

Evidence for long-term shift in plant community composition under decadal experimental warming

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Summary

1. Long-term, slow ecological processes such as changes in plant community structure and composition strongly regulate ecosystem responses to climate change. Shifts in plant community are expected in chronically altered environments under warming. However, experimental evidence for long-term shifts and the associated mechanisms is still scarce in temperate grasslands.

2. Here, we explore the long-term responses of a prairie plant community to 14-year (2000–2013) manipulations of climate warming and clipping in Oklahoma, USA. Infrared heaters were used to elevate soil temperature by about 2 °C all year round, and annual clipping was applied to mimic hay harvest.

3. Community composition was resistant to experimental warming in the first seven years, but started to show responses starting from the eighth year; clipping consistently affected community composition over the years. Compositional change under long-term warming was mainly due to one invasive species and three dominant species. The negative correlations in relative abundance between the invasive species and the dominant species suggest interspecific competition. Community structure (i.e. richness, evenness and diversity) had no overall response to experimental warming. However, in 2007, the extreme wet year, warming reduced species richness by 30%. Clipping promoted species richness by 10% on average over the 14 years but decreased community evenness. Warming did not interact with clipping in influencing the plant community variables.

4. *Synthesis.* Our study provides experimental evidence for long-term shifts in plant community composition due to warming and revealed novel mechanisms (i.e. species invasion and associated biotic interactions) underlying the long-term shift. The results also suggest that climate extremes may elicit or advance community responses to climate warming. The findings highlight that long-term climate change experiments are essential to reveal potential shifts in community composition.

Key-words: diversity, extreme climate, increased temperature, plant–climate interactions, prairie plant community, species invasion, tallgrass prairie, temperate grassland

Introduction

Global mean temperature has increased by 0.85 °C since the 1880s, and it is predicted to continue rising during the 21st century (IPCC 2013). Field experiments showed prompt ecosystem responses to climate warming (Rustad *et al.* 2001; Wu *et al.* 2011; Lu *et al.* 2013), which were due mainly to short-term, physiological mechanisms. However, ecosystem

responses to warming are strongly regulated by long-term, slow processes (Rastetter 1996; Luo *et al.* 2011) such as shifts in plant community structure and composition (Chapin *et al.* 1995; Saleska *et al.* 2002; Field *et al.* 2007; Luo 2007; Smith, Knapp & Collins 2009). Climate warming has the potential to alter plant community through shifting species dominance (Klanderud & Totland 2005; Prieto *et al.* 2009; Dieleman *et al.* 2015), facilitating species invasion (Dukes & Mooney 1999; Walther *et al.* 2009) and triggering species loss (Klein, Harte & Zhao 2004; Gedan & Bertness 2009). Therefore, shifts in community structure and composition are

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expected in chronically altered environment under long-term warming (Smith, Knapp & Collins 2009). However, experimental evidence for long-term shifts in community structure and composition to climate warming in temperate grasslands is still scarce.

Although plant communities in many temperate grassland ecosystems have shown no responses to experimental warming (Zavaleta *et al.* 2003; Dukes *et al.* 2005; Kardol *et al.* 2010; Hoepfner & Dukes 2012; Hoover, Knapp & Smith 2014) based on relatively short-term experiments (but see Grime *et al.* 2008), it may see major shifts in structure and composition with longer term change in temperature. A hierarchical response framework (HRF, Smith, Knapp & Collins 2009) was proposed to assess sequential ecosystem responses to chronic resource alterations induced by global change drivers such as elevated atmospheric CO₂ concentration, global climate warming and nitrogen deposition. Compared with initial, fast physiological and metabolic responses, significant changes in community structure and composition such as species reordering and species gain and loss are likely to be slow processes, as they are often affected by chronically altered resource availability over a long time (Smith, Knapp & Collins 2009). As a result, species reordering and turnover under chronic resource alteration is expected to have much greater consequences for ecosystem structure and functioning. For example, in moist tussock tundra, a pronounced response in the plant community was not revealed until the ninth year due to warming-induced slow accumulation of nutrient availability (Chapin *et al.* 1995). Additionally, chronically altered resource availability under warming can also change interspecific competition (Shaver *et al.* 2000) and may cause community compositional change. Therefore, long-term experiments are necessary to provide relatively complete understanding of climate change impacts on plant community structure and composition and reveal key mechanisms critical for long-term predictions of ecosystem responses (Rastetter 1996).

