

# The combined effects of an extreme heatwave and wildfire on tallgrass prairie vegetation

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## Abstract

**Questions:** Climate extremes are predicted to become more common in many ecosystems. Climate extremes can promote and interact with disturbances, but the combined effects of climate extremes and disturbances have not been quantified in many ecosystems. In this study, we ask whether the dual impact of a climate extreme and concomitant disturbance (wildfire) has a greater affect than a climate extreme alone.

**Location:** Tallgrass prairie in the Konza Prairie Biological Station, northeastern Kansas, USA.

**Methods:** We quantified the response of a tallgrass prairie plant community to a 2-year climate extreme of low growing-season precipitation and high temperatures. In the first year of the climate extreme, a subset of plots was burned by a growing-season wildfire. This natural experiment allowed us to compare community responses to a climate extreme with and without wildfire.

**Results:** In plots exposed to the climate extreme but not wildfire, community structure, diversity, and composition showed minor to insignificant changes, such as a 20% reduction in grass cover and a slight increase in species diversity. Plots exposed to both the climate extreme and wildfire underwent larger changes, including an 80% reduction in grass cover, 50% increase in forb cover, and increased plant diversity. Two years after the climate extreme, structural shifts in burned plots showed little sign of recovery, indicating a potentially lasting shift in plant community structure.

**Conclusions:** Our results suggest that community responses to climate extremes need to account for climate-related disturbances – in this case, high temperatures, drought and wildfire. This response diverged from our expectation that heat, drought, and an additional fire would favor grasses. Although growing-season wildfires in tallgrass prairie have been rare in recent decades, they will likely become more common with climate change, potentially leading to changes in grassland structure.

## KEYWORDS

climate change, climate extremes, drought, fire, pulses, regime shifts, resilience

## 1 | INTRODUCTION

Large deviations in temperature and precipitation, sometimes referred to as climate extremes, are predicted to become more common in many ecosystems, leading to more instances of drought, inundation, and heatwaves (Easterling et al., 2000; Jentsch, Kreyling, & Beierkuhnlein, 2007; Smith, 2011). The likely ecological responses to climate extremes are poorly understood, because extremes are always rare, regardless of range of climate variability, but can become more or less extreme with climate changes, or, in other words, the range of climate variability may shift (Smith, 2011). The interaction among climate extremes and disturbance is especially important in mesic grasslands, because these ecosystems are already exposed to high climate variability (Knapp & Smith, 2001), which will likely increase in the next century (Cook, Ault, & Smerdon, 2015). In addition, mesic grasslands are the product of complex disturbance regimes that often include frequent fires and grazing by native ungulates (Axelrod, 1985; Collins & Calabrese, 2012). As a consequence, climate extremes are likely to interact with disturbances in mesic grasslands and other disturbance-prone ecosystems under future scenarios of global environmental change.

Climate extremes can directly alter resource availability and act as a stressor, resulting in changes in community composition and structure. For example, extreme drought reduces soil moisture, affecting the growth, survival, and competitive ability of plants (Allen, Breshears, & McDowell, 2015; Smith, 2011). Declines in soil moisture may result in decreased primary productivity and greater dominance of drought-tolerant species (Breshears et al., 2005; Smith, 2011; Hoover, Knapp, & Smith, 2014; De Boeck, Hiltbrunner, Verlinden, Bassin, & Zeiter, 2018). Heatwaves can exacerbate moisture deficits (Krueger et al., 2016) and are a direct source of stress in many ecosystems, exemplified by widespread tree mortality (Allen et al., 2015) and coral bleaching (Hughes et al., 2017). Ecological responses to climate extremes often alter key ecosystem services, including forage and timber production (Allen et al., 2015; Isbell et al., 2015). However, in mesic grasslands, many experimental and observational studies find community structure either resistant to drought and heatwaves or initially altered, followed by quick recovery (Fuhlendorf & Smeins, 1997; Hoover et al., 2014; Isbell et al., 2015; Kreyling, Wenigmann, Beierkuhnlein, & Jentsch, 2008; Tilman & Downing, 1994; Vanderweide & Hartnett, 2015; Weaver, 1954; but see De Boeck et al., 2018). Few studies in grasslands, however, have assessed the community responses to the combined impacts of climate extremes and disturbance events, such as wildfire (Smit, Asner, Govender, Vaughn, & van Wilgen, 2016; Twidwell, West, et al., 2016; Wonkka, Twidwell, West, & Roger, 2016).

Climate extremes can increase the probability and intensity of disturbances. Elevated precipitation can facilitate or trigger floods and landslides (Ilg et al., 2008; Peters et al., 2011) and hot droughts increase the probability of wildfires (Allen et al., 2015; Jolly et al., 2015; Krueger et al., 2015; Turner, 2010), large-scale insect outbreaks (Raffa et al., 2008), and other disturbances (Peters et al.,

2011). While climate-related disturbances naturally occur in many ecosystems (Peters et al., 2011; Turner, 2010), alterations of disturbance regimes can have lasting impacts on ecosystem structure and alter the sensitivity to other perturbations (Paine, Tegner, & Johnson, 1998; Peters et al., 2011; Turner, 2010; Walker & Salt, 2006). For instance, recently disturbed shrublands and grasslands in Europe are less resistant to climate extremes (Grime et al., 2000; Kreyling, Jentsch, & Beierkuhnlein, 2011; Kröel-Dulay et al., 2015), suggesting synergistic interactions between climate extremes and disturbances on ecosystem processes. However, teasing apart the role of climate-related disturbances has proven difficult, because they are hard to replicate experimentally.

