

Press–pulse interactions: effects of warming, N deposition, altered winter precipitation, and fire on desert grassland community structure and dynamics

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Abstract

Global environmental change is altering temperature, precipitation patterns, resource availability, and disturbance regimes. Theory predicts that ecological presses will interact with pulse events to alter ecosystem structure and function. In 2006, we established a long-term, multifactor global change experiment to determine the interactive effects of nighttime warming, increased atmospheric nitrogen (N) deposition, and increased winter precipitation on plant community structure and aboveground net primary production (ANPP) in a northern Chihuahuan Desert grassland. In 2009, a lightning-caused wildfire burned through the experiment. Here, we report on the interactive effects of these global change drivers on pre- and postfire grassland community structure and ANPP. Our nighttime warming treatment increased winter nighttime air temperatures by an average of 1.1 °C and summer nighttime air temperature by 1.5 °C. Soil N availability was 2.5 times higher in fertilized compared with control plots. Average soil volumetric water content (VWC) in winter was slightly but significantly higher (13.0% vs. 11.0%) in plots receiving added winter rain relative to controls, and VWC was slightly higher in warmed (14.5%) compared with control (13.5%) plots during the growing season even though surface soil temperatures were significantly higher in warmed plots. Despite these significant treatment effects, ANPP and plant community structure were highly resistant to these global change drivers prior to the fire. Burning reduced the cover of the dominant grasses by more than 75%. Following the fire, forb species richness and biomass increased significantly, particularly in warmed, fertilized plots that received additional winter precipitation. Thus, although unburned grassland showed little initial response to multiple ecological presses, our results demonstrate how a single pulse disturbance can interact with chronic alterations in resource availability to increase ecosystem sensitivity to multiple drivers of global environmental change.

Keywords: aboveground net primary production, *Bouteloua eriopoda*, *Bouteloua gracilis*, desert grassland, fire, nighttime warming, nitrogen addition, soil moisture, species richness

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Introduction

Multiple drivers of global environmental change are expected to have dramatic impacts on ecosystem structure and function over the course of the next century (Sala *et al.*, 2000). Many of these environmental drivers are chronic ‘presses’ in that they are subtle, persistent, and in some cases accelerating over time. Examples include changing precipitation regimes (Min *et al.*, 2011; Beier *et al.*, 2012), increasing atmospheric nitrogen (N) deposition (Galloway *et al.*, 2008), and rising mean daytime and nighttime temperatures (Peng *et al.*, 2013). These chronic environmental drivers directly

and indirectly alter resource availability. For example, N deposition increases plant available N, whereas warming can decrease soil moisture availability (Wu *et al.*, 2011). The interactions of multiple global change drivers with contrasting effects (e.g., elevated CO₂ reduces transpiration losses, whereas warming decreases soil moisture availability) are often hard to predict because they may or may not be additive (Shaw *et al.*, 2002), and their effects likely change (Reich *et al.*, 2012) or may cancel out (Morgan *et al.*, 2011) over time.

Theory predicts that ecosystems will exhibit lagged responses to chronic alterations in resource availability through a hierarchy of mechanisms including physiological plasticity, genotypic variation, species reordering, and ultimately, species turnover (Smith *et al.*,

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2009). These time lags reflect, to some extent, delays in crossing environmental thresholds (Groffman *et al.*, 2006; D'Odorico *et al.*, 2012), as well as the ability of ecosystem processes to persist in the face of chronic changes in resource availability. For example, Avolio *et al.* (2013) found that increased precipitation variability altered genetic diversity of the dominant C₄ grass *Andropogon gerardii*, and Collins *et al.* (2012) found that 19 years of increased annual rainfall led to reordering of dominant species after an eight-year time lag in native tall grass prairie. This community reordering led to a significant increase in net primary production (Knapp *et al.*, 2012). Thus, ecosystems exhibit multiple patterns of response to chronic environmental presses that vary over time and can ultimately result in significantly altered ecosystem structure and function.

Natural disturbances are well-known drivers of change in ecosystems (White & Jentsch, 2001). Disturbances, such as fire, ungulate grazing, or wind throw, typically reduce the abundance of dominant species, which increases resource availability for subordinate and early-successional species (Pickett & White, 1985). As a consequence, disturbances often initiate patch dynamics, which can result in high overall species diversity at larger spatial scales (Connell, 1979; Wu & Loucks, 1995). Given that disturbances are a common feature of most terrestrial ecosystems, it is highly likely that disturbance events (ecological *pulses*) will interact with chronic resource alterations (ecological *presses*) to transform ecosystem structure and function now and in the future (Ives & Carpenter, 2008; Smith *et al.*, 2009; Kröel-Dulay *et al.*, 2015).

Aridland ecosystems, in particular, are predicted to be one of the mostly highly responsive ecosystems to anthropogenic change, particularly in the southwestern United States (Diffenbaugh *et al.*, 2008; Collins *et al.*, 2014; Knapp *et al.*, 2015). This region has experienced significant increases in mean annual temperature (Gutzler & Robbins, 2011) and N deposition (Fenn *et al.*, 2003; Báez *et al.*, 2007), as well as increasingly variable precipitation regimes (Notaro *et al.*, 2010; Petrie *et al.*, 2014) over the past century. Furthermore, climate models project increased frequency and intensity of ENSO-driven rainfall variability with global warming (Power *et al.*, 2013; Santoso *et al.*, 2013). Experiments demonstrate that greater precipitation variability (fewer but larger rain events) significantly increased seasonal soil moisture availability and net primary production in semiarid shortgrass steppe and desert grasslands (Heisler-White *et al.*, 2008; Thomey *et al.*, 2011). Experimental N addition increased aboveground net primary production (ANPP), especially by forbs, with no lasting effect on species richness in Chihuahuan Desert and Sonoran Desert plant communities (Hall *et al.*,

2011; Ladwig *et al.*, 2012). Experimental nighttime warming led to a significant increase in forb biomass and richness and a decrease in grass ANPP in shortgrass steppe (Alward *et al.*, 1999). Thus, because of their strong and rapid sensitivity to environmental variability (Chesson & Huntly, 1997), aridland ecosystems are ideal for understanding how natural disturbances interact with multiple drivers of global environmental change to alter ecosystem structure and function.

Given that N deposition, warming, and frequency of ENSO events are all projected to increase in the future, we established a long-term experiment in 2006 to determine the individual and interactive effects of these environmental changes on the structure and function of native desert grassland in central New Mexico, United States. Preliminary results demonstrated that growth rates of the dominant grasses were highly responsive to warming and N fertilization during an unusually wet summer monsoon (Collins *et al.*, 2010). In particular, the Chihuahuan Desert grass, *Bouteloua eriopoda*, increased with warming, but not N addition, whereas its shortgrass steppe congener, *B. gracilis*, increased with N addition, but not warming. Grass abundance may negatively impact the abundance of forbs (Mariotte *et al.*, 2013), ultimately reducing species diversity. Indeed, in a nearby experiment, forb biomass and richness increased following the removal of these dominant C₄ grasses (Peters & Yao, 2012). Thus, desert grassland responds to changes in these environmental drivers, which directly and indirectly affect community structure and diversity primarily through changes in the abundance of the dominant grasses.