The responses of a plant community to climate warming may vary strongly with land management practices (Harmens *et al.* 2004; Chapin *et al.* 2008; White *et al.* 2012). Land management practices in grassland ecosystems significantly affect plant community structure and composition (Collins *et al.* 1998; Borer *et al.* 2014; Koerner *et al.* 2014). For example, mowing or grazing often increases species richness by increasing light availability (Collins *et al.* 1998; Yang *et al.* 2012; Borer *et al.* 2014), and grazing suppresses growth of dominant species, increasing species richness (Koerner *et al.* 2014). As plant communities with higher diversity may be more resistant to environmental perturbations (Tilman, Reich & Knops 2006), clipping or grazing is likely to dampen warming effects on plant community structure and composition. Both observations and experiments have shown that clipping and grazing interact with climate warming in influencing the plant community. For example, clipping dampened the effect of warming on richness in alpine meadow and shrubland ecosystems on the Tibetan Plateau (Klein, Harte & Zhao 2004); grazing offset the warming impact on the plant

community in Arctic tundra ecosystems (Post & Pedersen 2008; Olofsson *et al.* 2009). Hay harvest in the southern Great Plains, where this study was conducted, is a common land management practice. In our study, annual clipping was used to mimic hay harvest. We therefore predicted that clipping would attenuate warming effects on community structure and composition in our study site.

An ongoing warming and clipping experiment was set up in a tallgrass prairie in central Oklahoma in November of 1999 (Luo *et al.* 2001). Besides monitoring carbon fluxes (Wan *et al.* 2005; Zhou, Wan & Luo 2007; Niu *et al.* 2013) and stocks (Luo *et al.* 2009; Niu *et al.* 2010; Xu *et al.* 2012a,b), plant community surveys including species richness and abundance have been conducted every year. Small warming effects on soil microclimate (Wan, Luo & Wallace 2002), soil nutrient dynamics (Wan *et al.* 2005) and ecosystem functioning (Zhou, Wan & Luo 2007; Luo *et al.* 2009) were found in previous studies, most of which reported experimental data from before 2008. Therefore, we first hypothesized that (i) experimental warming would have minimal impacts on plant community structure and composition in the short term, whereas clipping could have significant effects on the plant community due to its direct removal of plant species; (ii) secondly, we predicted that warming would alter plant community structure and composition over the long term through species reordering and/or species invasion based on the HRF; in addition, we hypothesized that (iii) clipping would dampen the warming effect on community structure and composition.

Materials and methods

STUDY SITE

The experiment was conducted in a tallgrass prairie on the Kessler Farm Field Laboratory in Oklahoma, USA (34°59'N, 97°31'W). The study site was neither cultivated nor grazed by large herbivores for the past 40 years prior to the start of the experiment. The grassland was dominated by the C₄ perennial grasses, such as *Schizachyrium scoparium* (*S. scoparium*) and *Sorghastrum nutans* (*S. nutans*), and the C₃ perennial forbs such as *Ambrosia psilostachya* (*A. psilostachya*), *Solidago nemoralis* (*S. nemoralis*) and *Solidago rigida* (*S. rigida*), with few annual grasses (*Aristida oligantha*) and forbs (e.g. *Croton glandulosus*). There are also a few subordinate legume species, such as *Dalea candida* (*D. candida*), *Dalea purpurea* (*D. purpurea*) and *Desmanthus illinoensis* (*D. illinoensis*). Mean annual temperature was 16.3 °C with a monthly mean temperature of 4.4 °C in January and 27.7 °C in July. Mean annual precipitation at the site is 914 mm (Oklahoma Climatological Survey, Norman, OK, USA). The soil was part of the Nash–Lucien complex with neutral pH, high available water-holding capacity (around 37%), and a moderately penetrable root zone (US Department of Agriculture 1979).

EXPERIMENTAL DESIGN

The experiment used a paired factorial split plot design. Warming was the main factor and clipping was nested within warming (Luo *et al.* 2001). Within each of six pairs of 2 m × 2 m plots, one plot

was subjected to continuous warming from an infrared heater (100 W m⁻²; Kalglo Electronics Inc, Bethlehem, PA, USA) hung 1.5 m above the ground since November 1999, while the other plot, equipped with a 'dummy' heater, served as a control. The distance between warmed and control plots was approximately 5 m. Each plot was divided into four 1 m × 1 m subplots. Plants in two diagonal subplots were clipped at a height of 10 cm above the ground annually to mimic hay harvest every year at peak biomass. Clipped materials including above-ground leaf, stem, inflorescence and fruit production were all taken away and not returned to the plots. The other two subplots were left unclipped. Thus, there were totally four treatments: unclipped and control (ambient) temperature (UC), unclipped and warmed (UW), clipped and control temperature (CC) and clipped plus warmed (CW).

SOIL TEMPERATURE, SOIL WATER CONTENT AND PRECIPITATION MEASUREMENTS

Soil temperature was measured by thermocouples at a depth of 2.5 cm in the centre of one clipped and one unclipped subplot in each plot. The thermocouples were connected to a data logger (Campbell Scientific Inc., Logan, UT, USA) and recorded soil temperature every 10 min. Volumetric soil water content (v/v %) was measured twice a month using portable Time Domain Reflectometry equipment (Soil Moisture Equipment Corp., Santa Barbara, CA, USA) at a depth of 1–15 cm. Precipitation data were obtained from an Oklahoma Mesonet Station (Washington Station) located approximately 200 m away from our experimental site.