We quantified the interactive effects of extreme heatwaves and wildfire on plant community composition in a native tallgrass prairie of the Central Great Plains of North America. Concurrent drought and wildfires are expected to increase in this region (Jolly et al., 2015; Krueger et al., 2016), but the effects of coupled climate extremes and wildfires on grasslands are poorly understood. In 2011 and 2012, drought and elevated growing-season temperatures occurred across much of the North American Great Plains (Knapp et al., 2015) and regionally, wildfires burned an area greater than any other year from 1985 to 2014 (Donovan, Wonkka, & Twidwell, 2017; Krueger et al., 2015, 2016). Increasing wildfire frequency, especially during the growing season, is a major departure from the region's historic fire regime, which has included only occasional wildfires (Allen & Palmer, 2011; Archibald, Lehmann, Gómez-Dans, & Bradstock, 2013; DeSantis, Hallgren, & Stahle, 2010; Stambaugh, Guyette, & Marschall, 2013). Instead, prescribed fires are more common and are generally conducted when many plants are still dormant and fires are easier to control (Mohler & Goodin, 2012), resulting in lower intensity fires (Choczynska & Johnson, 2009; Gibson, Hartnett, & Merrill, 1990). Wildfires in the growing season, in contrast, can have high fire intensities and occur after plants have broken dormancy (Smit et al., 2016; Twidwell et al., 2016b; Wonkka et al., 2016).

This study leverages long-term observational data and a natural experiment (Barley & Meeuwig, 2017) to track grassland community responses to drought, extreme heat, and wildfire at the Konza Prairie Biological Station, Kansas. We quantified the combined impacts of drought and wildfire by comparing long-term sampling plots that were either burned or untouched by a growing-season wildfire in 2011. We hypothesized that the heat and drought in 2011 and 2012 would temporarily increase warm-season grass ( $C_4$ ) dominance and decrease plant diversity (Hoover et al., 2014; Ladwig et al., 2016). Furthermore, we expected that exposure to wildfire would further favor warm-season grasses with neutral to positive effects on forbs, which reflects long-term studies that have manipulated fire in tallgrass prairie (Collins & Calabrese, 2012; Ewing & Engle, 1988; Towne & Kemp, 2008). These hypotheses were based on observations that drought, heatwaves and more frequent fires tend to favor grasses and alter community composition, in this and many other mesic grassland/savanna ecosystems

(Bond, 2008; Collins & Calabrese, 2012; Ehleringer et al. 1997; Hoover et al., 2014; Ratajczak, Nippert, & Ocheltree, 2014; Staal, Dekker, Hirota, & van Nes, 2015; Tilman & Downing, 1994; Weaver, 1954).

## 2 | METHODS

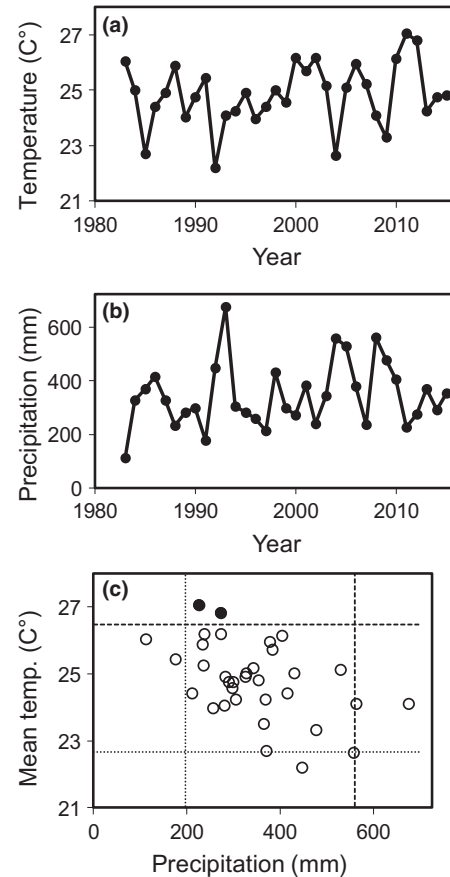
### 2.1 | Study region

This study occurred at the Konza Prairie Biological Station (KPBS), a long-term research site in native unplowed tallgrass prairie in the Flint Hills of northeastern Kansas, USA, one of the largest remaining regions of tallgrass prairie in North America. The topographic variation at KPBS ranges from 320 to 444 m above sea level. Upland soils, from the Florence series, are shallow, level, rocky, silty clay loams. Lowland soils, from the Tully series, are deeper, non-rocky, silty clay loams. In general, lowlands are more productive than uplands (Buis et al., 2009). KPBS and its associated fire treatments began in the late 1970s and early 1980s, before which the site was managed primarily for cattle production with an inter-fire interval of ~2 years.