In 2009, a lightning-caused wildfire burned through this experiment allowing us to assess how an ecological pulse (wildfire) interacted with ongoing ecological presses (nighttime warming, increased winter precipitation, and N fertilization) to affect postfire species composition and ANPP. Postfire recovery of dominant species in desert grasslands can take more than a decade (Parmenter, 2008; Ladwig *et al.*, 2014) in the absence of above-average rainfall. Based on these known responses, we tested the following hypotheses: (i) Following wildfire, the Chihuahuan Desert grass, *B. eriopoda*, would recover faster in warmed treatments, while the shortgrass steppe species, *B. gracilis*, would recover faster in N addition treatments compared with ambient plots; (ii) winter precipitation would not increase grass productivity, which responds primarily to summer precipitation (Muldavin *et al.*, 2008), but would increase forb NPP and species richness, which respond to spring soil moisture; (iii) forb richness would increase immediately following fire, and be highest in treatments receiving winter rainfall and N

fertilization. By testing these hypotheses, we can elucidate how this aridland community may respond to the individual and combined effects of multiple drivers associated with global environmental change.

Materials and methods

Study site

This study was conducted in the Sevilleta National Wildlife Refuge (SNWR), located at latitude 34°20'N and longitude 106°43'W in Socorro County, central New Mexico, United States. Prior to its designation as a wildlife refuge in 1973, the area had been grazed extensively for decades. Our experiment was located in native desert grassland codominated by *Bouteloua eriopoda* and *B. gracilis*. Overall, these grasses account for >90% of ANPP in this grassland. Other common species include scattered shrubs or subshrubs (e.g., *Yucca glauca* and *Ephedra torreyana*), as well as a mix of subdominant grasses (e.g., *Pleuraphis jamesii*, *Sporobolus* spp.) and forbs (*Cryptantha crassicarpa*, *Machaeranthera* spp., *Melampodium leucanthum*, *Sphaeralcea* spp.). Unvegetated soil and biocrusts account for ~25% cover in this ecosystem. Soils are Typic Haplargids derived from piedmont alluvium. Soil texture in the upper 20 cm, where highest root biomass occurs (Kurc & Small, 2004), is 68% sand, 22% silt, and 10% clay, with 2% calcium carbonate (Kieft *et al.*, 1998). Water holding capacity and nutrient reserves in these soils are very low (Zak *et al.*, 1994; Stursova *et al.*, 2006), and soils are highly erodible when vegetation cover and organic residues are removed, such as following fire (Ravi *et al.*, 2007).

On August 4, 2009, lightning ignited a ~3300-ha wildfire that burned through the experiment and its surroundings. Because desert grassland fires are patchy, not all of the replicate plots burned in the wildfire. Therefore, seven days after the wildfire was extinguished, the Sevilleta NWR Fire Crew thoroughly burned the remaining plots allowing us to assess experimentally the effects of interactions among multiple global change presses and a pulse disturbance on postfire grassland dynamics.

Average annual precipitation at this site is ~250 mm, more than half (~150 mm) of which occurs via convective storms that create intense but highly localized rain events during the summer monsoon, extending from July through early September (Pennington & Collins, 2007; Notaro *et al.*, 2010; Petrie *et al.*, 2014). Precipitation also comes as a mixture of snow and rain during winter and spring (Gosz *et al.*, 1995; Pockman & Small, 2010). Mean annual temperature is 13.2 °C. From 1989 to 2013, mean monthly maximum/minimum temperatures varied from 36/15 °C in June to 11/−9.5 °C in January.

Experimental treatments

Our experiment consisted of three factors (passive nighttime warming, increased winter precipitation, and N addition) in a fully crossed, completely randomized design, with five replicates of each treatment combination. There was a total of 40 plots and each plot was 3.0 × 3.5 m. Our nighttime

warming treatment was imposed on the full plot using lightweight aluminum fabric shelters mounted on rollers that were drawn across each warmed plot each night to trap outgoing long-wave radiation (Beier *et al.*, 2004). Dataloggers controlling shelter movements retracted the thermal blankets on nights when wind speeds exceeded a threshold value (to prevent damage) and when rain or snow occurred. Based on the long-term climate records, El Niño rains increase winter precipitation in our area by an average of 50%. We supplemented ambient winter precipitation each year using an irrigation system and reverse osmosis water. El Niño-type rains were added in six experimental storm events each winter that mimic actual El Niño winter-storm event size distribution (four 5-mm events, one 10-mm event, and one 20-mm event each winter) and amount (50 mm). For N deposition, we added 2.0 g m^{−2} yr^{−1} of N in the form of NH₄NO₃ because NH₄-N and NO₃-N contribute approximately equally to N deposition at SNWR (57% NH₄ and 43% NO₃; Báez *et al.*, 2007). The NH₄NO₃ was dissolved in 12 l of deionized water, equivalent to a 1-mm rainfall event, and applied with a backpack sprayer each year prior to the summer monsoon when most production occurs. Control plots received the same amount of deionized water.

Field measurements

From 2006 to 2009, air and soil temperature were measured in each plot with copper–constantan thermocouples positioned 20 cm above the ground and 2 cm below the soil surface beneath patches of grass. However, the soil sensors were unreliable in our warm and dry soils resulting in lengthy data gaps and high error rates. In 2011 following the fire, all copper–constantan thermocouples were replaced with Campbell Scientific CS107 temperature probes. Also starting in 2011, soil moisture was measured in each plot using 30-cm-long time domain reflectometry probes (Campbell Scientific CS-616) buried at a 45° angle to obtain an integrated measure of soil moisture in the top 15 cm of soil. Soil N availability was measured annually (except in 2011) from July through September using ion-exchange membrane Plant Root Simulator probes (WesternAg Industries, Calgary, Canada; Drohan *et al.*, 2005) placed in either *B. eriopoda* or *B. gracilis* patches in each plot.

Vascular plant standing biomass was estimated by species using a nondestructive volumetric method (Huenneke *et al.*, 2001; Muldavin *et al.*, 2008) that yields data on both species composition and aboveground net primary production. Volume measurements of all individual plants were recorded in spring (May) and fall (September) each year in two 1-m² permanent subplots in each treatment plot starting in April 2006. The two plots were centered under the long axis of the 3.0 × 3.5 m experimental unit. The subplots are separated by 25 cm leaving a one-meter buffer on each side of the short axis and a ~0.62-cm buffer on each end along the long axis.

