.06)	
Shaw 2	Burned	0.53 (0.04)	0.65 (0.07)	0.65 (0.05)	0.61 a (0.03)
	Non-burned	0.39 (0.03)	0.53 (0.03)	0.55 (0.10)	0.49 b (0.04)
	Mean	0.46 a (0.04)	0.59 a (0.04)	0.60 a (0.05)	

¹⁾ For a given study site, treatment means followed by the same lower case letter (a, b) are not significantly different ($P > 0.05$)

²⁾ For a given study site, year means followed by the same lower case letter (x, y) are not significantly different ($P > 0.05$)

³⁾ For a given study site, treatment means within a year followed by the same lower case letter (a, b) are not significantly different ($P > 0.05$).

⁴⁾ For a given study site, year means within a treatment followed by the same upper case letter (X, Y) are not significantly different ($P > 0.05$).

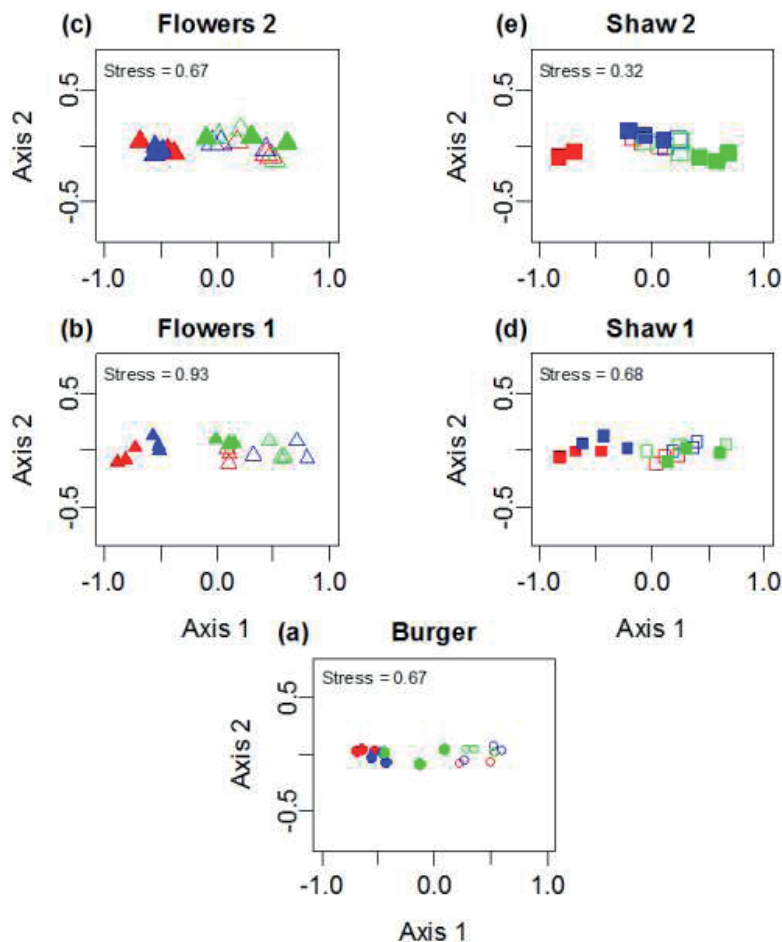


Figure 4. Nonmetric multi-dimensional scaling ordination diagram of ground cover composition on Mixedland Slopes sites following the East Amarillo Complex wildfires. Symbols as in Fig. 3.

Fire effects were apparent at each study site and were largely expressed along the first MDS axis. It is also true, however, that plant community response to wildfire differed among study sites. Two visual patterns can be identified in Fig. 3, b-f. At 3 study sites (Burger, Shaw 1 and Shaw 2), distances between burned and non-burned transects increased from 2006 through 2008. That is, wildfire effects became more apparent with the passage of time at these 3 study areas. In contrast, vegetation at Flowers 1 and 2 responded differently to wildfire. At these study areas, burned and non-burned transects were ordinated further from each other in 2007 (Fig. 3, c, d) than in 2006 or in 2008. In other words, at these 2 sites wildfire effects were most apparent 2 years post-fire (2007) and less apparent immediately after the fire (2006) and 3 years post-fire (2008).