Regionally, tallgrass prairie communities are dominated by warm-season ( $C_4$ ) grasses with a diverse subdominant community of forbs, grasses, sedges, and sub-shrubs (Collins & Calabrese, 2012; Gibson & Hulbert, 1987). Frequent fire is essential for maintaining this mesic grassland ecosystem (Anderson & Brown, 1986; Gibson & Hulbert, 1987). In our study region, the estimated average fire return interval over the last several hundred years is ~2.5–4 years (Allen & Palmer, 2011; DeSantis et al., 2010; Stambaugh et al., 2013). Currently, if the average interval between spring fires exceeds ~3–4 years, forb abundance and vulnerability to shrub and tree expansion increases, especially in lowlands (Collins & Calabrese, 2012; Ratajczak et al., 2014). Responses to declines in fire frequency are typically gradual at first, but can accelerate over time (Alstad et al., 2016; Ratajczak et al., 2014). Very frequent fires, such as annual burning, can result in grass-dominated communities with low diversity, especially in the absence of grazers (Collins & Calabrese, 2012).

### 2.2 | Climate and weather

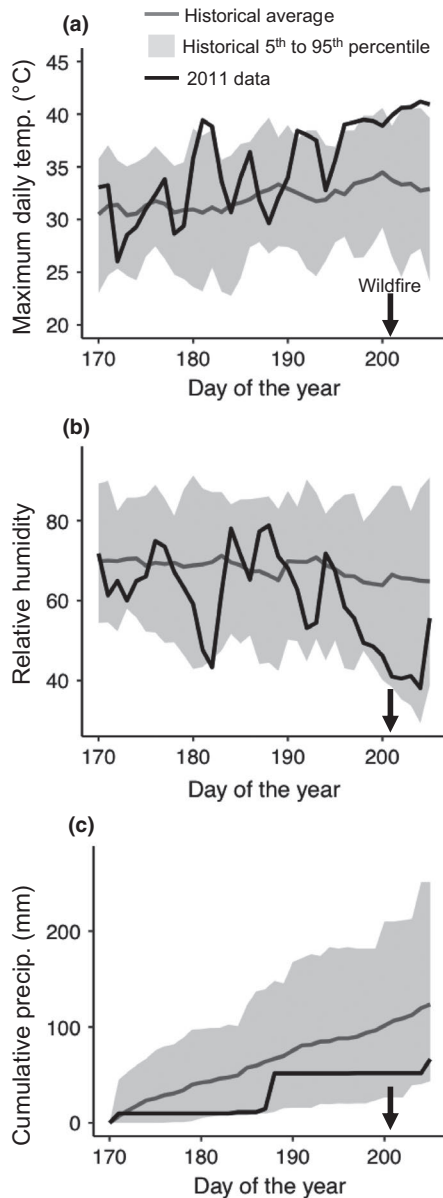
This study focuses on vegetation dynamics from 2008 to 2014. Growing-season precipitation and temperature in 2008, 2009, and 2010 were average to cooler/wetter (Figure 1). Weather during the 2011 and 2012 growing seasons was statistically extreme, as mean daily temperature and mean daily maximum temperature were above the 95th percentile of the historical (past 35 years) range of variability (Smith, 2011), and precipitation was below average during both years, and below the 5th percentile in 2012 (Figure 1). The 2-year average growing-season temperature and precipitation for 2011 and 2012 ranked as the warmest and 5th driest consecutive growing seasons from 1980 to 2014 (Appendix S1). In 2013 and 2014 the growing-season temperature and precipitation returned to average conditions (Figure 1).



**FIGURE 1** Changes in peak growing season (June through August) temperature and precipitation. (a) Average daily temperature; and (b) cumulative precipitation over the peak growing season. (c) A bivariate plot of annual peak growing-season precipitation and mean daily temperature, with black fills for 2011 and 2012. Dashed lines denote the respective 95th percentiles and dotted lines are 5th percentiles

### 2.3 | Study design

We focused on a management unit at KPBS, watershed r20b, where a growing-season wildfire in 2011 affected only a portion of the set of long-term vegetation plots. This area is part of a long-term study to determine how tallgrass prairie recovers from a legacy of annual burning (see Spasojevic et al., 2010; Ratajczak, D'Odorico, Collins, et al., 2017; Ratajczak, D'Odorico, Nippert, et al., 2017, for more information). Such a move from annual burning to longer fire return intervals has been advocated as a means to increase ecosystem heterogeneity (Fuhlendorf, Engle, Kerby, & Hamilton, 2009) and is occurring in up to 50% of grasslands in the region (Mohler & Goodin, 2012). This management unit was burned annually from 1983 to 2000 and then switched to an intermediate fire frequency from 2001 onwards, with a prescribed fire in 2008. This prescribed fire occurred in the spring under typical late winter/early spring burning conditions of low wind speeds (<25 kph) and moderate humidity (>50% mean relative daily humidity). On July 20th of 2011, an unplanned fire began at the southern border of KPBS. The wildfire spread north with the prevailing wind and uphill to the northeast, burning the eastern half