Biomass was calculated allometrically for spring and fall via linear regression models with intercepts through the origin that were developed for each species from the plants collected outside of the experimental plots (Muldavin *et al.*, 2008). Total yearly ANPP (g m^{−2}) on a quadrat basis is then the sum of spring and fall production values for each species. Species

richness is the cumulative number of species occurring in each plot over the growing season each year.

Analyses

We used three-way ANOVA to determine whether nighttime warming, winter precipitation, and N deposition increased air and soil temperature, soil moisture, and soil N availability, respectively, and to assess any potential interactions among treatments each year. We used repeated-measures ANOVA to assess the individual and interactive effects of nighttime warming, winter precipitation, and N deposition on (i) total aboveground net primary production (ANPP), (ii) grass ANPP, (iii) forb ANPP, (iv) total species richness, (v) grass species richness, and (vi) forb species richness. Pretreatment data from 2006 were not included in the repeated-measures ANOVA. One-way ANOVA was used to assess resilience of ANPP of the two dominant species, *B. eriopoda* and *B. gracilis*, following fire. Resilience of *B. eriopoda* and *B. gracilis* ANPP was calculated as $\ln(\text{ANPP}_{2013}/\text{aveANPP}_{2006-2008})$ (Tilman & Downing, 1994), where $\text{aveANPP}_{2006-2008}$ was the prefire average ANPP of *B. eriopoda* or *B. gracilis* from 2006 through 2008 and ANPP_{2013} was the ANPP of either *B. eriopoda* or *B. gracilis* in 2013, four growing seasons after the fire.

Plant community dynamics pre- and postfire were quantified using nonmetric multidimensional scaling (NMDS) based on a Bray–Curtis similarity matrix. Effects of warming, winter rain, and N addition on community composition across all years and again for each year individually (excluding 2006) were determined by PERMANOVA followed by SIMPER (similarity percentages) analysis. Community analyses were performed on data matrices with rare species (species with < four occurrences) removed (McCune *et al.*, 2002). NMDS, PERMANOVA, and SIMPER were performed using the 'VEGAN' package in R (Oksanen *et al.*, 2013; R Core Development Team, 2014).

Results

Treatment effects

Although total annual precipitation was generally at or above average from 2006 to 2013, monsoon precipitation, which drives seasonal ANPP and species richness, was at or above average only in 2006, 2008, and 2013 (Fig. S1). Significant main effects were found for most imposed treatments (warming, winter precipitation, N addition), but there were few significant interactions among treatment variables. From 2011 through 2013, there was a significant nighttime warming by winter precipitation interaction in which mean daily nighttime low air temperature (0000 through 0600 h) during the summer monsoon was increased by 1.4 C ($P < 0.0001$). Warming alone increased winter daily nighttime low air temperature by 1.1 C, but this effect was not statistically significant (Fig. S2; Table S1). Winter rain events (December through

March) significantly increased mean winter VWC by about 15% (13.0% vs. 11.1%, $P < 0.0001$ for precipitation vs. ambient plots, respectively) (Fig. S3). There were no significant warming by precipitation interactions for soil moisture. Fertilization with N significantly elevated soil N availability in 2008, 2012, and 2013, but otherwise N availability was highly variable among treatments and between years, although soil N availability was always higher on fertilized compared with unfertilized plots (Fig. S4).

Over all years, total ANPP ranged from a high of 98.7 g m⁻² on the winter precipitation treatment in 2007 to a low of 2.6 g m⁻² on the control plots in 2011, a year of very low monsoon rainfall. Despite the significant treatment effects, there were few significant richness or ANPP responses to winter precipitation, nighttime warming, or nitrogen addition within most years (Table 1). The strongest responses were in 2007 and 2008 prior to the fire where forb ANPP was highest in warmed and winter rain treatments or treatments receiving all three factors. Immediately following the fire in 2010, grass ANPP increased significantly under nitrogen addition. Although a significant treatment effect was found for forb richness in 2011, a year of very low precipitation, none of the post hoc comparisons were significantly different.

Temporal effects: aboveground net primary production

Not surprisingly, significant year effects occurred for total, grass, and forb ANPP given the high degree of interannual variation in precipitation that occurs in this aridland ecosystem (Fig. 1, Table 1). A number of significant interactions were found, as well. For example, a year by N (YN) interaction occurred for grass, forb, and total ANPP where forb ANPP differed in one pair of years, whereas grass ANPP and total ANPP were significantly different in nearly every interannual comparison. In general, forb ANPP showed some of the most complex responses to combinations of treatments. For example, a significant year by temperature by precipitation (YTP) interaction occurred for forb ANPP (Fig. 1, Tables 2 and S2). The YTP interactions occurred from 2007 to 2012 reflecting significant differences pre- and postfire and among postfire years as well. In this case, forb ANPP was generally higher under this treatment combination than on plots prior to the fire (Fig. 1).

Not only were temporal responses by forb ANPP complex in response to treatments and fire, effect sizes were generally greater after the fire compared with before the fire. That is, the ratio of treatment to control responses was much stronger for forb biomass under several treatment combinations after the burn

Table 1 Treatment responses within each year from 2007 through 2013 based on analysis of variance. Numbers in each row with different letters were significantly different based on post hoc tests. 2006 was a pretreatment year and not included in the analysis