Ground cover ordination

All ground cover ordinations yielded similar patterns: burned plots were plotted to the left relative to their non-burned plots at each study site. Additionally, the distance between burned and non-burned plots decreased from 2006 to 2008 at each site. Finally, there was a clear time trajectory among ordination scores: at all study sites, burned transects were plotted from left to right sequentially for data collected 1, 2 and 3 years post-fire. Thus, there is evidence of general recovery of residual dry matter over the 3-year monitoring period.

Discussion

We analyzed effects of the EAC wildfires on biomass standing crop (Rideout-Hanzak et al. 2011), a collective measure of the response of many species characterizing this landscape. Wildfire effects on standing crop were minimal the year following wildfire and diminished 2 and 3 years post-fire. The absence of wildfire effects on aboveground biomass production does not mean, however, that wildfire had no effect on this vegetation: we also found that frequency of grass mortality was higher on burned areas than on non-burned areas, an effect that also diminished 2 and 3 years post-fire but nevertheless was significant each of the 3 years post-fire. Unfortunately, it is virtually impossible to identify individual species of burned, dead perennial grasses, and so this measure, also a collective response variable, fails to describe fire effects on this plant community beyond a statement to the effect that “frequency of dead plants was higher in these burned areas.” When multivariate analyses are used, however, the ecological information expressed by each individual species can be captured and summarized in a way that enables inferences about the plant community *sensu stricto* (Gauch 1982)—using this approach, we have detected EAC wildfire effects on community composition that are site-specific and that change over time.

Our study sites had different initial species composition prior to wildfire (based on a test of equality of mean species composition among study sites in non-burned areas in 2006; Table 1). These differences likely were a result of past and

current management practices as well as legacy effects (see below). It is reasonable to suggest that these differences also affected response to wildfire (see below). For example, cattle had been removed from Flowers study areas the year prior to the wildfires, and so fine fuel was more abundant (242 g 0.25 m⁻²) than at the remaining sites (124 g 0.25 m⁻²; see Rideout-Hanzak et al. 2011) whose managers practiced moderate seasonal livestock grazing. Additionally, Shaw study sites were grazed following the wildfires whereas livestock grazing was deferred at Burger immediately after the wildfires.

We can identify 3 generalizations supported by these data, two of which deal with these wildfires’ effects on mean species composition and one that deals with these wildfires’ effects on homogeneity of species composition.

Effects on mean species composition

Relative to wildfire effects on mean species composition, we found: (1) weak immediate (2006) impacts of wildfire (at all but one study site), and (2) strong impacts at all study sites by 2008. Although these strong impacts varied among the study sites, two general patterns can be recognized. At 3 study sites (Burger, Shaw 1 and Shaw 2), wildfire effects became more evident over time, a pattern that was apparent from the permutational analysis of variance (Table 2) as well as ordination (Fig. 3). At two of these sites (Burger and Shaw 2), composition in non-burned areas was stable over time while composition changed in burned areas; at Shaw 1, mean composition varied over time at non-burned as well as at burned sites. The end result at these 3 sites was a progressive divergence in similarity between non-burned and burned areas: these wildfires set into motion changes that took mean species composition of burned and non-burned areas along different trajectories of change in species composition. In contrast, wildfire effects on mean composition at Flowers 1 and 2 were nonlinear over time (Fig. 3): compositional similarity between burned and non-burned areas at these sites was highest in 2006 and 2008 but lower in 2007. That is, wildfire effects were nonlinear and lessened over time.

Much of the research on the interaction between fire and grazing has been conducted in mesic grasslands (Kansas and Oklahoma, USA), where there is abundant evidence that these effects interact over spatial and temporal scales (Collins and Smith 2006) that involve fire season and frequency (Spasojevic et al. 2010, Collins and Calabrese 2012), kind of vegetation (Leonard et al. 2010), topography (Gibson and Hulbert 1987, Collins and Calabrese 2012) and climatic variables [e.g., precipitation and temperature before and after burning; Anderson (2006)]: effects cascade through these systems by affecting nutrient cycling (Johnson and Matchett 2001, Harris et al. 2007) and aboveground plant community structure (Coppedge et al. 1998) which in turn affects plant growth and development (Hulbert 1988), recruitment and survival (Benson and Hartnett 2006) dynamics as well as competitive interactions among plants (Zimmermann et al. 2008; also see Collins and Calabrese 2012)—the end result is a complex but scale-dependent (Collins and Smith 2006, Veen et al. 2008) interplay among biotic and abiotic