**FIGURE 2** Meteorology for the 30 days preceding the wildfire in 2011. (a) Time series of maximum daily temperature and (b) mean daily relative humidity during the peak growing season. (c) The cumulative precipitation during the peaking growing season (starting on day 170). In all panels, the black line is 2011, the gray line is average values from 1983 to 2014, and the grey area bounds the 5th to 95th percentile for 1983 to 2014. The arrow on each x-axis marks when the wildfire occurred

of the management unit (Figure 2). In the 2 weeks leading up to this fire, mean maximum daily temperatures were high and humidity was low (Figure 2a,b), with no precipitation during the preceding 13 days and only one precipitation event > 5 mm in the preceding 30 days (Figure 2c).

The focus of this study is on: (a) 20 permanent long-term vegetation-monitoring plots located in lowland vegetation on deeper soils, of which half were burned by the wildfire, and (b) 20 upland plots in the same watershed, all of which were burned by the wildfire. Fires

tend to spread downwind and uphill. Lowland plots that were affected by the wildfire were downwind of the fire spread, whereas plots unaffected by the wildfire were neither downwind or uphill of the fire spread. The lowland plots not affected by wildfire were just beyond the western edge of the wildfire (<150 m distance from burned plots) and slightly downhill of the burned plots (<5 m elevation difference). All upland plots were both downwind and uphill of the fire spread. Based on the pattern of fire spread, we have high confidence that the primary reason that plots differed in their exposure was due to the plots' position relative to the ignition and wind direction, rather than endogenous differences in fuel qualities (i.e., that unaffected plots did not burn because they lacked sufficient fuel or were too moist).

All plots were arrayed along 50-m transects, with five equally spaced 10-m<sup>2</sup> circular plots per transect. Detailed empirical observations suggest that the radius of community "patches" at this site is between 0.6 and 2.5 m (in areas without large ungulates; Koerner & Collins, 2013). We treated each plot as a replicate, because the edges of our plots are 6.4 m apart, suggesting that each plot represents a distinct patch separated by one to three patches (on average). However, we interpret our results cautiously, recognizing the limitations of not having multiple replicate wildfires and not having more widely spaced plots.

At the start and end of each growing season, the aerial coverage (per unit ground area) was estimated for all species present in each plot, using a modified Daubenmire cover class scale (see Collins & Calabrese, 2012). Cover class values were converted to their midpoints, and we used the maximum cover per species per plot per year to calculate all vegetation metrics (i.e., if a species had higher cover in the spring sampling, then cover from the spring sampling was used). In 2011, plots affected by the wildfire were not measured in autumn, and therefore, data from 2011 were excluded for all plots, because the methods were not comparable to other years.

We quantified changes in plant community metrics during the time period before ('Pre'; 2008–2010) and after ('Post'; 2012–2014) the 2011/2012 climate extreme. While we lacked a true control for the climate extreme (i.e., plots that did not experience a climate extreme), we were able to quantify if vegetation characteristics changed during the climate extreme and returned to their previous values after the climate extreme (similar to Isbell et al., 2015). The wildfire only affected two of the four lowland transects, creating a natural experiment with controls for wildfire exposure, which we used to assess how a growing-season wildfire affected the grassland community during the extreme climatic event. Thus, for lowlands, we had balanced sample sizes of plots with ( $n = 10$ ) or without wildfire ( $n = 10$ ), referred to hereafter as "F+" for burned plots and "F−" for non-burned plots (Figure 2b). The wildfire also affected 20 permanent plots in upland vegetation, leaving no control plots in uplands. For uplands, because we had years of pre-fire data, we could assess if and how the upland vegetation responded to the combination of the 2011/2012 climate extreme.

We evaluated seven response variables: three related to ecosystem structure (total plant cover, grass cover, forb cover), three

related to community diversity (species richness, Shannon diversity index, species evenness), and plant community composition (through multivariate analysis). Univariate responses (plant cover and diversity metrics) were analyzed using linear mixed models (LMM) in the package nlme in R version 3.2.3 (R Core Team, R Foundation for Statistical Computing, Vienna, Austria), where period (Pre or Post fire) and wildfire exposure (present [F+] or absent [F-]) were included as fixed effects, and plot was nested within transects as random effects to account for repeated measures sampling and the spatial structure of the data (Pinheiro, Bates, S., & D., 2014). We also included year as a random effect to account for potential successional changes after annual burning was discontinued in 2000. In the upland plots we could not include a fixed effect of wildfire, therefore we only considered the fixed effect of period (Pre/Post) and the same random effects as the lowland plots. Comparisons between upland and lowland areas were not conducted because they contain compositionally different vegetation (Collins & Calabrese, 2012). When at least one main effect was significant, pairwise comparisons among periods (Pre/Post) and wildfire exposure (F+/F-) were conducted using the package multcomp in R (Bretz, Hothorn, & Westfall, 2010).