	C	N	T	P	NT	NP	TP	NTP	F	P
Grass ANPP (g m⁻²)										
2007	48.9 + 6.1	77.2 + 16.5	51.3 + 16.1	93.3 + 27.1	52.7 + 14.4	65.2 + 14.1	76.4 + 27.6	49.2 + 8.6	0.86	0.55
2008	37.5 + 5.8	56.0 + 8.5	44.4 + 4.2	64.5 + 15.7	48.0 + 8.4	58.4 + 10.9	65.4 + 16.6	55.2 + 7.7	0.85	0.56
2010	14.8 + 1.4a	39.8 + 9.4b	17.7 + 4.1a	14.3 + 3.3a	19.0 + 2.9a	29.0 + 4.1ab	11.8 + 1.3a	13.7 + 4.2a	4.53	0.0013
2011	1.9 + 0.5	2.6 + 0.4	1.5 + 0.3	2.3 + 0.3	1.5 + 0.4	3.2 + 0.6	2.5 + 0.3	3.0 + 0.9	1.61	0.17
2012	20.6 + 2.3	33.0 + 6.1	20.2 + 5.6	18.1 + 5.6	14.1 + 2.5	18.1 + 3.5	21.0 + 7.1	15.2 + 3.1	1.57	0.18
2013	42.4 + 12.1	80.2 + 16.5	34.6 + 5.5	37.4 + 6.4	50.1 + 20.8	32.9 + 3.1	56.8 + 12.5	39.9 + 6.0	1.84	0.12
Forb ANPP (g m⁻²)										
2007	2.9 + 0.4ab	2.6 + 0.9ab	3.6 + 0.6ab	5.4 + 1.2a	2.7 + 0.8ab	1.6 + 0.7b	3.7 + 0.6ab	5.5 + 0.8a	3.00	0.0154
2008	1.7 + 0.4a	3.0 + 0.9ab	3.4 + 1.1ab	0.9 + 0.3a	2.8 + 0.8ab	2.3 + 0.6ab	6.6 + 0.9b	7.0 + 2.1b	4.68	0.0011
2010	2.3 + 0.6	4.4 + 0.7	3.7 + 0.9	3.6 + 1.0	5.5 + 1.0	6.4 + 2.1	4.1 + 1.6	5.7 + 1.9	1.00	0.44
2011	0.6 + 0.2	1.0 + 0.5	3.3 + 2.8	1.6 + 0.2	3.3 + 2.6	1.6 + 0.5	1.1 + 0.4	2.0 + 0.9	0.49	0.83
2012	5.0 + 0.6	3.7 + 0.9	6.3 + 1.9	7.8 + 1.5	6.0 + 0.9	10.8 + 2.3	4.8 + 1.6	7.3 + 1.5	2.09	0.0738
2013	4.6 + 2.3	4.9 + 1.0	6.7 + 1.3	8.9 + 2.7	12.7 + 5.2	13.0 + 6.9	8.0 + 4.4	19.4 + 7.8	1.17	0.34
Grass species richness (m⁻²)										
2007	3.0 + 0.0	3.0 + 0.3	3.2 + 0.2	2.6 + 0.4	3.4 + 0.4	2.6 + 0.2	3.0 + 0.3	3.2 + 0.2	0.97	0.47
2008	3.0 + 0.0	3.2 + 0.4	3.0 + 0.3	2.8 + 0.4	3.2 + 0.4	2.8 + 0.2	2.8 + 0.4	3.2 + 0.2	0.37	0.91
2010	3.0 + 0.0	2.6 + 0.3	3.0 + 0.3	2.4 + 0.5	3.2 + 0.4	2.6 + 0.2	3.0 + 0.3	3.2 + 0.2	0.95	0.48
2011	3.0 + 0.0	2.4 + 0.2	2.6 + 0.2	2.4 + 0.2	2.6 + 0.2	2.6 + 0.2	2.6 + 0.2	3.0 + 0.0	1.21	0.32
2012	3.0 + 0.0	2.4 + 0.2	2.6 + 0.2	2.6 + 0.4	2.8 + 0.2	2.6 + 0.2	2.6 + 0.2	3.4 + 0.2	1.60	0.17
2013	3.0 + 0.0	2.6 + 0.2	2.8 + 0.2	2.8 + 0.4	2.8 + 0.2	2.8 + 0.2	2.6 + 0.2	3.4 + 0.2	1.19	0.33
Forb species richness (m⁻²)										
2007	8.8 + 1.3	8.4 + 0.7	8.6 + 0.7	8.0 + 0.7	11.8 + 1.2	10.6 + 1.1	8.4 + 0.7	10.2 + 0.8	2.16	0.065
2008	5.2 + 0.7	4.6 + 0.8	4.8 + 0.5	5.8 + 0.7	5.6 + 0.7	5.2 + 0.8	5.0 + 0.7	4.8 + 1.0	0.29	0.95
2010	11.2 + 1.3	8.2 + 0.8	9.6 + 0.7	9.2 + 0.7	11.4 + 0.8	8.8 + 1.6	8.6 + 1.2	10.4 + 1.4	1.17	0.34
2011	4.8 + 0.9	2.0 + 0.4	3.0 + 0.7	4.0 + 0.6	2.6 + 0.4	3.6 + 0.5	2.8 + 0.6	4.4 + 0.7	2.34	0.0474
2012	7.2 + 0.9	6.2 + 0.9	6.8 + 0.6	7.8 + 1.4	8.0 + 0.4	5.0 + 0.9	5.4 + 1.1	7.8 + 0.6	1.64	0.16
2013	5.0 + 0.3	4.4 + 1.0	4.0 + 0.5	4.2 + 0.5	5.0 + 0.4	6.0 + 0.5	2.6 + 0.4	4.8 + 1.1	1.74	0.14

C = control; N = nitrogen addition; T = nighttime warming; P = winter precipitation. Values in bold are significant at $P < 0.05$.

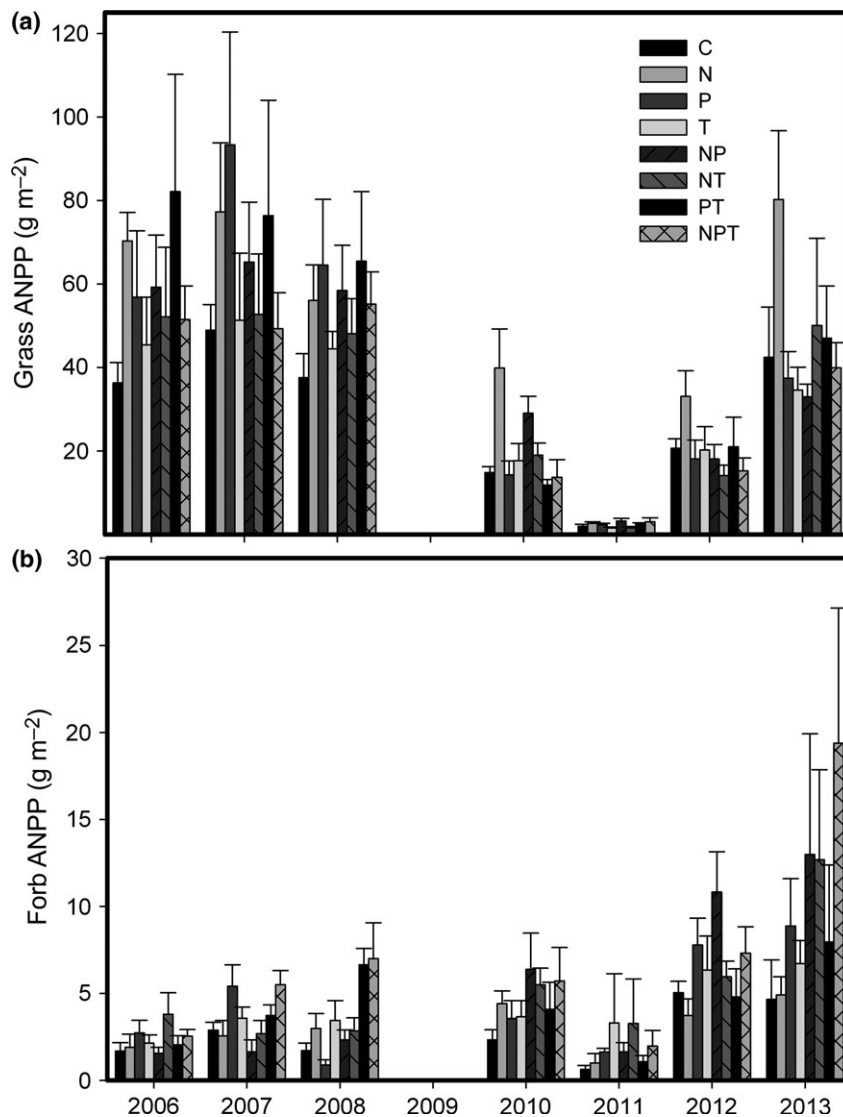


Fig. 1 Responses of (a) grass and (b) forb aboveground net primary production (ANPP) to nitrogen addition (N), winter precipitation (P), nighttime warming (T), and all possible combinations of treatments ($n = 5$) before and after a lightning-caused wildfire (2009) in Chihuahuan Desert grassland.

