Shifting grassland plant community structure drives positive interactive effects of warming and diversity on aboveground net primary productivity

JANE M. COWLES[1], PETER D. WRAGG[1], ALEXANDRA J. WRIGHT[2], JENNIFER S. POWERS[1,3] and DAVID TILMAN[1,4]

[1]*Department of Ecology, Evolution & Behavior, University of Minnesota Twin Cities, Saint Paul, MN 55108, USA,* [2]*Department of Science & Mathematics, FIT, New York, NY 10001, USA,* [3]*Department of Plant Biology, University of Minnesota Twin Cities, Saint Paul, MN 55108, USA,* [4]*Bren School of the Environment, University of California, Santa Barbara, CA 93106, USA*

Abstract

Ecosystems worldwide are increasingly impacted by multiple drivers of environmental change, including climate warming and loss of biodiversity. We show, using a long-term factorial experiment, that plant diversity loss alters the effects of warming on productivity. Aboveground primary productivity was increased by both high plant diversity and warming, and, in concert, warming (≈ 1.5 °C average above and belowground warming over the growing season) and diversity caused a greater than additive increase in aboveground productivity. The aboveground warming effects increased over time, particularly at higher levels of diversity, perhaps because of warming-induced increases in legume and C4 bunch grass abundances, and facilitative feedbacks of these species on productivity. Moreover, higher plant diversity was associated with the amelioration of warming-induced environmental conditions. This led to cooler temperatures, decreased vapor pressure deficit, and increased surface soil moisture in higher diversity communities. Root biomass (0–30 cm) was likewise consistently greater at higher plant diversity and was greater with warming in monocultures and at intermediate diversity, but at high diversity warming had no detectable effect. This may be because warming increased the abundance of legumes, which have lower root : shoot ratios than the other types of plants. In addition, legumes increase soil nitrogen (N) supply, which could make N less limiting to other species and potentially decrease their investment in roots. The negative warming × diversity interaction on root mass led to an overall negative interactive effect of these two global change factors on the sum of above and belowground biomass, and thus likely on total plant carbon stores. In total, plant diversity increased the effect of warming on aboveground net productivity and moderated the effect on root mass. These divergent effects suggest that warming and changes in plant diversity are likely to have both interactive and divergent impacts on various aspects of ecosystem functioning.

Keywords: biodiversity, biodiversity–ecosystem functioning, global change, grassland ecology, plant communities, primary productivity, warming

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Introduction

The functioning of ecosystems, and their ability to supply ecosystem services, will depend on ecosystem responses to the direct and interactive effects of two major drivers of global change, biodiversity loss, and warming. Global temperature is projected to increase 2–4.5 °C above pre-industrial levels by 2100 (Rogelj *et al.*, 2012). Overall, warming tends to have a positive effect on plant growth and other ecosystem processes such as nutrient cycling (Rustad *et al.*, 2001; Lin *et al.*, 2010; Wu *et al.*, 2011). Such effects tend to be strongest (most positive) toward the poles and in temperate climates, while warming can have deleterious effects in tropical systems (Corlett, 2011). Additionally, the effects of warming can be highly context-specific and indirect negative effects of warming on abiotic properties such as soil moisture can shift the overall productivity response to be negative (Dieleman *et al.*, 2012). The effect of warming on plant growth also depends on specific traits of the plant species. More drought tolerant species (e.g. warm season C4 grasses) can be less limited by the drying effects of warming (Ward *et al.*, 1999) than less drought tolerant cool season C3 grasses. Other groups, such as legumes, may experience increased nitrogen fixation at higher temperatures (Gundale *et al.*, 2012; Whittington *et al.*, 2012), and thus,

Correspondence: Jane Cowles, tel. +1 218 343 1519, fax +1 612 624 6777,
e-mail: janemcowles@gmail.com

warming could increase available nitrogen, therefore increasing biomass production.

Simultaneously, human activities are leading to species losses via habitat loss and fragmentation, simplification, and nutrient eutrophication, and to shifts in community composition and species dominance (Vitousek *et al.*, 1997). Recent research has questioned the universality of global biodiversity loss at small spatial scales (Dornelas *et al.*, 2014); however, as most North American prairies have been converted from high-diversity natural communities to monoculture crops or low diversity pasture systems, the overall question of how local biodiversity can affect ecosystems is still important. The effects of this loss on ecosystem properties have been well studied in many long-term biodiversity experiments. Overall, increasing species richness has a positive effect on plant productivity (van Ruijven & Berendse, 2003; Roscher *et al.*, 2005; Balvanera *et al.*, 2006; Cardinale *et al.*, 2011; Hooper *et al.*, 2012; Tilman *et al.*, 2012, 2014; Zhang *et al.*, 2012; Allan *et al.*, 2013), and these effects tend to increase over time (Cardinale *et al.*, 2007; Reich *et al.*, 2012).