We examined the effect of fire (F+/F-) and time period (Pre/Post) on plant community composition based on a Bray-Curtis dissimilarity matrix, with species relativized by maximum cover to reduce the impact of rare species on sample differences (McCune & Grace, 2002) using the Adonis function for perMANOVA in the R package vegan (R Core Team, R Foundation for Statistical Computing, Vienna, Austria). Our full model included an interaction between wildfire exposure and time period, with strata set at a combination of year and transect ID. Pairwise comparisons of wildfire exposure and time period were determined using the pairwise Adonis package in R that included a Bonferroni correction for multiple comparisons (R Core Team, R Foundation for Statistical Computing, Vienna, Austria).

### 3 | RESULTS

#### 3.1 | Lowlands

Before the climate extreme (in the 'Pre' period), total cover, grass cover, and forb cover were similar in plots that were (F+) and were not (F-) ultimately affected by wildfire (Appendix S3; Figure 3). No changes in total cover were statistically significant after the fire (Appendix S3; Figure 3a). Grass cover decreased significantly in both F+ and F- plots, but the reduction was only 15% in the F- plots, from an average of ~100% cover to 85% cover. Whereas grass cover decreased from an average of ~90% cover to an average of 20% cover in F+ plots, explaining the statistically significant interaction between time period and wildfire (Appendix S3; Figure 3b). After the climate extreme, forb cover increased slightly in F- plots and approximately doubled in F+ plots ( $p < 0.05$  for both); the interaction between period and wildfire was not significant, however (Appendix S3; Figure 3c).

Before the climate extreme, F- and F+ plots had similar species richness, but species diversity (Shannon index) and evenness were higher in F+ plots (Appendix S3; Figure 3e,f). Species richness increased in both fire treatments, but these increases were not significant (Figure 3d). Shannon diversity index and evenness increased in both F- plots and F+ plots, with larger increases in F+ plots ( $p > 0.05$  for both; Appendix S3; Figure 3e,f).

Time period (perMANOVA,  $F_{1,119} = 12.0$ ,  $p < 0.01$ ), wildfire exposure (perMANOVA,  $F_{1,119} = 14.4$ ,  $p < 0.01$ ), and their interaction (perMANOVA,  $F_{1,119} = 4.3$ ,  $p < 0.01$ ) separated multivariate plant community composition in lowlands (Figure 4). Community composition differed between all combinations of wildfire exposure and time periods ( $p = 0.01$ ; Figure 4). Before the climate extreme, F- and F+ plots were somewhat differentiated along the first NMDS axis, but largely overlapped in multivariate space. After the climate extreme, F+ and F- plots no longer overlapped along the first NMDS axis. In the post period, composition in F- plots largely overlapped with F- plots before the climate extreme. In F+ plots, multivariate composition in the post-extreme period showed almost no overlap with multivariate composition in the pre-period (note in Figure 4 the separation of ellipses). This indicates a large shift in plant species composition in F+ plots.

#### 3.2 | Upland plots

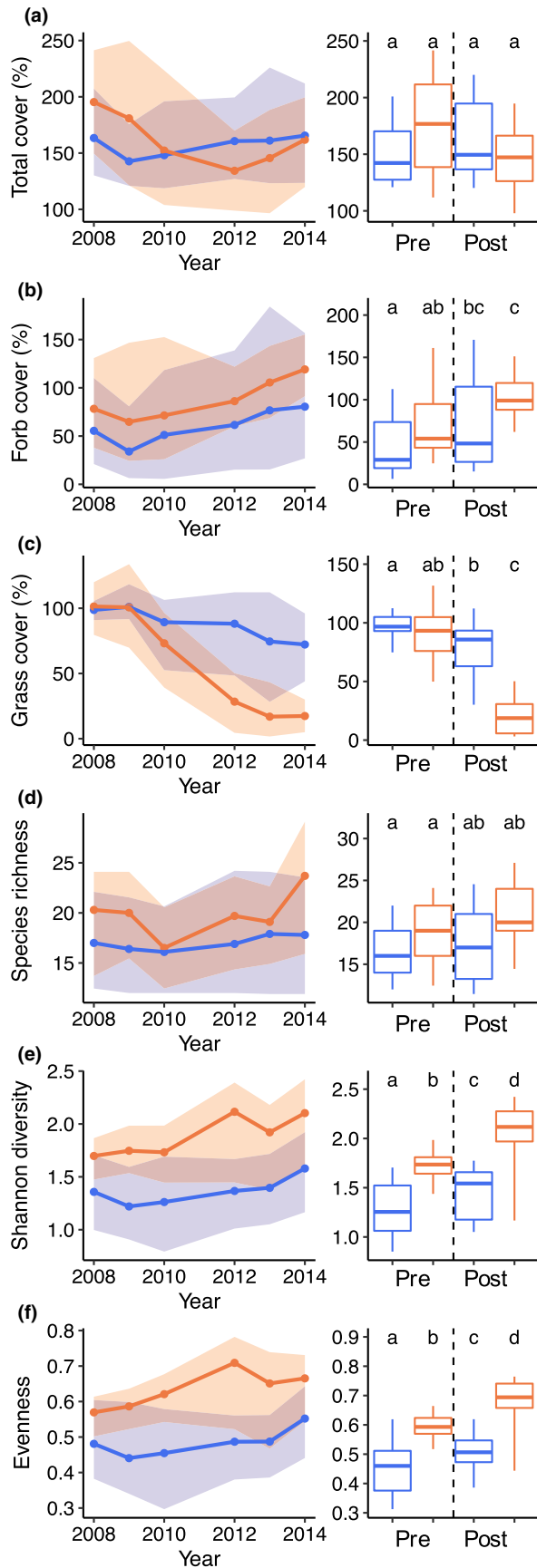
In uplands plots, all variables except total cover underwent statistically significant changes between the pre- and post-fire periods (Appendix S4). Grass cover decreased by more than 50% and forb cover increased by 100 (Figure 5a-c). Additionally, species richness, diversity, and evenness all increased after the wildfire and climate extreme (Figure 5d-f). For example, the median species richness went from 17 species per plot before 2011 to 23 species per plot after 2011. All of these changes in plant cover and species diversity were statistically significant (Appendix S4). Multivariate community composition also shifted after the wildfire and climate extreme (perMANOVA,  $F_{1,119} = 28.4$ ,  $p < 0.01$ ; Appendix S2).