compared with before the burn (Figs 2, S5–S7). To some extent, this response was modulated by NPP in a given year, which reflects the interactions between precipitation and the experimental treatments.

Temporal effects: plant species richness

Over all years, total richness ranged from a high of 15.2 species m^{-2} on the warmed, N addition treatment in 2007 to a low of 4.4 species m^{-2} on the N addition treatment in 2011. Like ANPP, significant year effects also occurred for total and forb richness with most treatment interactions occurring following the fire (Fig. 3, Tables 3 and S3). There were no significant treatment

effects on grass richness, which only ranged, on average, from 2.4 to 3.2 species m^{-2} (Fig. 3). Forb species richness was far more dynamic, ranging from a low of 2.0 species m^{-2} on fertilized plots in 2011 to 11.8 species m^{-2} on warmed, fertilized plots in 2007. As a consequence, all significant responses by total richness mirrored those of forb richness, which was significantly different in nearly every year-by-year comparison. In addition, a YN interaction occurred in all years in which forb richness on fertilized plots was slightly lower than on control plots in each year following the fire. A TN interaction also occurred for forb richness following the fire. Richness was generally higher on plots that were fertilized and warmed compared with

Table 2 Results of repeated measures analysis of variance for forb, grass and total aboveground net primary production. Data from the pre-treatment year (2006) were not included

Source of variation	Forb			Grass			Total		
	df	F	P	df	F	P	df	F	P
Year	5,28	19.66	<0.0001	5,28	103.1	<0.0001	5,28	113.26	<0.0001
T	1,32		0.0961	1,32		0.15	1,32		0.29
P	1,32	4.45	0.427	1,32		0.8	1,32		0.47
N	1,32		0.09	1,32		0.5	1,32		0.29
Year × T	5,28	3.15	0.0233	5,28		0.22	5,28		0.15
Year × P	5,28		0.18	5,28		0.12	5,28		0.28
Year × N	5,28	2.65	0.0442	5,28	3.56	0.0129	5,28	4.56	0.003
Year × T × P	5,28	3.28	0.0187	5,28		0.5	5,28		0.45
Year × T × N	5,28		0.12	5,28		0.0577	5,28		0.07
Year × P × N	5,28		0.48	5,28		0.38	5,28		0.55
Year × T × P × N	5,28		0.22	5,28		0.9	5,28		0.97
T × P	1,32		0.5564	1,32		0.5	1,32		0.6
T × N	1,32		0.4757	1,32		0.17	1,32		0.22
P × N	1,32		0.37	1,32	4.89	0.0343	1,32		0.0524
T × P × N	1,32		0.71	1,32		0.39	1,32		0.35

T = nighttime warming; P = winter precipitation; N = nitrogen addition. Values in bold are significant at $P < 0.05$.

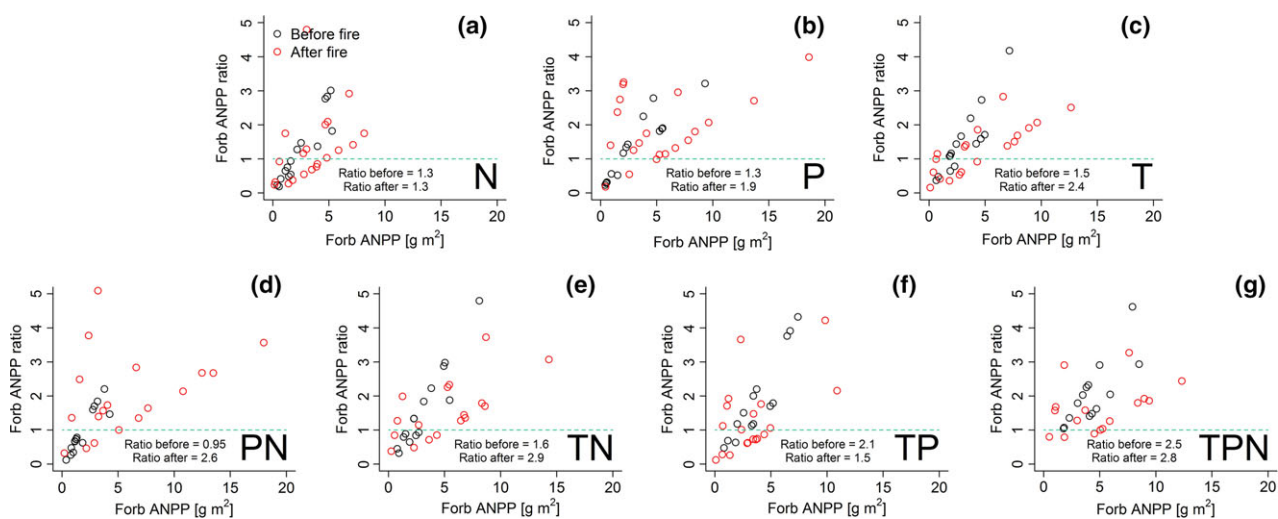


Fig. 2 Effect size of forb biomass responses before and after the fire for each of the experimental treatments (a–c) and treatment combinations (d–g). In each case, the symbols show the ratio of the mean treatment response ($n = 5$) to the mean control ($n = 5$) relative to mean control plots in each year. Larger ratios indicate stronger effect sizes.

plots that received either treatment independently (Fig. 3, Tables 3 and S3).

Community composition

Based on PERMANOVA results, all three treatments had significant effects on community structure over the full time series of the experiment, and all treatment interactions were also significant (Table 4). Despite these significant treatment results, NMDS ordination showed

the strongest drivers of community dynamics to be fire and interannual variability likely caused by strong differences in precipitation among years (Fig. 4). Plots from each year tended to occupy relatively discrete space within the ordination with high variability among treatments in 2011, a year of very low total precipitation (Fig. S1). In general, prefire samples fall to the right side of the figure and postfire samples to the left, with the exception of 2013 when vegetation began converging with prefire composition.