Although both warming and loss of diversity are known to affect ecosystem functioning, their potential interactive effects are poorly understood. Because warming can decrease species richness over time (Klein *et al.*, 2004; Gedan & Bertness, 2009), experiments that only examine warming are unable to parse the direct effects of warming (likely positive if water is sufficient) from the indirect effect through the loss of diversity (likely negative). Our experiment is a full-factorial combination of three levels of plant diversity with three levels of warming that is designed to determine how and why these global change factors directly and interactively affect ecosystems. As such, it is the first long-term field experiment to examine the independent and interactive effects of warming and diversity loss on the functioning of an ecosystem.

Materials and methods

Our Biodiversity and Climate experiment ('BAC') is nested within the existing long-term biodiversity experiment at Cedar Creek Ecosystem Science Reserve in Minnesota, USA, described in detail in previous papers (Tilman *et al.*, 2001, 2006). To summarize, 168 plots, 9 m × 9 m each, were seeded at equal densities in 1994 with random combinations of prairie perennial species at differing diversity levels, with compositions maintained by hand weeding. Weeding occurs when nonfocal species are small to minimize disturbance and nutrient loss through weeding. The subset of 32 plots used in the BAC experiment consists of 14 monoculture plots, 10 4-species plots, and 8 16-species plots. The species in the 4- and 16-species plots are randomly selected from the experimental species pool, which is comprised of four functional categories [C3

grasses, C4 grasses, nonleguminous forbs, and legumes; each containing four species (Tilman *et al.*, 2001)].

Low warming (600 W) and high warming (1200 W) treatments were imposed on 2.5 m × 3 m subplots within each of the 32 plots using infrared heaters (Kimball *et al.*, 2007) suspended from metal frames at a height of 1.8 m above the ground. Control subplots in each of the 32 plots had a metal shade the same size, shape, and height as heaters. Heaters were in continuous operation, 24 h day^{-1}, March through November, focusing on the bulk of the growing season, since 2009. The diversity and warming treatments were fully factorial, with a high, a low, and a control warming treatment nested within each of the 32 diversity plots (Whittington *et al.*, 2013).

No experimental warming treatment to date has been found to precisely replicate the various environmental conditions expected under global climate change (Aronson & McNulty, 2009; Amthor *et al.*, 2010; Rich *et al.*, 2015). While bare ground experimental trials at our field site indicated our treatments increased soil temperature at 1 cm depth by approximately 1.5 and 3 °C above ambient in the low and high warming treatments, the actual warming is expected to depend on the wind conditions (Kimball *et al.*, 2011), time of day (Kimball *et al.*, 2011; Wall *et al.*, 2011), plot productivity (Luo *et al.*, 2010), soil moisture (McDaniel *et al.*, 2013; Wall *et al.*, 2013), and soil depth (Luo *et al.*, 2010). Thus, we directly measured various aboveground and belowground abiotic conditions to quantify the realized effect of warming on each subplot.

To quantify the efficacy and abiotic effects of our treatments, soil temperature, soil moisture, and air humidity were measured throughout the growing season. Soil temperature was measured via iButton data loggers (Maxim, Sunnyvale, CA, USA) at 1 cm depth in all years, with multiple depths measured in 2012 (1 and 10 cm), 2013 (1 and 10 cm), and 2014 (1, 10, 20, and 30 cm). iButtons deeper than 1 cm were affixed to a wooden stake inserted into the soil. Relative air humidity and air temperature were measured hourly from 2012 to 2014 in each subplot using iButton data loggers attached to wooden stakes and sheltered from direct sunlight and rainfall under white plastic cups elevated 10 and 25 cm above the soil surface to assess microclimate conditions at various points in the canopy. As the plant canopy height increased through the season, the aerial iButtons were gradually sheltered by plant biomass in addition to the white plastic cup, thus measuring the combined direct effects of treatments and indirect effects through biomass changes on humidity and temperature. The air humidity and temperature data were used to calculate vapor pressure deficit (VPD). Soil moisture was measured in the top 6 cm every 2 weeks each growing season at six points per subplot using Thetaprobe ML2 and SM150 soil moisture sensors (Delta-T Devices, Cambridge, UK). Plots were burned each spring, removing essentially all aboveground biomass and as such, biomass harvested late in the growing season measures annual aboveground net primary productivity (minus any productivity removed by small mammal and insect herbivory).