VEGETATION SAMPLING AND COMMUNITY STRUCTURE CALCULATION

Species abundance was estimated at peak biomass in August from 2000 to 2013. We measured species abundance using the point-quadrat method. From 2000 to 2004, a grid frame (1 m × 0.5 m) with 36 points was placed once in the centre of each subplot. The plant species touched by a pin placed at each point on the grid was recorded as one hit. Beginning in 2005, community assessment was combined with the pin-contact method. Ten pins, 5 cm apart between any adjacent two pins, were held at a 60° angle in a frame placed in each subplot four times (once in each of the four cardinal directions), and pins could be raised within the frame to count hits up to 1 m high. One hit was recorded for each species if they touched any part of the pins, and species having no contact with any of the pins was recorded as one hit.

The number of hits in the two subplots under each treatment was summed together before any calculation or statistical analysis. To calculate relative abundance of each species, the number of hits for each species was divided by the total number of hits for all species in the two subplots under each treatment. Species richness (*S*) was calculated as the total number of plant species in the two subplots. We calculated the Shannon–Weiner diversity index (*H'*) as follows: $H' = -\sum p_i * \ln(p_i)$ where p_i is the relative abundance of species *i*; evenness (*E*) as follows: $E = H' / \ln(S)$.

STATISTICAL ANALYSIS

We used repeated-measures ANOVA to examine main and interactive effects on soil temperature, soil water content, species richness, diversity and evenness, with warming and clipping as main effects, year as

the repeated factor and plot pair as a random effect. Linear regressions were performed to explore the relationships between community structure (i.e. species richness, diversity and evenness) and abiotic variables (i.e. soil temperature and soil water content) over time in each treatment and all treatments together. All statistical analyses were conducted using SAS v.8.1 (SAS Institute Inc., Cary, NC, USA).

To examine the main and interactive effects of the treatments on plant community composition, we used a two-way permutational analysis of variance (PERMANOVA) on the Bray–Curtis similarity index of species relative abundance, with warming and clipping as fixed effects in the model and plot pair as a random effect. PERMANOVA was conducted within each year with all plant species. Species relative abundance data were arcsine-square-root transformed to ensure normal distribution. A similarity percentage (SIMPER) analysis was performed to quantify the contribution of individual species to compositional divergence among the treatments. Principle coordinates analysis (PCO) ordination was performed to visualize whole plot composition in a two-dimensional space. Because the first two axes explained the majority of the variation in plot location in multivariate space, we used PCO axes 1 and 2 scores as an index of community composition. The multivariate community analyses PERMANOVA, SIMPER and PCO were performed using PRIMER (version 1.0.3; Plymouth Marine Laboratory, Plymouth, UK).

Results

PRECIPITATION AND SOIL MICROCLIMATE

Annual precipitation varied from 515 mm in 2005, which was the driest year in the last 54 years, to 1307 mm in 2007, which was the wettest year in the last 54 years with a mean of 874 mm during the 54 years (Fig. S1, Supporting Information). There was strong interannual variability in soil temperature and water content (Table 1). Experimental warming elevated soil temperature by 1.3 °C on average in the unclipped plots and 2.2 °C on average in the clipped plots (Fig. S2a). Clipping increased soil temperature by 0.5 and 1.3 °C in unwarmed and warmed plots, respectively. Warming decreased soil water content by 1.5% on average across the 14 years (Fig. S2b), and clipping decreased soil water content by 0.6% on average (Fig. S2c). Warming did not interact with clipping to impact soil water content (Table 1).

SPECIES RICHNESS, DIVERSITY AND EVENNESS

The number of species was ca. 10% greater in the clipped plots than in the unclipped plots, whereas no significant difference was found between the warmed and unwarmed plots in most years (Fig. 1a,b; Table 1). However, in 2007, the wettest year, species richness was 30% more in the unwarmed plots than in the warmed plots. Community diversity and evenness did not respond to warming (Fig. 1c,e), whereas clipping tended to decrease evenness (Fig. 1f). Interactive effects of clipping and year on diversity were significant (Fig. 1d). There was strong interannual variability in species richness, diversity and evenness (Table 1).

Table 1. Results of repeated-measures ANOVA (*F* and *P* values) for responses of soil temperature (T_{soil}), soil water content (W_{soil}), species richness (*S*), Shannon–Weiner diversity index (H'), evenness (*E*), grass species richness (GR *S*), forb species richness (Forb *S*) and legume species richness (LE *S*) to warming (*W*), clipping (*C*), year (*Y*) and their interactions. Significant results ($P < 0.05$) are bolded