### 4 | DISCUSSION

While plots unaffected by wildfire showed minor responses to a 2-year climate extreme, in plots affected by wildfire and the climate extreme, forb cover increased substantially, grass cover decreased by 75% and community diversity increased (Figures 3-5). These results underscore that climate extremes can have far greater effects when they initiate disturbances, leading to large, novel, and potentially lasting shifts in grassland communities (Paine et al., 1998; Walker & Salt, 2006).

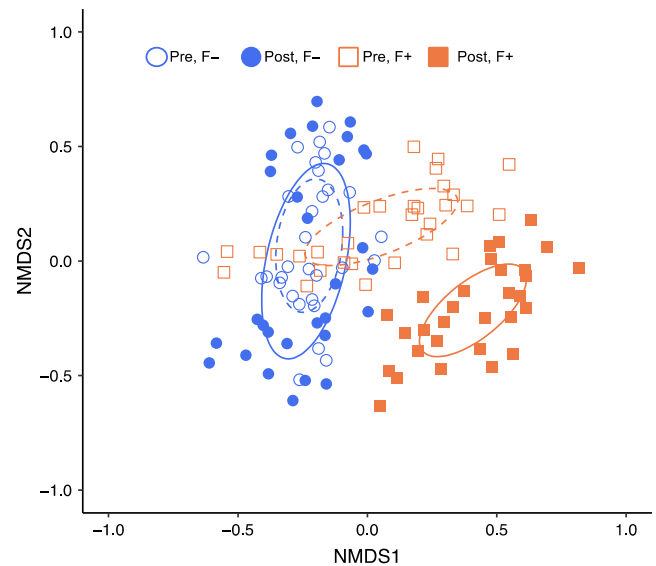
Based on past species and community responses to drought and heat waves at our study site (Hoover et al., 2014; Ladwig et al., 2016) and elsewhere (Isbell et al., 2015; Tilman & Downing, 1994; Volder, Briske, & Tjoelker, 2013), we hypothesized that even without wildfire, the high heat and low precipitation of 2011 and 2012