For 2009–2014, aboveground biomass was annually harvested in one 0.1 × 3 m (2009), two 0.1 × 1.5 m (2010–2011), two 0.1 × 2 m (2012), or two 0.1 × 1 m (2013–2014) clip strips
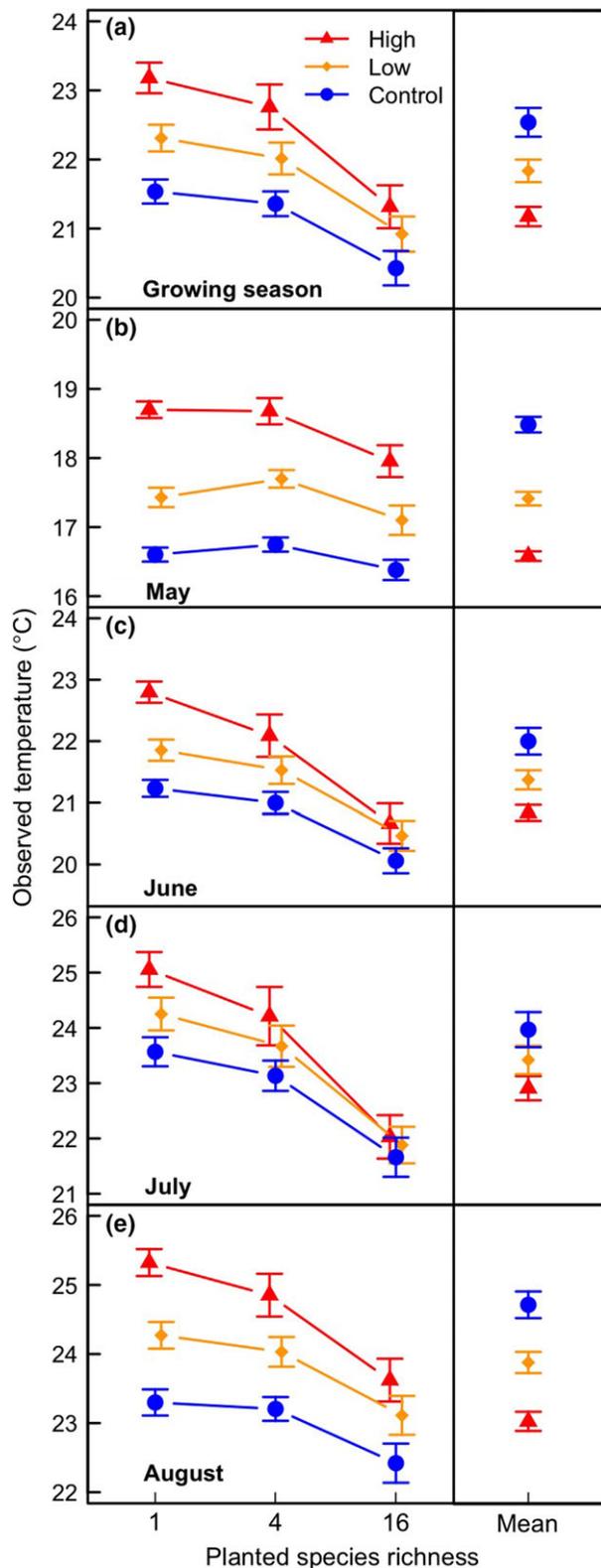
Fig. 1 Observed effects of warming and diversity treatments on temperature averaged across all depths/heights (25, 10 cm above surface, 1, 10, 20, 30 cm below surface) in 2014 (left) and the mean effect of warming across all diversity levels and depths/heights (right). Measurements were recorded via iButton data loggers from May 10, 2014–August 31, 2014. Aerial iButtons (25 and 10 cm above surface) were affixed to a wooden stake and sheltered from wind and direct sunlight by an inverted lightweight, white plastic cup. Belowground iButtons were inserted into the ground affixed to a wooden stake. Panel (a) is the average across all seasons, and subsequent panels are monthly averages for May (b), June (c), July (d), and August (e), respectively. Error bars are standard error of the mean.

immediately afterward in 2009, 2010, and 2012 using pooled, replicate 5 cm diameter × 30 cm deep root cores. Each root sample was gently rinsed on a 1.5 mm mesh screen to remove all soil, dried, and weighed.