d.f.	T_{soil}		W_{soil}		<i>S</i>		H'		<i>E</i>		GR <i>S</i>		Forb <i>S</i>		LE <i>S</i>	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
1, 5	132.5	< 0.0001	42.0	0.0001	0.9	0.001	0.3	0.60	0.4	0.56	8.8	0.03	0.4	0.54	1.0	0.35
1, 270	108.3	< 0.0001	56.7	< 0.0001	14.2	0.0002	1.6	0.21	17.1	< 0.0001	3.6	0.06	17.3	< 0.0001	3.4	0.07
1, 270	7.4	0.0068	0.07	0.80	0.2	0.67	1.4	0.24	1.55	0.21	2.6	0.11	0.08	0.78	0.02	0.89
13, 270	2217	< 0.0001	35.2	< 0.0001	34.2	< 0.0001	10.4	< 0.0001	17.3	< 0.0001	16.1	< 0.0001	45.7	< 0.0001	4.5	< 0.0001
13, 270	1.2	0.28	0.79	0.66	1.77	0.05	0.3	1	0.46	0.94	1.2	0.29	1.6	0.09	1.7	0.07
13, 270	4.7	< 0.0001	0.2	1	0.71	0.75	1.9	0.03	2.17	0.1	0.8	0.69	1.13	0.33	0.7	0.80
13, 270	2.1	0.016	0.08	1	0.14	1.00	1.5	0.11	0.72	0.74	0.4	0.98	0.24	1	1	0.49

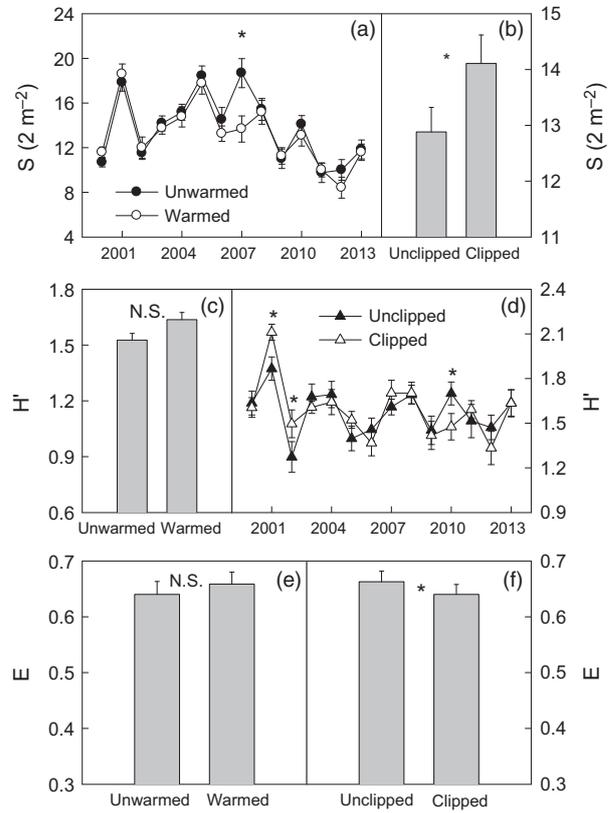


Fig. 1. Effects of warming and clipping on species richness, *S* (a, b), Shannon–Wiener diversity index, H' (c, d) and Pielou's evenness index, *E* (e, f) (Mean \pm 1SE). 'N.S.' stands for not significant; '*' indicates significant ($P < 0.05$).

Grass, forb and legume richness differed in their responses to warming and clipping treatments. Grass species richness was 13% higher on average in the unwarmed plots than in the warmed plots, whereas clipping did not yield a significant response (Fig. S3a,b; Table 1). Forb species richness was 19% greater on average in the clipped plots than in the unclipped ones, whereas warming had no impact (Fig. S3c, d). Clipping increased legume richness with marginal significance ($P = 0.07$), whereas warming did not affect legume richness (Fig. S3e,f). Warming did not interact with clipping in influencing species richness of any functional group (Table 1).

RELATIONSHIPS OF INTERANNUAL VARIATIONS IN COMMUNITY STRUCTURE WITH SOIL MICROCLIMATE

Soil temperature and soil water content significantly correlated with the species richness across all treatments and years (Fig. 2). However, none of the relationships were significant for any individual treatment (Fig. S4). Multiple linear regression showed that soil water content was the dominant climatic factor in controlling interannual variation in species richness ($r^2 = 0.18$, $P < 0.01$). Community diversity and evenness did not significantly correlate with soil temperature or soil water content (Fig. S5).

Fig. 2. Relationships of species richness with soil temperature (a) and soil water content (b) across all treatments from 2000 to 2013. Each point represents mean value in each year under each treatment. UC, unclipped with control (ambient) temperature; UW, unclipped and warmed; CC, clipped with control temperature; CW, clipped and warmed.

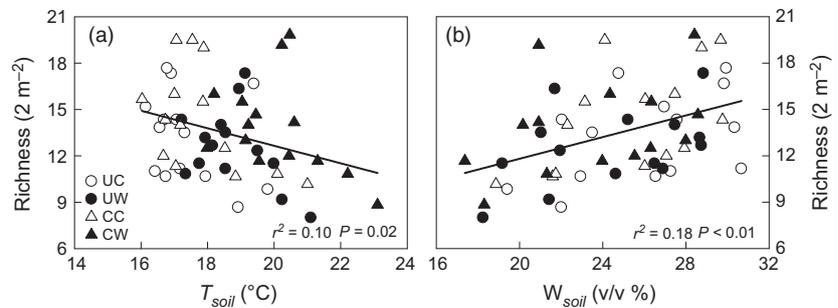


Table 2. Results from two-way permutational anovas (F and P values) and SIMPER analyses of the effects of warming (W), clipping (C) and their interactions on Bray–Curtis plant community composition in each year within 2000–2013. Significant results ($P < 0.1$) are bolded. Percentage contribution of different plant species to community divergence between control and treatments (i.e. warming and clipping) was based on SIMPER analysis (shown are the key species contributing the most). ‘–’ not applicable. Bi: *Bothriochloa ischaemum*; Di: *Desmanthus illinoensis*; Do: *Dichantherium oligosanthes*; Pv: *Panicum virgatum*; Sc: *Sporobolus compositus*; Sn: *Sorghastrum nutans*; Ss: *Schizachyrium scoparium*