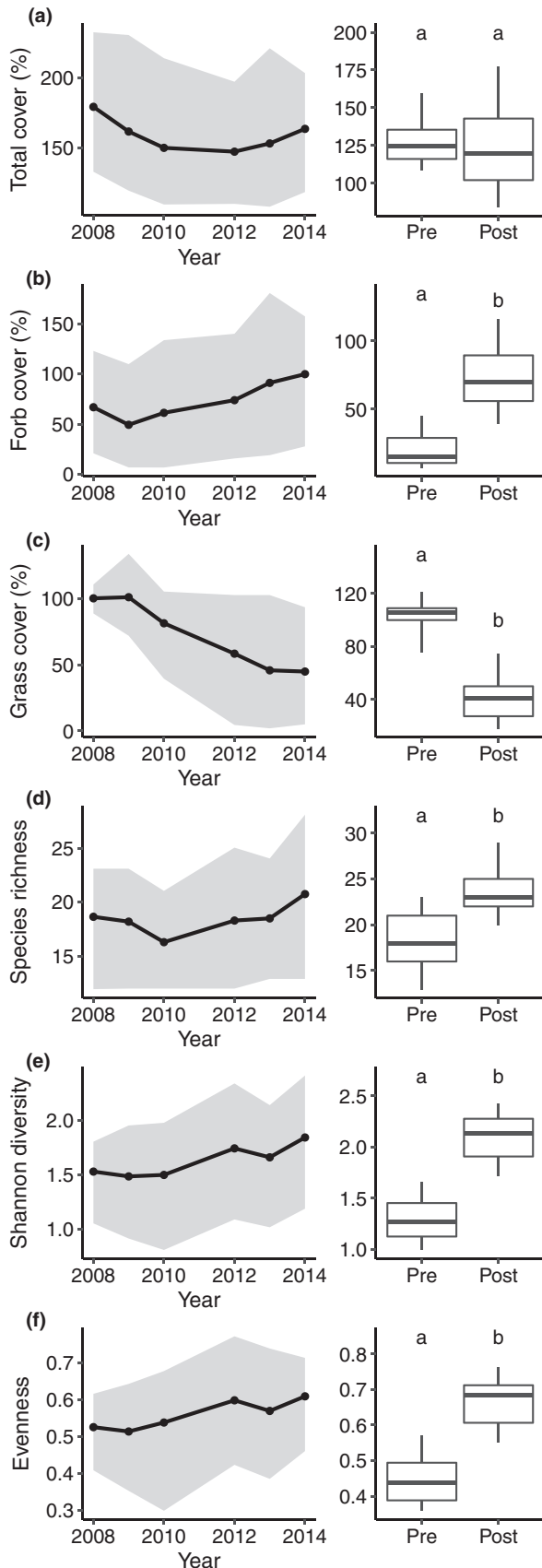


**FIGURE 3** Univariate results from lowland plots, shown as time series (left hand panels) and boxplots (right hand panels) for: (a) total cover, (b) forb cover, (c) grass cover, (d) species richness, (e) Shannon diversity index, and (f) species evenness. Orange coloring denotes plots affected by wildfire, blue denotes plots not affected by fire. In time series, points mark annual averages and shaded areas span the 5th to 95th percentile. In boxplots, period is on the x-axis, separating data from before (Pre; 2008–2010) and after the climate extreme (Post; 2012–2014). Boxes indicate 25% and 75% quartiles, and vertical lines indicate 95% confidence intervals. Within each panel, different letters denote differences among interacting periods and wildfire ( $p < 0.05$ ) based on pairwise comparisons. Note that y-axes differ for annual averages and corresponding box plots [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

would temporarily favor grasses at the expense of other species. Instead, community metrics in non-burned plots were either static (species richness, total cover) or changed in the opposite direction of our expectations (decreased grass cover; increased forb cover and Shannon diversity; Figure 3). The minor decrease in grass cover in non-burned plots probably resulted from the long-term decrease in fire frequency since year 2000, which typically leads to decreases in grass cover in tallgrass prairie that play out over decades (Alstad



**FIGURE 4** Nonmetric Multidimensional Scaling ordination of lowland plant community composition in burned (F+, blue coloring and circle markers) and unburned (F-, orange coloring and square markers) plots before (Pre, white fill) and after the extreme climate event (Post, solid fill). Stress is 0.26 for the final two-axis solution. Ellipsoids denote centroids for each combination of wildfire exposure and time period. Differences among plots were visualized using the metaMDS function in the package vegan for non-metric multi-dimensional scaling (NMDS) based on the Bray–Curtis dissimilarity metric [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 5** Univariate results from upland locations, shown as time series of annual averages (left hand panels) and boxplots (right hand panels) for: (a) total cover, (b) forb cover, (c) grass cover, (d) species richness, (e) Shannon diversity index, and (f) species evenness. In time series, points mark annual averages and shaded areas span the 5th to 95th percentile. In boxplots, period is on the x-axis, separating data from before (Pre; 2008–2010) and after the climate extreme (Post; 2012–2014). Boxes indicate 25% and 75% quartiles, and vertical lines indicate 95% confidence intervals. Within each panel, different letters denote differences among interacting periods and wildfire ( $p < 0.05$ ) based on pairwise comparisons. Note that y-axes differ for annual averages and corresponding box plots

Willms, 2010; Hulbert, 1988; Knapp & Seastedt, 1986). Or, it may take longer and more intense changes in temperature and precipitation to force a shift in the plant community (Ratajczak, D'Odorico, Collins, et al., 2017; Schwinning & Sala, 2004).

In plots affected by both the 2011 climate extreme and wildfire, we expected an increase in grass cover and concomitant decline in diversity (Collins & Calabrese, 2012), but the opposite occurred (Figures 3–5). Plots affected by wildfire in both uplands and lowlands experienced a nearly complete loss of grasses and a large increase in forb cover (Figures 3b, 5b), which runs counter to the handful of studies on growing-season wildfires in mesic grasslands and savannas (Smit et al., 2016; Twidwell, Rogers, Wonkka, Taylor, & Kreuter, 2016). These shifts in structure, diversity, and composition persisted for 2 years after the climate extreme, indicating that the combination of a climate extreme and wildfire might have exceeded the ability of this system to return to its prior ecological state (i.e., a regime shift; Paine et al., 1998; Walker & Salt, 2006). However, more years of data will be needed to firmly assess this hypothesis. At the very least, recovery after wildfire appears to be slow, during which some ecosystem services will likely be altered (e.g., pollination Welts & Joern, 2018).