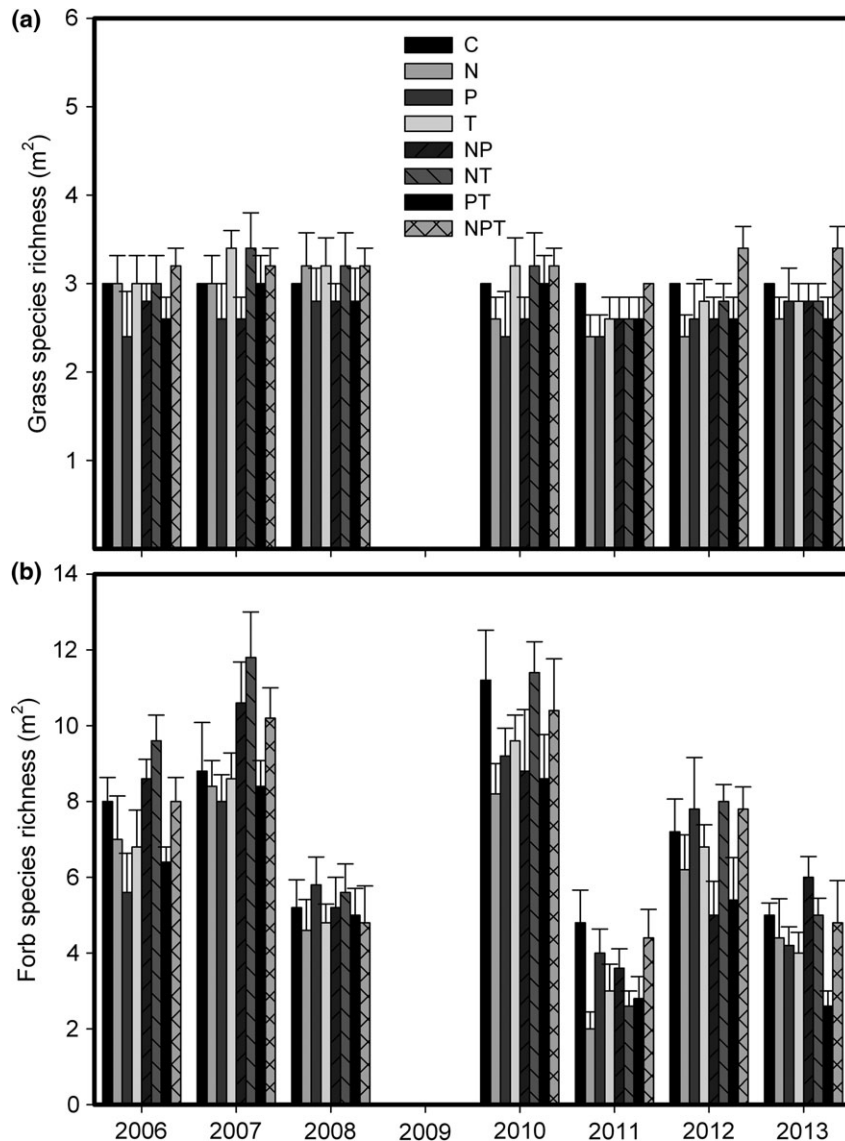


Fig. 3 Responses of (a) grass and (b) forb species richness to nitrogen addition (N), winter precipitation (P), nighttime warming (T), and all possible combinations of treatments ($n = 5$) before and after a lightning-caused wildfire (2009) in Chihuahuan Desert grassland.

Based on PERMANOVA for each year separately, there were significant main effects of N addition, nighttime warming, and winter precipitation in three years (Table 4). All but one of the significant effects occurred in the years following the fire, indicating strong press-pulse effects on plant community composition in this grassland. To a large extent, these differences reflect changes in the abundance and richness of forbs under main effects of nitrogen, warming, and winter precipitation.

Together, *B. eriopoda* and *B. gracilis* were by far the two dominant species in this grassland, accounting for an average of 93.8% of ANPP over the three years prior

to the wildfire. There were no significant treatment effects on the rate of recovery (resilience) of these two species based on three-way ANOVA (*B. eriopoda* $P = 0.467$, *B. gracilis* $P = 0.447$), although for *B. eriopoda* the N effect within the model was marginally significant ($P = 0.0591$). Surprisingly, the recovery of *B. eriopoda* ANPP was slightly inhibited by N addition. In 2013, ANPP of *B. eriopoda* was 23% and 29% of average prefire levels on N addition vs. non-N addition treatments, respectively. In contrast, N addition had no effect on *B. gracilis* resilience. Rather, by 2013, ANPP of *B. gracilis* was 272% and 268% higher than prefire ANPP in N addition vs. non-N addition treatments, respectively.

Table 3 Results of repeated-measures analysis of variance for forb, grass, and the total species richness. Data from the pretreatment year (2006) were not included

Source of variation	Forb			Grass			Total		
	df	F	P	df	F	P	df	F	P
Year	5,28	96.2	<0.0001	5,28		0.058	5,28	99.73	<0.0001
T	1,32		0.8	1,32		0.16	1,32		0.4
P	1,32		0.7	1,32		0.63	1,32		0.6
N	1,32		0.4	1,32		0.6	1,32		0.28
Year × T	5,28		0.12	5,28		0.063	5,28		0.0613
Year × P	5,28		0.25	5,28		0.17	5,28		0.34
Year × N	5,28	6.57	0.0004	5,28		0.75	5,28	5.39	0.0014
Year × T × P	5,28		0.47	5,28		0.99	5,28		0.46
Year × T × N	5,28	2.91	0.03	5,28		0.22	5,28	2.64	0.0449
Year × P × N	5,28		0.2	5,28		0.62	5,28		0.17
Year × T × P × N	5,28		0.059	5,28		0.45	5,28		0.097
T × P	1,32		0.4	1,32		0.37	1,32		0.6
T × N	1,32	5.73	0.02	1,32		0.19	1,32	8.56	0.0063
P × N	1,32		0.3	1,32		0.27	1,32		0.16
T × P × N	1,32		0.5	1,32		0.95	1,32		0.5

T = nighttime warming; P = winter precipitation; N = nitrogen addition. Values in boldface are significant at $P < 0.05$.

Table 4 PERMANOVA analysis of the effects of passive nighttime warming (T), nitrogen fertilization (N), and winter precipitation (P) on plant community composition in native desert grassland across all years (excluding pretreatment year 2006) and in each year individually

All years	2007	2008	2010	2011	2012	2013
T**	T*			T*		T*
P**			P*	P**	P**	
N**			N**	N*	N*	
T × P*						
N × P*						
N × T**						
N × T × P**						

* $P < 0.05$, ** $P < 0.01$.