Year	$P_{(\text{perm})} W$ (Pseudo- F)	$P_{(\text{perm})} C$ (Pseudo- F)	$P_{(\text{perm})} W \times C$ (Pseudo- F)	Contribution (%)		
				W	C	$W \times C$
2000	0.63 (0.72)	0.63 (0.63)	0.29 (1.25)	–	–	–
2001	0.45 (0.96)	0.10 (1.82)	0.85 (0.58)	–	52% (Di, Ss, Pv)	–
2002	0.92 (0.49)	0.02 (2.75)	0.91 (0.51)	–	43% (Di, Do, Sc)	–
2003	0.16 (1.45)	0.02 (3.09)	0.92 (0.45)	–	42% (Sc, Ss, Sn)	–
2004	0.53 (0.89)	0.43 (1.00)	0.62 (0.81)	–	–	–
2005	0.45 (0.97)	0.03 (2.72)	0.74 (0.70)	–	44% (Sc, Sn, Ss)	–
2006	0.39 (1.06)	0.003 (3.35)	0.68 (0.75)	–	45% (Sn, Ss, Sc)	–
2007	0.08 (1.90)	0.07 (2.60)	0.49 (0.93)	47% (Di, Bs, Ss)	46% (Di, Ss, Sn)	–
2008	0.08 (1.70)	0.006 (3.32)	0.25 (1.29)	43% (Sn, Sc, Di)	43% (Sc, Sn, Di)	–
2009	0.02 (2.61)	0.13 (1.67)	1.00 (0.09)	44% (Ss, Sn, Sc)	–	–
2010	0.03 (2.76)	0.01 (3.76)	0.15 (1.94)	49% (Ss, Bi, Sn)	48% (Ss, Sc, Bi)	–
2011	0.07 (2.38)	0.01 (4.63)	0.11 (2.15)	56% (Ss, Bi, Sc)	57% (Ss, Bi, Sc)	–
2012	0.04 (2.58)	0.15 (1.92)	0.47 (0.94)	53% (Ss, Bi, Sn)	–	–
2013	0.01 (2.81)	0.17 (1.66)	0.63 (0.76)	57% (Bi, Sn, Ss)	–	–

WARMING AND CLIPPING EFFECTS ON COMMUNITY COMPOSITION

Warming interacted with year in influencing community composition starting in 2007, with marginal significance in 2007, 2008 and 2011 (Table 2; Fig. 3). Clipping had significant impacts on community composition in most of the years (Table 2; Fig. 3). The interactive effect of warming and clipping on composition was not found (Table 2).

The three dominant species, *S. scoparium* (Ss, 40% relative abundance under control, Table S1), *S. nutans* (Sn, 12% relative abundance under control) and *S. compositus* (Sc, 11% relative abundance under control), together with the invasive species, *Bothriochloa ischaemum* (*B. ischaemum*, Bi), contributed to the significant compositional change under warming treatment (Table 2). *S. scoparium* and *S. compositus* showed negative responses to warming. *S. nutans* was generally more abundant in the warmed plots. *B. ischaemum* codominated with the other three species in the warmed plots (Fig. S6). Relative abundance of the invasive species (Bi) negatively correlated with the relative abundance of the two dominant species (Ss and Sc) from 2007 to 2013 (Fig. 4), suggesting interspecific competition among them. The species

Ss, Sn, Sc and Di (*Desmanthus illinoensis*) together contributed to the compositional change under clipping treatment (Table 2). Clipping often favoured Ss and Di, but suppressed Sn and Sc.

Discussion

SENSITIVITY OF COMMUNITY STRUCTURE AND COMPOSITION TO CLIMATE WARMING

A growing body of literature has demonstrated that climate warming alters plant community structure and composition in cold regions. Elevated temperature increased the cover of deciduous shrubs and graminoids in Arctic tundra ecosystems (Arft *et al.* 1999; Walker *et al.* 2006) and caused loss of plant species in some critical ecosystems such as alpine meadows and wetlands (Klein, Harte & Zhao 2004; Gedan & Bertness 2009). In temperate grasslands, however, plant communities are rather resistant to increased temperature alone (Zavaleta *et al.* 2003; Harmens *et al.* 2004; Dukes *et al.* 2005; Grime *et al.* 2008; Kardol *et al.* 2010; Arnone *et al.* 2011; Hoepfner & Dukes 2012; Hoover, Knapp & Smith 2014; White, Bork