We analyzed data using linear mixed effect models in the nlme package in R 2.14.1 (https://www.r-project.org/). All models included subplot and plot (nested random intercept effects) and experiment year (fixed effect; categorical variable except where explicitly testing for time by treatment interactions) along with variables discussed below. Warming (coded as 0, 1, and 2 for control, low, and high warming, respectively) and $\log_e$[diversity treatment] were included as continuous fixed effects. Models of species proportional abundance only include plots planted with >1 species. All response variables were transformed to meet normality assumptions. As such, all responses were log transformed except aboveground biomass (no transformation), C4 grass absolute biomass (square root transformed), C4 grass proportional biomass (square root transformed), surface soil moisture (no transformation), and VPD (no transformation). Wald chi-squares from Type II ANOVAs are presented for all results. Thus, the presented statistics assess the effects of each predictor after accounting for all other noninteraction effects.

Results

The abiotic effects of the warming treatments were dependent on the time of the season and diversity of the plots (Figs 1 and S1). The measured temperature increase with warming was the greatest at 1 cm below the surface throughout the season. Across the entire growing season (May–August) and across all heights and soil depths (from 25 cm aboveground to 30 cm belowground), the average warming effect measured was ≈1.5 °C above ambient in the high warming treatment and ≈0.75 °C in the low treatment, relative to controls. The observed effect of warming treatment was greatest at the beginning of the growing season in May (High warming ≈2 °C above control) and smallest at peak biomass in July (≈1 °C increase in High warming treatment). Diversity strongly decreased the measured effect of warming treatment on temperatures (Fig. 1;

in early August, sorted to species, dried, and weighed. Clip strips varied in size and location to avoid year-to-year overlap in sampling location. Belowground biomass was sampled

negative warming × diversity interaction, average of all depths across entire growing season: *P* = 0.0002), especially below the canopy and in the middle of the growing season (Fig. S1).

Along with impacting temperatures, our treatments also impacted soil moisture and air humidity (measured as VPD). Surface soil moisture increased with diversity (Fig. 2a; *P* = 0.0002) and decreased with warming (Fig. 2a; *P* < 0.0001), but there was no significant interactive effect of warming and diversity on surface soil moisture (Fig. 2a; *P* = 0.878 NS). Diversity decreased VPD (increased humidity) averaged across iButtons at 10 and 25 cm above soil surface (Fig. 2b; *P* < 0.0001) while warming increased VPD (decreased humidity) (Fig. 2b; *P* < 0.0001), and the effect of warming on VPD was smaller in the high-diversity treatments (*P* = 0.033). Mean soil moisture throughout the soil profile did not show significant effects of warming, even though the temperature effect reached the deepest sensors at 30 cm in our experiment (Fig. S1), and reached 105 cm in a similarly structured warming experiment in Oklahoma, USA (Sherry *et al.*, 2008).

Across all years, net aboveground primary productivity, as estimated by total aboveground living biomass, responded positively and significantly to both warming and planted diversity, and had a significant, positive warming by diversity interaction (Figs 3, S2 and S3; Diversity: *P* < 0.0001; Warming: *P* < 0.0001, Interaction: *P* = 0.0003). The main effect of warming increased significantly over time (Fig. S2; Year × Warming interaction: *P* = 0.008), as did the effect of diversity (Fig. S2, Year × Diversity interaction: *P* < 0.0001).

Root mass (belowground biomass) also increased with warming and diversity in our experiment, but there was a significant negative interaction between the two factors, because the effect of warming on belowground biomass trended toward negative at high diversity (Figs 3 and S3; Diversity: *P* < 0.0001, Warming:

P = 0.0443, Interaction: *P* = 0.0281). Combined with the positive interaction on aboveground biomass, this led to a marginal decrease in root to shoot ratio in the high-diversity–high-warming plots (not shown, interaction: *P* = 0.0639). Further, because of the high proportion of biomass that is belowground in our system, the results for the sum of aboveground plus belowground biomass to 30 cm (total biomass) in 2009, 2010, and 2012 mirrored the belowground results. Total biomass increased with diversity (Fig. 3; *P* < 0.0001) and warming (Fig. 3; *P* = 0.0047), and the effect of warming on total biomass marginally decreased with increasing diversity (Fig. 3; *P* = 0.0639).