factors that determines composition, structure and function of plant communities (Fuhlendorf and Engle 2001, 2004). In arid environments, however, there is little evidence that fire and grazing interact in their effect, either at the individual plant level or the community level (Valone et al. 2002), and effects of drought can override potential fire/grazing interaction effects (Drewa and Havstad 2001). Our study sites occur between the mesic grasslands (characterized by the Konza Prairie in Kansas with 81 cm of annual precipitation) and the arid grasslands of southern New Mexico (with 28 cm of annual precipitation). Our study was not designed to test wildfire/grazing interaction effects; nevertheless, to the extent that vegetation changes over time varied among our study sites (which differed in livestock management both prior to and following wildfire), these results suggest a possible interaction between the EAC wildfires and grazing.

Effects on diversity and variation in species composition

From a community perspective, variation in species composition is often studied with metrics related to species diversity (e.g., Belsky 1992, Warwick and Clarke 1993, Capitanio and Carcaillet 2008, see below) or with ordination analyses through interpretation of the “spread of points” (e.g., Gibson and Hulbert 1987, Warwick and Clarke 1993) or “length of axes” (e.g., Biondini et al. 1989, Fuhlendorf et al. 2006). We chose Clarke and Warwick’s (2001) “index of multivariate dispersion” (IMD), a descriptive measure that ranges from +1 (indicating that non-burned vegetation is maximally more homogeneous than burned vegetation—i.e., all similarities among non-burned transects are higher than any similarities among burned transects)—to -1 (indicating the converse). This measure may be more meaningful than one that is based on dispersion of distances in 2-dimensional MDS ordination space because the latter is generally not an exact representation of the rank order of similarities among transects in higher dimensional space (Clarke and Warwick 2001).

Although immediate impacts of the EAC wildfires on vegetation heterogeneity varied among study sites, we found that (regardless of whether burned vegetation was more homogeneous or less homogeneous than non-burned vegetation in 2006) the change between 2007 and 2008 was toward more homogeneity in burned vegetation relative to non-burned vegetation, a pattern that was detected at each of our study sites. We also found, however, that although species richness was largely unaffected by wildfire, both species diversity and evenness generally were higher in burned areas than in non-burned areas at most of our study sites. At first, it may seem counterintuitive that diversity was generally higher in burned areas while at the same time there was more homogeneity in compositional variation in burned vegetation relative to non-burned vegetation as the study period progressed. These two results can be reconciled when it is realized that Shannon’s index is maximized (for a given richness) when all species are equally abundant. In the context of the EAC wildfires, our data indicate that whereas wildfire had little effect on species richness it increased species diversity as well as species evenness, and that these effects resulted in less compo-

sitional variation among transects in burned areas relative to non-burned areas, a trend that was especially evident between 2007 and 2008.

The literature addressing impacts of fire on species diversity reports a wide variety of effects that generally depend on season and frequency as well as scale of measurement (Collins and Smith 2006); time since fire, topography and climatic variability (Gibson and Hulbert 1987); plant functional group (Peterson and Reich 2008, Uys et al. 2004); photosynthetic (C_3 or C_4) pathway (Harnett et al. 1996); grazing (Collins and Smith 2006, Harnett et al. 1996, Fuhlendorf and Engle 2006); and geological/soil characteristics (Harrison et al. 2002). Long-term (*ca.* 50 yrs) data sets (e.g., Furley et al. 2008) are relatively rare. It is difficult to relate our results specifically to this broader context because our data reflect short-term responses to two simultaneous wildfires on a relatively homogenous landscape dominated by warm-season grasses with a variable (and uncontrolled) grazing influence.

It is also difficult to relate our results to literature dealing with frequency of burning, much of which indicates that infrequently burned grasslands are more stable (in Collins’ (2000) sense that they do not show statistically significant changes in composition and abundance) over time than more frequently burned areas (e.g., Collins 2000, Fuhlendorf et al. 2006)—i.e., annual burns can lead to low temporal variation and set into motion directional changes (i.e., they destabilize communities) whereas infrequent burns lead to higher year-to-year variation and weaker patterns of directional changes. The fire history of our study sites is only incompletely known: cooperating land owners indicated to us that although wildfires had affected their properties in the past, no wildfires had occurred within the past 10 or more years prior to the EAC and none were involved in a prescribed burning program. In this light, we suggest that our study areas were exposed to episodic (rather than frequent) fire disturbance which should have had little effect on compositional variability; our results do not support this prediction (e.g., Fraterrigo and Rusak 2008) and they differ from results in more mesic grasslands.