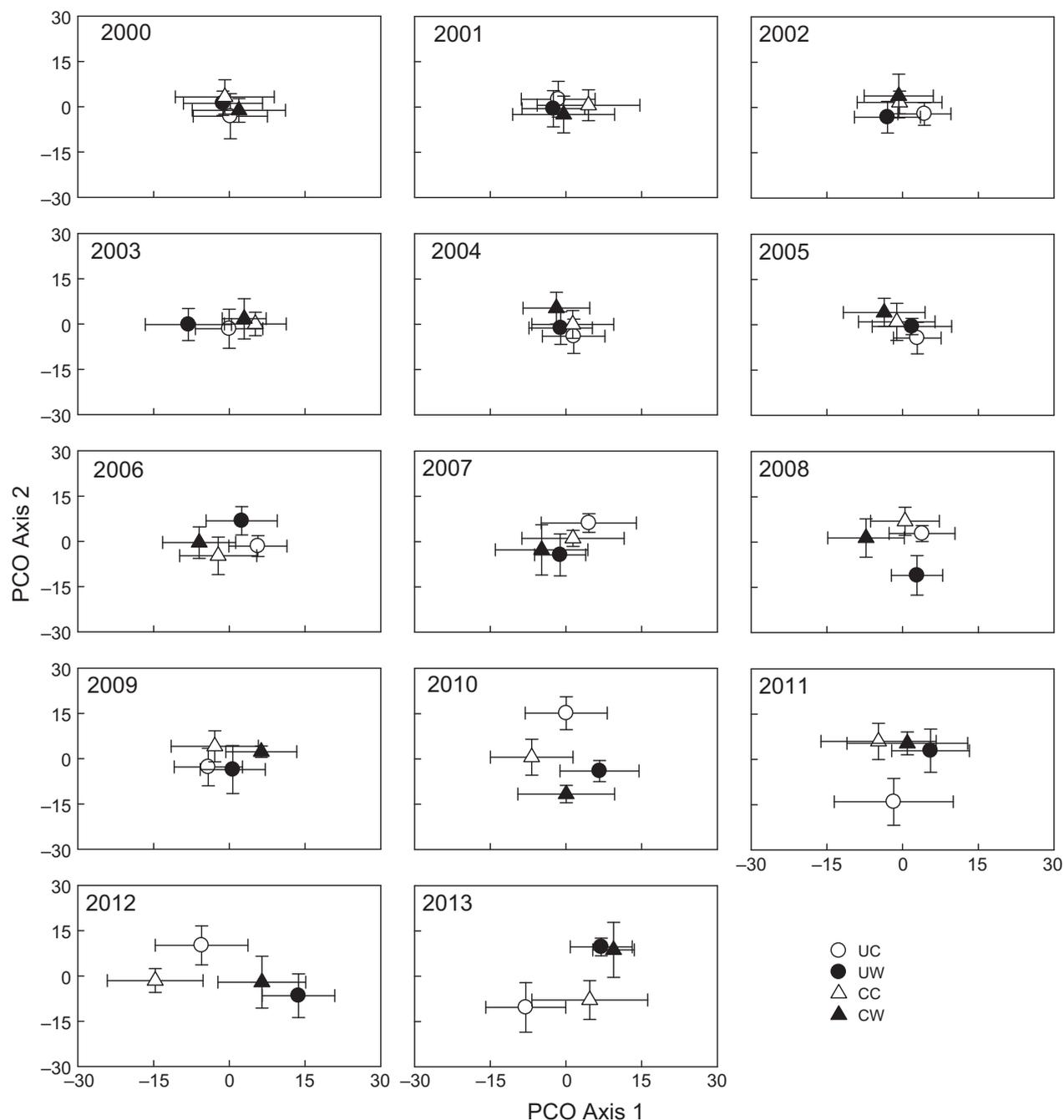


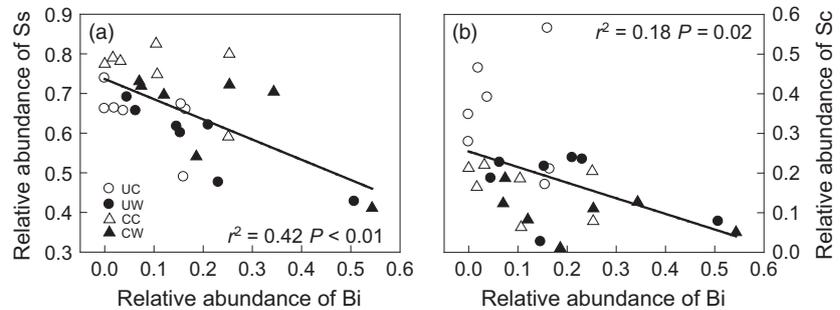
Fig. 3. PCO ordination plots within each year from 2000 to 2013, with axes 1 and 2 scores. Each point represents mean coordinates (with 1 SE) under each treatment in each year. See Fig. 2 for treatments abbreviations.