Functional groups responded differentially to warming. Legumes increased in abundance in the warmed treatments relative to controls, both absolutely (Fig. 4; Warming: *P* < 0.0001) and as a proportion of total aboveground biomass (Fig. 4; Warming: *P* < 0.0001). C4 grasses, dominant in our study system (the tallgrass prairie), increased in absolute abundance with warming (Fig. 4; Warming: *P* = 0.0013) but not in proportional abundance (Fig. 4; Warming: *P* = 0.219 NS) because of the much larger response of legumes to warming. Forbs did not respond to warming in absolute abundance (Fig. 4; Warming: *P* = 0.204 NS) or in proportional abundance (Fig. 4; Warming: *P* = 0.155). C3 (cool season) grasses decreased in both absolute (Fig. 4; Warming: *P* = 0.0029) and proportional aboveground abundance with warming (Fig. 4; Warming: *P* < 0.0001).

Discussion

Aboveground effects

Our study found that warming and diversity had positive individual and interactive effects on aboveground biomass. Moreover, the strength of this warming effect
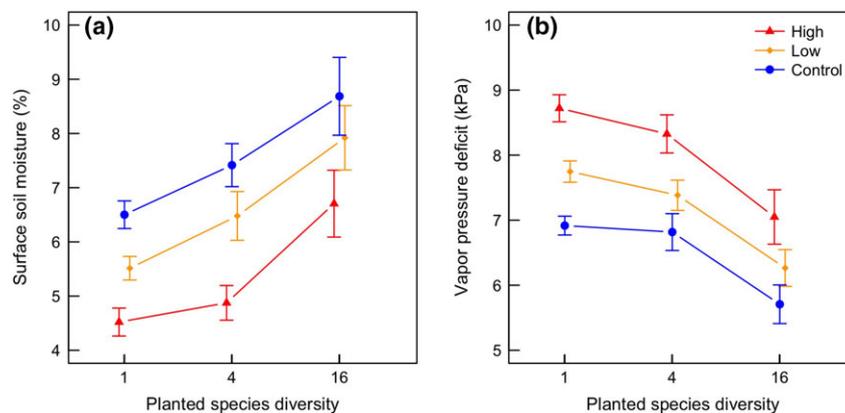

Fig. 2 Planted diversity moderated the impacts of warming on soil moisture to 6 cm depth (a) and vapor pressure deficit (averaged across the iButtons at 10 and 25 cm above soil surface) (b). Error bars depict standard error of the mean.
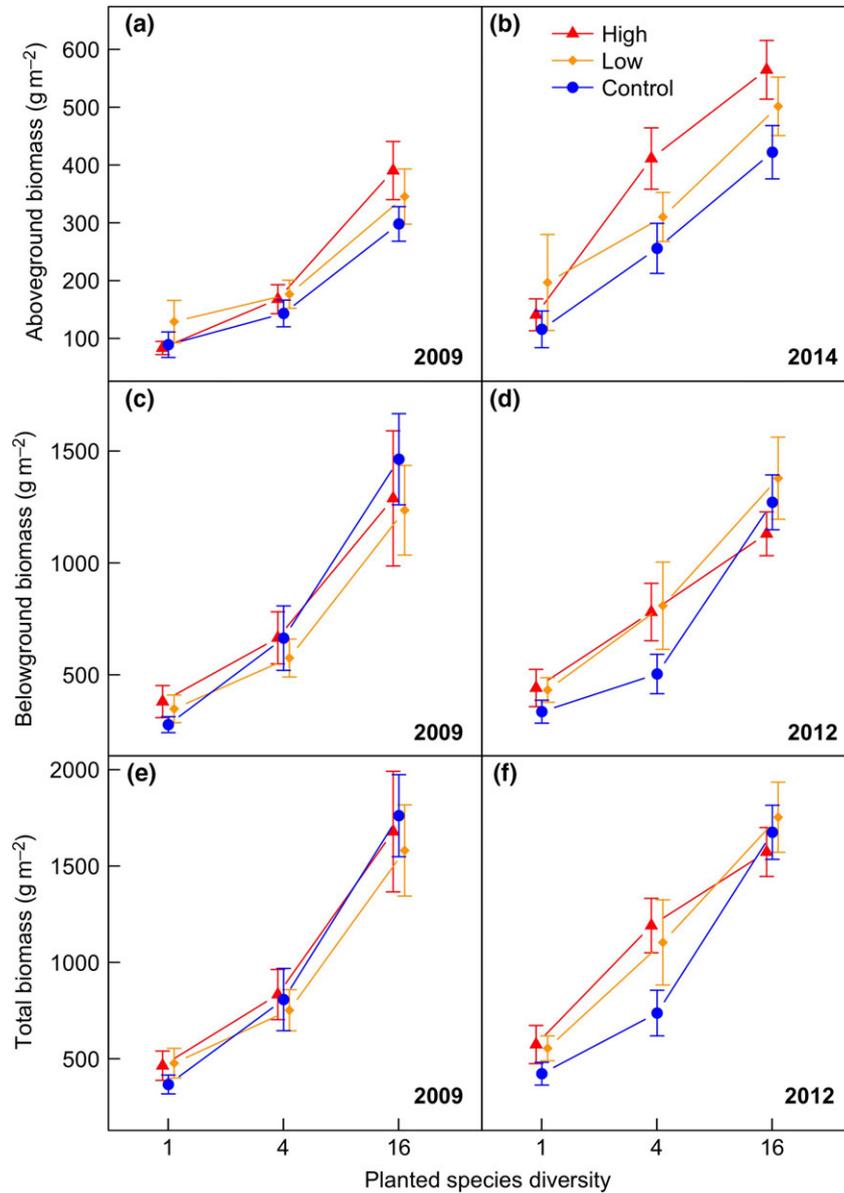
Fig. 3 The effect of warming and diversity on aboveground biomass (a, b), belowground biomass (0–30 cm; c, d), and total biomass (sum of above- and belowground biomass; e, f) in the first year of the experiment (a, c, e) and the final year of data collection for the variable (b, d, f). Roots were most recently sampled in 2012, aboveground biomass in 2014. Error bars depict standard error of the mean.