It was beyond the scope of this study to explore specific mechanisms involved in changes in species composition following the EAC wildfires. However, these changes ultimately are the combined results of differential mortality and/or recruitment of plants. Relative to plant mortality, we have previously reported (Rideout-Hanzak et al. 2011) high frequency of mortality of perennial grasses immediately following the EAC wildfires; further, frequency of mortality in burned areas remained higher for 3 years following wildfires (although they also diminished over this time period). Although these data were not species-specific (it is difficult to identify species from the remains of burned crowns), the literature on prescribed burning (Wright 1971, Wright and Bailey 1982) clearly shows that mortality varies widely among perennial grasses. Relative to recruitment, opportunities for plant establishment are enhanced with the creation of gaps (Burke and Grime 1996) and our ground cover ordination clearly shows that bare ground increased dramatically following wildfires. However, residual dry matter ground cover recovered to non-burned conditions by 3 years post-wildfires and so the

temporal window for seedling recruitment was relatively short-lived. Many perennial grasses (the dominant species group in our study area) typically rely on vegetative (rather than sexual) reproduction (Benson and Hartnett 2006), and so recruitment of individuals into gaps created by the wildfires likely would be largely the result of surviving plants extending vegetatively into these gaps. Vegetative reproduction of surviving plants into gaps created by the wildfires—the success of which varied among species—could explain (i) a change in mean composition, (ii) increases in diversity and evenness but not species richness, and (iii) reduced variation in burned areas compared to non-burned areas that we observed following these wildfires.

Conclusions

We conclude that community compositional changes in our burned areas were likely the result of dominance relationships that changed over time among plants that survived the EAC wildfires rather than the result of seedling recruitment of new species into gaps created by dead plants; in particular, we observed no non-native invasive species during field sampling. This explanation is consistent with our findings that (i) whereas immediate effects on mean composition were weak, these effects were far more evident 3 years post-fire; and (ii) burned areas had higher species diversity, higher evenness, and less variability in species composition than non-burned areas but similar species richness 3 years post-fire. The growth form of grasses (with relatively little aboveground structural material so that most regrowth can photosynthesize and thus contribute to growth) allows these plants to recover quickly from fire (D'Antonio and Vitousek 1992) and contributes both to resistance and resilience of these grasslands to disturbances including fire (Tilman and Downing 1994, Tilman et al. 2006, Thompson et al. 2009). The changes thus set into motion by the EAC wildfires—changes in mean species composition and decreased variability in species composition at all 5 study sites 3 years post-fire (compared to non-burned areas), together with increased species diversity and evenness without accompanying changes in species richness—are short-term (1-3 years post-fire) effects. Given the resilience of grasslands to fire, and the fact that fire is an important factor that affected not only the historical development and expansion of these C₄-dominated ecosystems (Axelrod 1985, Anderson 2006) but also currently affects their structure, function and composition (Wright and Bailey 1982, Anderson 2006), it is not likely that longer-term effects of the EAC wildfires on vegetation of our study areas would be significant.