& Cahill 2014). Most of these experiments were relatively short term, less than 5 years long (but see Grime *et al.* 2008). Resistance of community structure and composition to experimental warming in the first 7 years of our study is consistent with previous findings in temperate grasslands.

Background climate variability, dominant species traits, biodiversity and biogeochemistry are often proposed as key factors to define sensitivity of an ecosystem to disturbances (Grime *et al.* 2000; Smith, Knapp & Collins 2009). Tallgrass prairies are exposed to naturally high interannual climate variability, but plant species composition remains relatively

constant (Knapp *et al.* 1998). C_4 grasses dominated our studied system and are considered well-adapted to heat and drought conditions (Christie & Delting 1982; Seastedt *et al.* 1994). Slow rates of biogeochemical cycling (Wan *et al.* 2005; Zhou, Wan & Luo 2007), low nitrogen content (Niu *et al.* 2010) and relative low productivity at our study site (Luo *et al.* 2009) might also constrain the response of the ecosystem to climatic perturbations. Indeed, previous studies at our site reported small warming effects on soil microclimate (Wan, Luo & Wallace 2002), soil nutrient dynamics (Wan *et al.* 2005) and ecosystem functioning (Zhou, Wan &

Fig. 4. The relationships between relative abundance of the invasive species Bi (*Bothriochloa ischaemum*) and Ss (*Schizachyrium scoparium*) (a) and Sc (*Sporobolus compositus*) (b) from 2007 to 2013. Each point represents mean value in each year under each treatment. See Fig. 2 for treatments abbreviations. Note that the relative abundance was arcsine-square-root-transformed for normality.



Luo 2007; Luo *et al.* 2009). The aforementioned factors might together determine the resistance of the plant community in our study site to climate warming from 2000 to 2006.

The shift from resistance to responsiveness of community composition to warming since 2007 was intriguing. The HRF predicts that chronically altered environments under long-term climate change can induce nonlinear changes in community structure and composition through species reordering and/or species invasion (Smith, Knapp & Collins 2009). In our study, the three dominant C₄ species (*S. scoparium*, *S. nutans* and *S. compositus*) and one invasive species (*B. ischaemum*) contributed most to the warming-induced changes in community composition since 2007. *B. ischaemum*, a warm-season C₄ grass, is known as an invasive species to the Great Plains prairies (Schmidt *et al.* 2008; Wilson, Hickman & Williamson 2012). Because habitats with highly fluctuating resource availability are susceptible to invasion (Davis, Grime & Thompson 2000), the extreme wet year in 2007 likely facilitated the invasion of *B. ischaemum* in the environment chronically altered by warming. The negative responses of *S. scoparium* and *S. compositus* to warming may partly be caused by interspecific competition with the invasive species, which is suggested by the negative correlations in relative abundance between *B. ischaemum* and *S. scoparium* and *S. compositus*. Natural disturbances such as extreme precipitation events are expected to interact with climate warming to elicit or accelerate shifts in plant community structure and composition (Jentsch, Kreyling & Beierkuhnlein 2007; Smith, Knapp & Collins 2009). In other words, natural disturbances can reduce resistance of a system to climate change (Jentsch & Beierkuhnlein 2003). For example, extreme wet conditions can increase the invasibility of a plant community due to either direct effects on water supply or through enhanced nutrient availability (Dukes & Mooney 1999; Davis, Grime & Thompson 2000). Warming may interact with the extreme scenarios by increasing nutrient availability due to the elevated mineralization (Bai *et al.* 2013) in wet years. Therefore, warming may interact with natural disturbances to cause permanent shifts in community structure and composition.

Multiple linear regression showed that soil moisture was the controlling factor for interannual variation in species richness across all treatments in our study site. Therefore, we expected that warming would decrease species richness due to its negative effect on soil water content. Surprisingly, warming did not cause any loss in total species richness in most years due possibly to the limited reduction (ca. 2%) in soil

water content by warming. Another possible explanation is that the low variation (18%) explained by soil moisture may indicate that some other factors, such as nutrient status (Clark *et al.* 2007) and surface light availability, could contribute significantly to the interannual variation in species richness. Unfortunately, we did not collect relevant data over the entire course of the experiment. However, significant reduction (ca. 30%) in species richness occurred in the warmed plots relative to the unwarmed plots in 2007, the extreme wet year, suggesting interaction between long-term warming and natural disturbances. Warming-induced reduction in species richness in 2007 was likely caused by competition due to increased biomass and decreased ground light in the warmed plots, which were probably triggered by increased available nitrogen under warmed condition in the extreme wet year.