increased from the first through the sixth year of this experiment. This has several important implications. First, to maximize aboveground productivity, our results suggest that the restoration and maintenance of high-diversity ecosystems will be increasingly important as climate changes, as the positive effect of biodiversity on surface soil moisture can at least in part counter the negative drying effect of warming (for other examples, see Wright *et al.*, 2014, 2015). Further, our observed increasing strength of warming effects over time, when combined with emerging trends from long-

term diversity experiments (Reich *et al.*, 2012), suggests that the effect of both factors may be underestimated by short-term experiments.

Our results on the interactive effects of biodiversity and warming on aboveground net primary productivity and on root mass support an emerging trend: biodiversity often interacts with other drivers of global change in its effects on productivity. Earlier studies have found interactive effects of plant diversity and elevated CO_2 on aboveground productivity (Reich *et al.*, 2001), plant diversity and nitrogen addition on
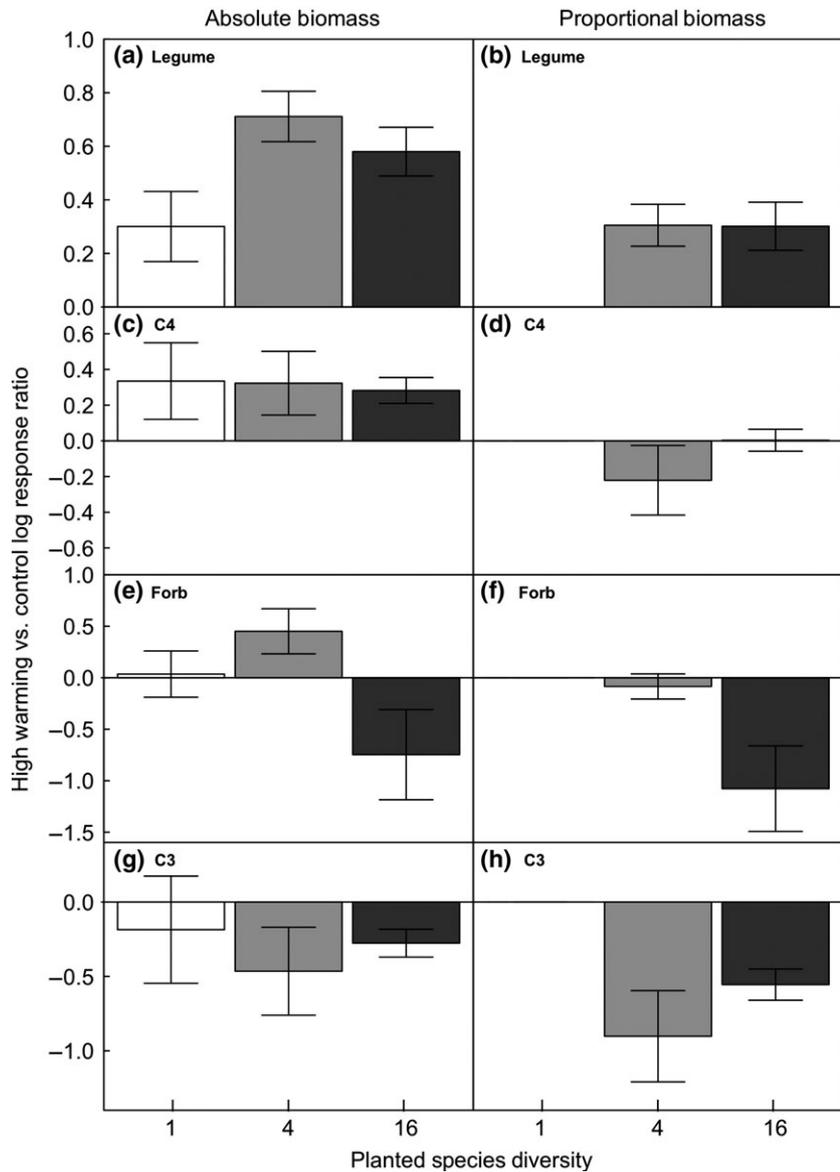
Fig. 4 Log (base e) ratio (log response ratio; LRR) of aboveground biomass (left) or proportional biomass (right) in high warming to control for legume (a, b), C4 grass (c, d), Forb (e, f), and C3 grass (g, h) functional groups across all years. Low warming had an overall intermediate effect and is not shown. A positive LRR indicates a positive effect of warming, and a negative LRR indicates warming reduced biomass relative to controls. Error bars depict standard error of the mean.