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References

- Anderson, M.M. 2001. A new method for non-parametric multivariate analysis of variance. *Austral. Ecol.* 26:32-46.
- Anderson, R.C. 2006. Evolution and origin of the Central Grassland of North America: Climate, fire and mammalian grazers. *J. Torrey Bot. Soc.* 133:626-647.
- Ansley, R.J. and Castellano, M.J. 2007. Texas wintergrass and buffalograss responses to seasonal fires and clipping. *Rangeland Ecol. Manage.* 60:154-164.
- Augustine, D.J. and Milchunas, D.G. 2009. Vegetation responses to prescribed burning of grazed shortgrass steppe. *Rangeland Ecol. Manage.* 62:89-97.
- Axelrod, D.I. 1985. Rise of the grassland biome, central North America. *Bot. Rev.* 51:163-201.
- Belsky, A.J. 1992. Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland community. *J. Veg. Sci.* 3:187-200.
- Benson, E.J. and Harnett, D.C. 2006. The role of seed and vegetative reproduction in plant recruitment and demography in tallgrass prairie. *Plant Ecol.* 187:163-177.
- Bidwell, T.G. and Engle, D.M. 1992. Relationship of fire behavior to tallgrass prairie herbage production. *J. Range Manage.* 45:579-584.
- Bidwell, T.G., Masters, R.E., Weir, J.R. and Engle, D.M. 2005. *Fire Effects in Native Plant Communities*. Oklahoma Cooperative Extension Service [NREM-2877], Stillwater, OK, USA.
- Biondini, M.E., Steuter, A.A. and Grygiel, C.E. 1989. Seasonal effects of fire on the diversity patterns, spatial distribution and community structure of forbs in the Northern Mixed Prairie, USA. *Vegetatio* 85:21-31.
- Bond, W.J. and Midgley, J.J. 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends Ecol. Evol.* 16:45-51.
- Burke, M.J.W. and Grime, J.P. 1996. An experimental study of plant community invisibility. *Ecology* 77:776-790.
- Capitanio, R. and Carcaillet, C. 2008. Post-fire Mediterranean vegetation dynamics and diversity: A discussion of succession models. *For. Ecol. Manage.* 255:431-439.
- Clarke, K.R. and Warwick, R.M. 2001. *Change in Marine Communities—An Approach to Statistical Analysis and Interpretation*. 2nd ed. PRIMER-E, Plymouth, UK.