Discussion

Pulse disturbances are likely to have profound impacts on community structure and ecosystem processes subjected to combinations of global change presses, such as warming, N deposition, and altered precipitation regimes. In our perennial-dominated, semiarid grassland, the strongest drivers of change were interannual precipitation variability and fire (pulse disturbance). Experimental nighttime warming, increased winter precipitation, and N addition significantly altered abiotic conditions and resource availability in this desert grassland, but resulted in weak and often inconsistent responses in ANPP, species richness, and community composition prior to the fire. These results contrast

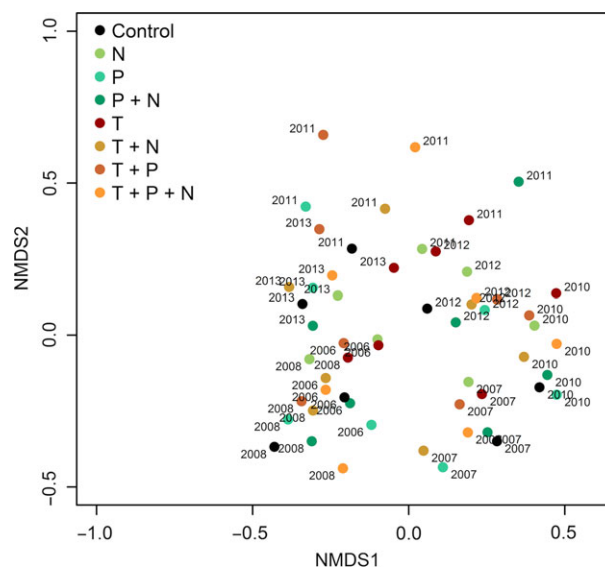


Fig. 4 Nonmetric multidimensional scaling (NMDS) ordination of plant community composition by year and treatment. Sites are separated along the first axis between prefire (2006–2008) and postfire (2010–2013) time periods. 2006 was a pretreatment year, but is included in the ordination for context. The analysis shows that interannual variation and fire have larger impacts than treatment effects within years.

with Shaw *et al.* (2002) who found that ANPP of serpentine grassland, which is dominated by annual grasses, increased 84% after three years under this same combination of treatments. Indeed, there were few responses in community composition and structure to

any of the experimental treatments, and few interactions occurred among treatments, prior to the wildfire in 2009 (Figs 1 and 2). Rather, most treatment effects on community structure emerged following the fire. Thus, fire (a pulse disturbance) had a much greater impact on community structure and function than the more subtle abiotic presses, but following the fire interactions among these ecological presses influenced community structure during postdisturbance succession.

Our results are consistent with Kröel-Dulay *et al.* (2015) who found in a cross-site experiment in Europe that successional systems following a disturbance were more sensitive to environmental change drivers than more mature ecosystems. They attributed these responses to differential sensitivities of species to environmental drivers during early compared to later life stages (e.g., Roleda *et al.*, 2007; Medeiros *et al.*, 2012). This mechanism may not apply to our desert grassland, however, because most of these grassland species propagate asexually and gradually regain cover following fire (Parmenter, 2008; Ladwig *et al.*, 2014). Community composition in this grassland includes annual and perennial forbs that depend primarily on winter and spring soil moisture (Xia *et al.*, 2010), and long-lived perennial C₄ clonal grasses, which generally respond most strongly to summer monsoon precipitation (Muldavin *et al.*, 2008; Collins & Xia, 2015). Thus, as we hypothesized, burning reduced the competitive dominance of the perennial grasses allowing forbs to increase in abundance in response to a combination of environmental drivers.

Overall, fire reduced the abundance of the dominant grass, *B. eriopoda*, by more than 80% in some plots, whereas forb richness and ANPP increased. In the absence of strong competitive dominance by perennial grasses (Peters & Yao, 2012), richness and ANPP of forbs continued to increase, and as we hypothesized, forb ANPP was highest on warmed treatments that received winter rain and added N. Indeed, four years after the fire, forb ANPP on warmed, fertilized plots that received winter rain was 7.5 times greater than forb ANPP in this same combination of treatments at the start of the experiment (Fig 1).

In contrast to our hypothesis, none of the global change drivers significantly affected the rate of recovery by the dominant grasses. Prior to the fire, ANPP of *B. eriopoda* was nearly double that of *B. gracilis*. By 2013 following an above-average monsoon season, ANPP of *B. eriopoda* was still only 38.3 g m⁻² across all the treatments, or 33.7% of prefire levels. In contrast, postfire ANPP of *B. gracilis* was 1.75 times that of prefire conditions (46.5 vs. 26.6 g m⁻², respectively), but still less than half that of prefire ANPP of *B. eriopoda* (113.7 g m⁻²). Thus, in 2013, total grass abundance was

still much lower than prefire conditions, creating conditions for forbs to persist (Fig 1).

The increase in forb ANPP observed in this study is consistent with forb responses to warming and increased precipitation in other systems. In shortgrass steppe, Alward *et al.* (1999) reported that increased nighttime temperature was correlated with an increase in forb species richness. Zhang *et al.* (2015) reported that warming increased forb abundance in a temperate meadow in China. Zavaleta *et al.* (2003) found few consistent responses in species richness to warming, precipitation, and N fertilization, but those differences in richness that did occur were primarily driven by the changes in forb richness. Together, these studies along with our results suggest that forb abundance and richness are likely to be highly sensitive to multiple drivers of global environmental change, through both direct (e.g., increased grass ANPP with N addition) and indirect (e.g., altered competitive regimes with perennial grasses following fire) mechanisms.

We hypothesized that winter precipitation would have a limited effect on grass productivity, but would increase forb ANPP and species richness. Our winter precipitation treatment significantly increased soil VWC during the nongrowing season by 9.3%, but this additional soil moisture was generally depleted prior to the monsoon season. Following the fire, forb ANPP was highest on the warmed, fertilized plots that received additional winter rain. Forb richness and ANPP in this Chihuahuan Desert grassland are tightly correlated with soil moisture accumulated during winter and spring precipitation events (Xia *et al.*, 2010; Mulhouse *et al.*, 2016), but grass ANPP is driven primarily by soil moisture derived from monsoon precipitation (Muldavin *et al.*, 2008). Thus, winter moisture is more likely to affect forb rather than grass richness and ANPP. Climate models predict a decrease in winter precipitation in our region (Gutzler & Robbins, 2011), likely reducing forb ANPP and richness in the future.