aboveground productivity (Reich *et al.*, 2001), and plant diversity and climatic extremes on resistance of aboveground productivity (Isbell *et al.*, in press). In a correlational study, higher plant diversity was associated with smaller declines in productivity when water availability declined during drought (Tilman & Downing, 1994; Tilman *et al.*, 1996).

Might such interactive effects of diversity with global change factors share some underlying causes? Communities that are more diverse contain species with a greater range of traits, allowing fuller use of limiting resources, for example, soil nitrogen, soil moisture,

light or atmospheric CO_2, and greater tolerance of novel conditions, which could cause greater aboveground net primary productivity at higher diversity. The same mechanism may apply to the diversity by warming interaction we observed for aboveground productivity. Soil temperature data from 2012 indicate that warming extended the growing season (days with mean temperature >10 °C) by 14 and 7 days in the high- and low-warming treatments, respectively. Thus, the diverse communities containing a variety of species, some that grow preferentially in the early season and some that grow later, would best capitalize on this

increased growing season length. Warming-dependent increases in legume and C4 grass abundances may contribute to the positive diversity by warming interaction on aboveground productivity, as one factor causing higher productivity at higher diversity in our biodiversity experiment is a positive legume by C4 grass interaction (Fornara & Tilman, 2008). Elevated temperature has caused similar compositional shifts in other grassland experiments (Niu et al., 2010; Cantarel et al., 2012; but see Alward et al., 1999 and discussion below). Finally, the positive effects of biodiversity on surface soil moisture may be an additional reason for the diversity by warming interaction.

Although aboveground biomass production increased with warming in our study and others (Rustad et al., 2001; Lin et al., 2010; Wu et al., 2011), the effects of warming may be mediated by water availability, nutrient availability, humidity, and growing season length (Dieleman et al., 2012), possibly with an overall larger response of productivity to warming in cooler, wetter ecosystems (Rustad et al., 2001) and a smaller response if warming causes marked soil drying (Zhou et al., 2012; Bai et al., 2013). Thus, warming can affect biomass production positively, as we saw, or negatively, depending on environmental context.

Belowground effects

Both warming and diversity increased standing root biomass. Increases in root biomass with increased species richness have been well documented in biodiversity experiments (Mueller et al., 2013; Ravenek et al., 2014). As in our aboveground effects, the positive main effect of warming belowground was the reverse of other warming studies (De Boeck et al., 2007; Zhou et al., 2012) and may indicate many warming results are situational. Many of the species in this study are located toward the northern (more polar) end of their geographic ranges, and thus, temperature increases and longer growing seasons likely have positive effects on biomass compared with species at the southern (more equatorial) edge of their range (Reich et al., 2015). This may explain differences between our study and that of Zhou et al. (2012), conducted with similar species composition but at the southern edge of the species range limits.