- Collins, S.L. 2000. Disturbance frequency and community stability in native tallgrass prairie. *Amer. Nat.* 155:311-325.
- Collins, S.L. and Smith, M.D. 2006. Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. *Ecology* 87:2058-2067.
- Collins, S. and Calabrese, L.B. 2012. Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie. *J. Veg. Sci.* 23:563-575.
- Coppedge, B.R., Engle, D.M., Toepfer, C.S. and Shaw, J.H. 1998. Effects of seasonal fire, bison grazing and climatic variation on tallgrass prairie vegetation. *Plant Ecol.* 139:235-246.
- D'Antonio, C.M. and Vitousek, P.M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* 23:63-87.
- Drewa, P.B. and Havstad, K.M. 2001. Effects of fire, grazing and the presence of shrubs on Chihuahuan desert grasslands. *J. Arid Env.* 48:429-443.
- Duff, T.J., Bell, T.L. and York, A. 2013. Managing multiple species or communities? Considering variation in plant species abundances in response to fire interval, frequency and time since fire in a healthy *Eucalyptus* woodland. *Forest Ecol. Manage.* 289:393-403.
- Evans, R.A. and Love, R.M. 1957. The step-point method of sampling: a practical tool in range research. *J. Range Manage.* 10:208-212.
- Fraterrigo, J.M. and Rusak, J.A. 2008. Disturbance-driven changes in the variability of ecological patterns and processes. *Ecol. Letters* 11:756-770.
- Fritsch, K.S. and Hsu, J.C. 1999. Multiple comparison of entropies with application to dinosaur biodiversity. *Biometrics* 55:1300-1305.
- Fuhlendorf, S.D. and Engle, D.M. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *Bioscience* 51:625-632.
- Fuhlendorf, S.D. and Engle, D.M. 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. *J. Appl. Ecol.* 41:604-606.
- Fuhlendorf, S.D., Harrell, W.C., Engle, D.M., Hamilton, R.G., Davis, C.A. and Leslie, D.M., Jr. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. *Ecol. Appl.* 16:1706-1716.
- Furley, P.A., Rees, R.M., Ryan, C.M. and Saiz, G. 2008. Savanna burning and the assessment of long-term fire experiments with particular reference to Zimbabwe. *Progr. Phys. Geogr.* 36:611-634.
- Gauch, H.G. 1982. *Multivariate Analysis in Community Ecology*. Cambridge University Press, New York, US.
- Gibson, D.J. and Hulbert, L.C. 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. *Vegetatio* 72:175-185.
- Gould, S.J. 1985. The median isn't the message. *Discover* June, 40-42.
- Gould, S.J. 1996. *Full House, The Spread of Excellence from Plato to Darwin*. Harmony Books, New York, US.
- Harnett, D.C., Hickman, K.R. and Fischer, L.E. 1996. Effects of bison, fire and topography on floristic diversity in tallgrass prairie. *J. Range Manage.* 49:413-420.
- Harris, W.N., Moretto, A.S., Distel, R.A., Boutton, R.W. and Boo, R.M. 2007. Fire and grazing in grasslands of the Argentine Caldenal: effects on plant and soil carbon and nitrogen. *Acta Oecol.* 32:207-214.
- Harrison, S.B., Inouye, D. and Safford, H.D. 2002. Ecological heterogeneity in the effects of grazing and fire on grassland diversity. *Conserv. Biol.* 17:839-845.
- Hulbert, L.C. 1988. Causes of fire effects in tallgrass prairie. *Ecology* 69:46-58.
- Johnson, L.C. and Matchett, J.R. 2001. Fire and grazing regulate belowground processes in tallgrass prairie. *Ecology* 82:3377-3389.
- Jost, L. 2010. The relation between evenness and diversity. *Diversity* 2:207-232.
- Kirk, R.E. 1995. *Experimental Design: Procedures for the Behavioral Sciences*. Brooks Cole, Belmont, CA, US.
- Kempthorne, O. 1952. *The Design and Analysis of Experiments*. John Wiley, NY.
- Landres, P.B., Morgan, P. and Swanson, F.J. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecol. Appl.* 9:1179-1188.
- Leonard, S., Kirkpatrick, J. and Marsden-Smedley, J. 2010. Variation in the effects of vertebrate grazing on fire potential between grassland structural types. *J. Appl. Ecol.* 47:876-883.
- Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D. and Schabenberger, O. 2006. *SAS for Mixed Models*. SAS Institute, Inc., Cary, NC, USA.
- Manjarres-Martinez, L.M., Gutierrez-Estrada, J.C., Hernando, J.A. and Soriquer, M.C. 2012. The performance of three ordination methods applied to demersal fish data sets: stability and interpretability. *Fisheries Manage. Ecol.* 19:200-213.
- Marlon, J.R., Martlein, P.J., Walsh, M.K., Harrison, S.P., Brown, K.J., Edwards, M.E., Higuerra, P.E., Power, M.J., Anderson, R.S., Briles, C., Brunelle, A., Carcaillet, C., Daniels, M., Hu, F.S., Lavoie, M., Long, C., Minckley, T., Richard, P.J.H., Scott, A.C., Shafer, D.S., Tinner, W., Umbanhowar, C.E., Jr., and Whitlock, C. 2009. Wildfire responses to abrupt climate change in North America. *Proc. Nat. Acad. Sci.* 106:2519-2524.
- McCune, B. and Grace, J.B. 2002. *Analysis of Ecological Communities*. MjM Software, Gleneden Beach, OR, US.
- NIFC. 2013. Historically significant wildfires. Available at: http://www.nifc.gov/fireInfo/fireInfo_stats_histSigFires.html. Accessed 4 December 2013.
- Orlaci, L. 1978. *Multivariate Analysis in Vegetation Research*. 2nd ed. Junk, The Hague, NL.
- Peterson, D.W. and Reich, P.B. 2008. Fire frequency and tree canopy structure influences on plant species diversity in a forest-grassland ecotone. *Plant Ecol.* 194:5-16.
- Pyne, S.J. 1984. *Introduction to Wildland Fire: Fire Management in the United States*. Wiley, NY.
- Rideout-Hanzak, S., Wester, D.B., Britton, C.M. and Whitlaw, H. 2011. Biomass not linked to perennial grass mortality following severe wildfire in the southern High Plains. *Rangeland Ecol. Manage.* 64:47-55.
- Rogers, J.A. and Hsu, J.C. 2001. Multiple comparisons of biodiversity. *Biometrical J.* 43:617-625.
- Scheintaub, M.R., Derner, J.D., Kelly, E.F. and Knapp, A.K. 2009. Response of the shortgrass steppe plant community to fire. *J. Arid Env.* 73:1136-1143.
- Spaeth, K.E., Pierson, F.B., Robichaud, P.R. and Moffet, C.A. 2007. Hydrology, erosion, plant, and soil relationships after rangeland wildfire. In: Sosebee, R.E., Wester, D.B., Britton, C.M., McArthur, E.D. and Kitchen, S.G. (comps.) *Proceedings: Shrubland Dynamics—Fire and Water*, 2004 August 10-12; Lubbock, TX. [Rocky Mountain Research Station, RMRS-P-47]. United State Department of Agriculture, Forest Service, Fort Collins, CO, US.