SENSITIVITY OF COMMUNITY STRUCTURE AND COMPOSITION TO CLIPPING

In our study, clipping had significant effects on community composition in most years. We expected clipping to have greater impact on community structure and composition with time. Because removing all clipped plant materials including inflorescences could have cumulative effects on soil fertility and plant reproduction, long-term clipping might have pronounced effects over time. In contrast to our expectation, the responses of plant community composition to clipping differed little between the short term and the long term. Three dominant species (*S. scoparium*, *S. nutans* and *S. compositus*) consistently contributed the most to the compositional change under clipping over time. Clipping generally favoured the most dominant species (*S. scoparium*) and suppressed the two subdominant species (*S. nutans* and *S. compositus*). The long-term above-ground biomass data can indirectly support that clipping did not have cumulative effects on soil fertility as above-ground biomass did not decrease with time in the clipped plots (Luo *et al.* 2009; Niu *et al.* 2010).

Our finding that clipping increased species richness has been widely recognized (Collins *et al.* 1998; Foster & Gross 1998; Klein, Harte & Zhao 2004; Yang *et al.* 2012). Increase in species richness from clipping is often attributed to alleviated interspecific competition (Koerner *et al.* 2014) and decreased litter accumulation, which increases ground-level light availability in a variety of grassland ecosystems (Borer *et al.* 2014). In our study site, harvesting the plants significantly reduced litter accumulation (Cheng *et al.* 2010).

Additionally, clipping-stimulated species richness in our study enhanced a number of forb species, consistent with previous studies (Harmens *et al.* 2004; Yang *et al.* 2012).

SENSITIVITY OF COMMUNITY STRUCTURE AND COMPOSITION TO WARMING AND CLIPPING INTERACTIONS

We expected significant interactive effects between warming and clipping on community structure and composition for at least three reasons. First, warming and clipping interacted to influence soil temperature. The interactive effect on soil microclimate could propagate into the plant community. Secondly, clipping was expected to have a negative, cumulative effect on soil fertility, which could alter community responses to warming. Thirdly, clipping increased species diversity and more diverse plant communities could be more resistant to warming. However, our analysis demonstrated that there were no interactive effects of warming and clipping on community structure and composition, suggesting that their effects were additive rather than interactive. We have argued that clipping did not have a cumulative effect on soil fertility. The interactive effect of warming and clipping on soil temperature was likely too small to affect the plant community. In addition, the clipping-induced increase in species richness was low (10%). A synthesis of global change experiments also showed that there were typically few interactions between global change factors and land management in temperate grassland communities (White *et al.* 2012).

However, interactive effects of warming and clipping (or grazing) were reported in previous studies, with clipping usually dampening the warming effect on the plant community (Klein, Harte & Zhao 2004; Post & Pedersen 2008; Olofsson *et al.* 2009; Post 2013). Clipping (or grazing) was rarely reported to exacerbate warming effects. The neutral response in our study, combined with clipping attenuating or amplifying the effect of warming in other experiments, suggests that the responses could be contingent on the type of ecosystem (tundra vs. temperate grassland), management practices (e.g. frequency of clipping or grazing) or extent of management (e.g. light or heavy grazing). Nonetheless, lack of an interactive response to warming and clipping in our study site indicates that hay harvesting in this area is unlikely to affect the trajectory of the impact of warming on the tallgrass prairie.

Conclusions

Our results showed that species richness in a tallgrass prairie was resistant to long-term warming, but was increased by clipping. Taken together with other studies (e.g. Borer *et al.* 2014; Hautier *et al.*, 2014), our results indicate that grassland species richness in warm or temperate regions is more susceptible to land management practices such as clipping, grazing and fertilization than to climate warming. The finding that warming significantly decreased species richness and induced a shift in composition in an extremely wet year suggests possible interactions between warming and extreme events (e.g.

Peñuelas *et al.*, 2007; Hoeppepner & Dukes 2012; De Boeck *et al.*, 2011). The predicted greater frequency of extreme weather events in the future could therefore interact with climate warming and lead to a large and rapid loss of plant species and significant change in community composition in this area and possibly large impact on ecosystem functioning and services. Indeed, in conjunction with a long-term shift of community composition under warming, we found amplified warming effects on above-ground biomass and soil respiration after 2007 (Xu *et al.* 2015; Y. Q. Luo, X. Xu, R. Sherry, S. L. Niu, D. J. Li & J. Y. Xia, in prep.). Together, the long-term shift in community composition and ecosystem functioning provides direct experimental evidence of the predictions by HRF and suggests that dynamics of community composition should be carefully studied in order to accurately predict long-term ecosystem response to climate warming. Meanwhile, more research explicitly investigating the interaction between climate warming and extreme precipitation events is necessary and urgent.

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Data accessibility

Data are available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.1v339> (Shi *et al.* 2015).

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Supporting Information

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

Table S1. List of common species in the experimental site across the 14 years.

Figure S1. Annual precipitation from 1960 to 2014.

Figure S2. Effects of warming and clipping on soil temperature at 2.5 cm depth (a), and soil water content at ~15 cm depth (b, c) (Mean ± 1 SE).

Figure S3. Effects of warming and clipping on GR richness (a, b), Forb richness (c, d) and LE richness (e, f).

Figure S4. Relationships of species richness with soil temperature and water content.

Figure S5. Relationships of community diversity and evenness with soil temperature and water content.

Figure S6. Abundance rank curve in UC (a), UW (b), CC (c) and CW (d) in 2013.