Warming can have a number of direct and indirect effects on ecosystem processes. For example, in a multi-site study of mesic herbaceous communities across Europe, warming, on average, increased aboveground plant biomass (Peñuelas *et al.*, 2004), rate of litter decomposition (Emmett *et al.*, 2004), soil respiration (Emmett *et al.*, 2004), and N loss (Schmidt *et al.*, 2004). A recent meta-analysis (Wu *et al.*, 2011) reported that warming resulted in an overall increase in ANPP, although other studies suggest that warming indirectly affects ANPP by decreasing soil moisture availability (e.g., Sherry *et al.*, 2008; Xia & Wan, 2012; Xu *et al.*, 2013). Yang *et al.* (2016) reported that warming enhanced drought resistance in temperate steppe vegetation. The soil moisture response we observed under

our nighttime warming treatment differed from those experiments where warming typically decreased moisture availability. Surprisingly, we found that soil moisture was slightly higher in warmed compared with ambient plots during the summer monsoon when most ANPP occurs. Thus, our nighttime warming treatment did not negatively impact soil moisture during the peak growing season when daytime soil surface temperatures can reach 60 °C. As a consequence, ANPP in our system responded to seasonal soil moisture availability, as expected, but soil moisture did not decrease under our nighttime warming treatment.

Nitrogen fertilization significantly increased plant available N in our experiment (Fig. S4), and again, most significant effects of N addition occurred following the wildfire (Fig. 1, Table 4). Nitrogen enrichment has been shown to increase aboveground net primary production and decrease plant species richness in mesic herbaceous communities (Clark & Tilman, 2008; Lebauer & Treseder, 2008), whereas fertilization effects in arid and semiarid systems are often contingent on soil moisture (Hall *et al.*, 2011; Ladwig *et al.*, 2012). For example, N fertilization increased forb richness and ANPP during wet years in shortgrass steppe (Lauenroth *et al.*, 1978), Chihuahuan Desert grassland (Ladwig *et al.*, 2012), and Sonoran Desert winter annual communities (Hall *et al.*, 2011). Previous studies have found that *B. eriopoda* is relatively unresponsive to the levels of N addition used in our experiment (2.0 g m⁻² yr⁻¹), whereas *B. gracilis* is highly responsive to low amounts of N addition (Báez *et al.*, 2007). Nevertheless, our N addition treatment had no significant impact on postfire recovery of *B. gracilis* and appeared to slightly inhibit that of *B. eriopoda*. Thus, postfire recovery of ANPP in this semiarid grassland reflects the innate differences between perennial C₄ grasses and short-lived C₃ forbs to fire and other abiotic drivers of global environmental change.

Although we implicate fire as the cause of community responsiveness to global change drivers, other uncontrolled factors, such as lag effects or drought, could also play a role in postfire community dynamics. Indeed, there is evidence for one-year lag effects in ANPP response to interannual variation in precipitation (Sala *et al.*, 2012; Petrie *et al.*, 2015), but such lags should occur across the temporal span of our experiment. Even though lags may occur, arid ecosystems are known to be highly responsive to interannual variation in precipitation (Huxman *et al.*, 2004). Drought could be another factor affecting the community response given that precipitation was well below average in 2011 and 2012 (Knapp *et al.*, 2015), but recovery from drought can be quite rapid (Báez *et al.*, 2013). Thus, we feel confident that the increased responsiveness to

global change drivers noted in our experiment was a consequence of the fire and the dramatic reduction in abundance of the dominant grass, *B. eriopoda*.

The independent impacts of altered precipitation, warming, and N addition on grassland production and diversity have been well documented (e.g., Knapp & Smith, 2001; Suding *et al.*, 2005; Lebauer & Treseder, 2008; Wu *et al.*, 2011). Studies on the interactive effects of various environmental change drivers on plant community structure and ecosystem function have resulted in few strong generalities, perhaps because the effects of one driver may cancel the effects of another (Rustad *et al.*, 2001; Morgan *et al.*, 2011; Wu *et al.*, 2011). Moreover, the long-term response to single or combined environmental drivers may change as species composition responds to changes in resource availability (Isbell *et al.*, 2012; Wu *et al.*, 2012; Avolio *et al.*, 2014), further challenging generality. As a consequence, calls for additional long-term studies on the interactive effects of environmental change drivers on community structure and ecosystem function are common (e.g., Wu *et al.*, 2011; Xu *et al.*, 2013).

Arid and semiarid ecosystems, which cover approximately 40% of terrestrial environments (Reynolds *et al.*, 2007; Maestre *et al.*, 2012), are predicted to be highly sensitive to increased interannual climate variability (Diffenbaugh *et al.*, 2008). Climate models project increased within- and between-season variability, with little change in total growing season precipitation (Gutzler, 2013). However, increased precipitation variability in the form of larger, less-frequent precipitation events can have strong, positive effects on semiarid grassland structure and function (Heisler-White *et al.*, 2008; Knapp *et al.*, 2008; Thomey *et al.*, 2011). By the end of this century, regional mean temperatures are predicted to increase by 3–4 °C leading to longer drought cycles, greater aridity, and significantly lower soil moisture availability (Seager *et al.*, 2007; Cook *et al.*, 2015). Although inorganic N deposition is expected to increase by 2.0–6.0 g m⁻² yr⁻¹ in the future across the southwestern United States (Fenn *et al.*, 2003; Báez *et al.*, 2007), increased aridity is likely to offset any potential positive impacts of elevated rates of N deposition on ANPP. Overall, the combined effects of increased aridity, N deposition, and more intense El Niño events on species interactions and changes in species composition remain unclear. Although some significant effects occurred in our long-term experiment, these differences were often ephemeral and variable among treatments and years, and most changes in community structure in response to these global change drivers occurred during postfire recovery. Together, our results demonstrate how pulse disturbances can interact with chronic alterations in resource availability to

increase ecosystem sensitivity to multiple drivers of global environmental change.

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Supporting Information

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

Figure S1 Monsoon (June–September, gray bars) and total annual precipitation (blue bars) for each year during the study period.

Figure S2 Average daily air and soil temperature during winter (December–February) and summer monsoon (June–September) seasons from 2011–2013 in control (C), warmed (W), increased winter precipitation (P), and warmed plus increased winter precipitation (WP) treatments.

Figure S3 Average daily soil volumetric water content (0–15 cm depth) from 2011–2013 in control (C), warmed (W), increased winter precipitation (P), and warmed plus increased winter precipitation (WP) treatments by season.

Figure S4 Plant available soil nitrogen during the monsoon season measured by Plant Root Simulator probes (Drohan *et al.*, 2005).

Figure S5 Effect size of grass biomass responses before and after fire for each of the experimental treatments and treatment combinations.

Figure S6 Effect size of forb richness responses before and after fire for each of the experimental treatments and treatment combinations.

Figure S7 Effect size of grass richness responses before and after fire for each of the experimental treatments and treatment combinations.

Table S1 Summary statistics for mean daily air and soil temperature, and soil volumetric water content (VWC) for control (C), warmed (W), winter precipitation (P), and warmed plus winter precipitation treatments (WP) for winter (December–February) and monsoon (June–September) seasons.

Table S2 Contrasts for aboveground net primary production (ANPP) from Repeated Measures ANOVA.

Table S3 Contrasts for species richness (m^{-2}) from Repeated Measures ANOVA.