- Spasojevic, M.J., Aicher, R.J., Koch, G.R., Marquardt, E.S., Mirotnick, N., Troxler T.G. and Collins, S.L. 2010. Fire and grazing in a mesic tallgrass prairie: impacts on plant species and functional traits. *Ecology* 91:1651-1659.
- Thompson, I., Mackey, B., McNulty, S. and Mosseler, A. 2009. Forest resilience, biodiversity and climate change: a synthesis of the biodiversity/resilience/stability relationship in forest ecosystems. Secretariat of the Convention on Biological Diversity [Technical Series no. 43], Montreal, CA.
- Tilman, D.A. and Downing, J.A. 1994. Biodiversity and stability in grasslands. *Nature* 367:363-365.
- Tilman, D.A., Reich, P.B. and Knops, J.M.H. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* 441:629-632.
- USDA. 2008. Ecological Site Description, Natural Resources Conservation Service. Available at http://esis.sc.egov.usda.gov/esis_report. Accessed 16 July 2009.
- Uys, R.G., Bond, W.J. and Everson, T.M. 2004. The effect of different fire regimes on plant diversity in southern African grasslands. *Biol. Conserv.* 118:489-499.
- Valone, T.J., Nordell, S.E. and Ernest, S.K.M. 2002. Effects of fire and grazing on an arid grassland ecosystem. *Southwestern Nat.* 47:557-565.
- Veen, G.F., Blair, J.M., Smith, M.D. and Collins, S.L. 2008. Influence of grazing and fire frequency on small-scale plant community structure and resource availability in native tallgrass prairie. *Oikos* 117:859-866.
- Vermeire, L.T. and Roth, A.D. 2011. Plains prickly pear response to fire: Effects of fuel load, heat, fire weather, and donor site soil. *Rangeland Ecol. Manage.* 64:404-413.
- Vermeire, L.T., Crowder, J.L. and Wester, D.B. 2011. Plant community response and soil environment response to summer fire in the northern Great Plains. *Rangeland Ecol. Manage.* 64:37-46.
- Vermeire, L.T., Crowder, J.L. and Wester, D.B. 2014. Semiarid rangeland is resilient to summer fire and postfire grazing utilization. *Rangeland Ecol. Manage.* 67:52-60.
- Warwick, R.M. and Clarke, K.R. 1993. Increased variability as a symptom of stress in marine communities. *J. Exp. Marine Biol. Ecol.* 172:215-226.
- West Texas Mesonet. 2007. Available at <http://www.mesonet.ttu.edu/mesonet-precipitation.htm>. Accessed 30 October 2009.
- Wester, D.B. 1992. Viewpoint: Replication, randomization and statistics in range research. *J. Range Manage.* 45:285-290.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R. and Swetnam, T.W. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science* 313:1069-1083.
- Wright, H.A. 1971. Why squirreltail is more tolerant to burning than needle-and-thread. *J. Range Manage.* 24:277-284.
- Wiens, J.A. and Parker, K.R. 1995. Analyzing the effects of accidental environmental impacts: Approaches and assumptions. *Ecol. Appl.* 5:1069-1083.
- Wright, H.A., Bunting, S.C. and Neuenschwander, L.F. 1976. Effect of fire on honey mesquite. *J. Range Manage.* 29:467-471.
- Wright, H.A. and Bailey, A.W. 1982. *Fire Ecology: United States and Southern Canada*. John Wiley and Sons, New York, NY.
- Zane, D., Henry, J., Lindley, C., Pendergrass, P.W., Galloway, D., Spencer, T. and Stanley, M. 2006. *Surveillance of Mortality during the Texas Panhandle Wildfires (March 2006)*. Texas Department of State Health Service and Texas Forest Service.
- Zimmermann, J., Higgins, S.L., Grimm, V., Hoffmann, J., Münkemüller, T. and Linstädter, A. 2008. Recruitment filters in a perennial grassland: the interactive roles of fire, competitors, moisture and seed availability. *J. Ecol.* 96:1033-1044.

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