Species composition may play a role in study-specific effects of warming on communities. The use of C_3 grasses in a warming and diversity greenhouse study (De Boeck et al., 2007) might account for the difference in results between our study and theirs, as our and other studies report C_4 grasses responding positively and C_3 grasses responding negatively to warming (Sherry et al., 2008; Cantarel et al., 2012). However,

Alward et al. (1999) found that the dominant native C4 grass decreased with warming and an exotic C3 grass became more dominant in a four-season nighttime warming experiment in the shortgrass steppe. Their hypothesis, that the reversal is caused by early season growth of C3 grasses preempting the reduced soil moisture supply for the C4 grasses in the spring, could be a reason for the opposite effects seen in the two studies. The warming treatments in our experiment do melt snow in March and April, but May and June are the two wettest months of the growing season, so any effects of early spring C3 grass growth on soil moisture would likely not impact C4 grasses, which begin growing in mid-May when soils are frequently brought to full water holding capacity by numerous rains.

We observed a small but significant negative interactive effect of warming and diversity on root biomass that may be due to greater legume abundance and/or higher availability of soil nitrogen at higher diversity and warmer temperatures (Fornara & Tilman, 2008; Dijkstra et al., 2010). Legumes have smaller root : shoot ratios than other functional groups in our system (Craine et al., 2002) and decomposition of their N rich roots would increase soil available N (Fornara et al., 2009). Increased N availability would be expected to favor lower allocation to roots in nonlegume plant species. If warming was to consistently lower root allocation over a long period, soil carbon stores might decrease. Soil carbon stores could also decline if, as has been reported (Rustad et al., 2001), warming increases decomposition rates. As belowground biomass and soil organic carbon are a large proportion of the carbon in grassland systems, these possibilities merit further attention. Further, although the soils at Cedar Creek are strongly N-limited, increased dominance of legumes and increased N availability may lead to phosphorus limitation in legumes (Ritchie & Tilman, 1995), potentially damping the positive warming effects through time.

It is important to note that our study was conducted in a perennial grassland system with frequent disturbance via burning. Because of this, the effects of diversity and warming that we observed likely occurred more quickly than they would in some other systems. Forests, for instance, could take much longer to respond to climatic changes due to longer generation times and thus slower changes in species abundances and composition. Because system-specific responses may play an important role in ecosystem responses to global changes (Shaver et al., 2000), caution is needed in extrapolating the results of one system to other systems.

Our experimental design, which utilizes random species combinations rather than the nonrandom

species losses that might be expected under various climate change scenarios, allows a test of the effects of biodiversity *per se* and climate warming on ecosystem functioning. Our experiment provides a first test of how these two important global change factors may interactively affect ecosystem functioning. However, as experiments with nonrandom species loss may exhibit both greater and smaller ecosystem effects than random species loss (Tilman *et al.*, 2014), further experimentation with climate-induced species loss patterns will be necessary.

Conclusions

Biodiversity is known to be a major determinant of ecosystem productivity and of the stability of productivity when climate extremes occur. Our work shows that biodiversity is also an important determinant of an ecosystems' response to climate warming. The observed positive interactive effect of warming and diversity on aboveground productivity was not mirrored in belowground or total biomass, perhaps because of shifts in community structure. This indicates that while high-diversity ecosystems may have a higher ability to respond positively aboveground to warming in our system, positive effects of warming on belowground biomass may be smaller, even absent in diverse communities. Consequently, the impacts of global change on ecosystem services associated with aboveground biomass (e.g. forage quality) may not be mirrored in the impacts on ecosystem services associated with belowground biomass (e.g. carbon storage). However, our results still corroborate previous findings that biodiversity strongly and positively influences both above and belowground biomass, indicating that preserving biodiversity is still essential to promoting both aboveground and belowground ecosystem services in grassland ecosystems.

Acknowledgements

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Supporting Information

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

Figure S1. (a) The effect of warming and diversity on air and soil temperature in May (left) and June (right) 2014. Error bars depict standard error of the mean. (b) The effect of warming and diversity on air and soil temperature in July (left) and August (right) 2014. Error bars depict standard error of the mean.

Figure S2. The effect of planted diversity and warming on aboveground biomass production for the six years of the experiment (a–f). Error bars depict standard error of the mean.

Figure S3. Mixed-effects model parameter estimates for effects of diversity (loge species number), warming (nominal degrees C of warming), and the interaction of the two on aboveground biomass (a) and belowground biomass (b). Error bars depict standard errors of the estimates.