Our results support the idea that multiple perturbations are more likely to result in state changes (Paine et al., 1998). For instance, wildfire in the Chihuahuan desert altered the response to ongoing experimental warming and precipitation manipulations (Collins et al., 2017) and following experimental warming in shrublands across Europe, recently disturbed areas experienced greater vegetation loss than undisturbed areas (Kröel-Dulay et al., 2015). Similar synergistic relationships between climate extremes and disturbance have been proposed for ecosystems ranging from semi-arid woodlands (Allen & Breshears, 1998) to tropical forests (Brando et al., 2014; Staal et al., 2015) and coral reefs (Mumby, Wolff, Bozec, Chollett, & Halloran, 2014). At our study site, the responses to experimental increases in temperature (Hoover et al., 2014), decreases in precipitation (Vanderweide & Hartnett, 2015), and repeated summer burning during non-drought conditions (Towne & Kemp, 2008) have not matched the immediate, large, and (potentially) persistent decline of grass cover reported in this study (Figures 3–5).

The reason(s) grasses declined so sharply after climate extreme and wildfire are not immediately clear, but we suspect that

et al., 2016; Collins & Calabrese, 2012). The somewhat surprising resistance to the 2011/2012 climate extreme could result from a build-up of shading litter since the last prescribed fire (Deutsch, Bork, &

fire-induced death of below-ground grass meristems played an important role. Below-ground meristems, or bud banks, are the primary source of grass recruitment in tallgrass prairie and one of the key mechanisms that reinforces grass dominance (Benson & Hartnett, 2006). The steep decline of grasses in plots affected by the wildfire strongly suggests that high temperatures along with the 2011 wildfire resulted in substantial bud mortality, allowing other species, such as forbs, to expand. Death of below-ground buds is usually rare for rhizomatous grasses in this system, even during droughts and under frequent prescribed burning (Benson & Hartnett, 2006; Ewing & Engle, 1988; Vanderweide & Hartnett, 2015; Volder et al., 2013). However, the 2011 wildfire likely had a higher intensity than typical spring burns and other fires in past studies of tallgrass prairie (Benson & Hartnett, 2006; Collins & Calabrese, 2012; Ewing & Engle, 1988; Gibson et al., 1990; Ratajczak et al., 2014); In the weeks leading up to the 2011 wildfire, the weather conditions matched those predicted to foster high-intensity fires (Govender, Trollope, & Van Wilgen, 2006; Rothermel, 1972; Twidwell et al., 2016b), including consistently high air temperatures, low relative humidity and almost no precipitation (Figure 2a–c). This inferred higher fire intensity may have exceeded the thermal tolerance of grass seeds and vegetative buds (Gagnon et al., 2015), especially considering that dry soils can conduct more heat below-ground (Choczynska & Johnson, 2009). Overall, the switch from grasses to forbs suggests that predicting the response to wildfires will require a better understanding of how the traits of perennial grasses and forbs affect their response to combinations of environmental drivers.

Some have proposed using prescribed fires during heatwave and drought conditions (sometimes referred to as “extreme fire”) to prevent or reverse expansion by woody species, thereby increasing the dominance of grasses and other herbaceous species (Smit et al., 2016; Twidwell et al., 2016b; Twidwell, Rogers, et al., 2016). To date, the ability of these “extreme fires” to favor grasses has only been tested in a few locations and has sometimes reversed woody plant expansion (Smit et al., 2016; Twidwell et al., 2016a; Wonkka et al., 2016). Nevertheless, our results suggest that “extreme fires” can sometimes have unintended consequences, such as declines in grass cover and related ecosystem services (e.g., forage production and carbon storage).

## 5 | CONCLUSIONS

In this study, a wildfire associated with a hot drought led to a shift in community composition and structure, which did not occur in areas unaffected by wildfire. Many experimental and observational approaches do not account for disturbances facilitated by climate extremes and therefore may not accurately reflect the potential ecological consequences of predicted increases in the frequency and intensity of climate extremes. Natural experiments, however, can provide valuable insights on how climate extremes and disturbance interact, especially when pre-disturbance data are available (Barley & Meeuwig, 2017). Understanding the response to climate

extreme-facilitated wildfires is critical, because the number and extent of wildfires are increasing in the U.S. Great Plains and in North America in general (Donovan et al., 2017; Jolly et al., 2015; Krueger et al., 2016). The response of this grassland community to a simultaneous climate extreme and related growing-season wildfire resemble theoretical predictions that multiple pressures are more likely to elicit lasting ecological changes (Paine et al., 1998), which has important implications for understanding the theoretical importance of climate anomalies and grassland management during climate extremes and other perturbations (Westerling, Walker, & Noy-Meir, 1989).

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## DATA ACCESSIBILITY

Plant species cover data can be assessed at Collins (2016). Climate data can be accessed at O’Neal (2016).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1.** Two-year rolling averages of (A) the annual average daily (black fill) and maximum (open fill) temperature during the peak growing season (June to August) and (B) precipitation during the peak growing season.

**Appendix S2.** Visualization of dissimilarity in vascular plant community composition between plots among different periods (Pre and Post 2011 fire) showing NMDS scores for axis 1 and 2

**Appendix S3.** ANOVA results for lowland plots

**Appendix S4.** ANOVA results for upland plots

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