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GLOBAL CHANGE ECOLOGY – ORIGINAL RESEARCH

Imposing antecedent global change conditions rapidly alters plant community composition in a mixed-grass prairie

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Abstract Global change drivers are altering climatic and edaphic conditions of ecosystems across the globe, and we expect novel plant communities to become more common as a result. In the Colorado Front Range, compositional changes have occurred in the mixed-grass prairie plant community in conjunction with shifts in winter precipitation and atmospheric nitrogen (N) deposition. To test whether these environmental changes have been responsible for the observed plant community change, we conducted an in situ manipulative experiment in a mixed-grass meadow near Boulder, CO. We simulated historical conditions by reducing N availability (+500 g C m^{-2} $year^{-1}$) and winter precipitation (with rainout shelters) for 2 years (2013–2014) and compared vegetation response to these treatments with that of ambient conditions. The site experienced an extreme precipitation event in autumn 2013 which allowed comparison of an exceptionally wet year with an average year. We measured pre-treatment species composition in 2012, and treatment responses in the spring and summer of 2013 and 2014. As predicted, simulating historical low N-winter dry conditions resulted in a plant community dominated by historically abundant species. Cool-season introduced species were significantly reduced in low N-winter dry plots, particularly the annual plants *Bromus tectorum* and *Alyssum parviflorum*. These same species responded strongly to the extreme precipitation event with large increases, while native grasses and forbs showed little change in productivity or composition under varying climatic or edaphic conditions. This work provides clear evidence linking on-going global change drivers to altered plant community composition in an otherwise relatively undisturbed grassland ecosystem.

Keywords *Bromus tectorum* · *Erodium cicutarium* · Nitrogen deposition · Novel ecosystem · Precipitation seasonality

Introduction

As global change agents alter the edaphic and climatic conditions that define terrestrial ecosystem boundaries, we can expect to see shifts in plant communities and ecosystem function (Seastedt et al. 2008). Increasing temperature, changing precipitation patterns, altered atmospheric composition, and anthropogenic nitrogen deposition have already resulted in significant changes to sensitive (e.g., alpine ecosystems; Bowman et al. 2012) and impacted systems (e.g., those close to urban centers; Rao et al. 2011), and are expected to affect even the most remote and protected locations (Pauchard et al. 2009). Coupled with these on-going directional shifts, ecosystems may experience

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disturbances or extreme events which act to cause rapid change in community composition or ecosystem function, pushing the system over some threshold (Jentsch et al. 2007; Suding and Hobbs 2009). Such changes have been well-documented in arid systems and rangelands (e.g., Walker 1993), and it has been increasingly recognized that non-linear ecosystem dynamics are likely to be common in other types of ecosystems (Suding and Hobbs 2009), but documented case studies are still rare. The Colorado Front Range mixed-grass prairie ecosystem has experienced changes in both plant community composition and ecosystem function over the last several decades (Beals et al. 2014), and is an ideal location to test hypotheses about mechanisms of change.

Native vegetation of the Colorado mixed-grass prairie includes grasses and forbs with C_3 and C_4 photosynthetic pathways, with highest productivity often occurring during the summer season. Over the last several decades, the plant community has shifted toward increased cover of forbs at the expense of native grasses (Beals et al. 2014). In urban and suburban areas of the Front Range occupied by the black-tailed prairie dog (*Cynomys ludovicianus*), this shift has occurred four to ten times faster than in unoccupied areas, and exotic forbs and bare ground now dominate much of the landscape (Beals et al. 2014). Consequences of this loss of native vegetation include rapid soil erosion followed by dust storms, which were not previously reported in this area (Seastedt et al. 2013). In contrast, the black-tailed prairie dog has historically played a keystone role in western US grasslands by maintaining high levels of diversity and providing multiple ecosystem services (e.g., Miller et al. 1994). Although the changing impacts of prairie dogs in this human-dominated landscape are well-documented (Beals et al. 2014), many unanswered questions remain about mechanisms driving altered plant–prairie dog trophic interactions and shifting community composition of grasslands unoccupied by prairie dogs. Management of these complex human-dominated systems requires a better understanding of the drivers of both directional shifts in community composition and ecosystem properties, and thresholds. Here, we focus on the latter question: what are the mechanisms that allow cool-season introduced species to become dominant in the Colorado Front Range in the absence of prairie dogs?

Changes in climate, atmospheric composition, and biogeochemical cycling have been occurring over the past century in the Front Range of Colorado, with accelerated speed during the last several decades (Lukas et al. 2014). Carbon dioxide concentrations (Morgan et al. 2007), anthropogenic nitrogen deposition (Baron et al. 2000), and mean (Lukas et al. 2014) and maximum (McGuire et al. 2012) temperatures are increasing, while precipitation seasonality has shifted toward wetter winters (Prevéy 2014), and earlier snowmelt has been linked to an expansion of the growing season (CaraDonna et al. 2014). Each trend is predicted to continue, resulting in climatic and edaphic conditions that native species in the region have never before experienced. Under these novel environmental conditions, changes in plant community composition are expected (Seastedt et al. 2008). It is clear that rainfall seasonality is a major influence over the distribution of grasslands (Parton et al. 1994; Knapp et al. 2008), and nutrient availability can have large effects on productivity of these systems (Parton et al. 1994). It is likely that the changes that have been documented in Front Range mixed-grass plant communities over the last two decades are linked to on-going global change.

Of the global change drivers occurring in the region, those that increase resource availability during the cool-season (when most introduced species are active and native species are dormant) are most likely to be responsible for documented changes in community composition. Past research has found that shifting seasonality of precipitation in the Front Range toward wetter winters is likely to facilitate the increased abundance of exotic grasses (Prevéy and Seastedt 2014). We, therefore, hypothesized that: (H_1) the combination of higher soil water and N availability during the cool-season (made available through shifts in precipitation and increased N deposition) has been facilitating the increased abundance of cool-season introduced forbs and grasses in the region. Furthermore, by favoring introduced species, global change drivers may have additional indirect impacts on species composition. Prevéy and Seastedt (2014) found that introduced grass cover in the early spring is associated with reduced moisture availability later in the season, with potential consequences for warm-season grasses and forbs. In addition, it has been found elsewhere that increased N deposition can lead to losses in biodiversity (Stevens et al. 2004; Dise and Stevens 2005). One explanation for this trend is that the excess soil N availability allows fast-growing and/or early germinating species to attain high biomass, leading to reduced light availability for slower or later growing species (Hautier et al. 2009). Thus, we further hypothesized that: (H_2) increases in introduced forb and grass cover in the spring would lead to losses in native species abundance and plant diversity in both the spring and summer seasons; and (H_3) increased nitrogen deposition at this site is leading to losses in plant diversity. To test these hypotheses, we set up an in situ manipulative experiment in 2012 in a mixed-grass meadow ecosystem just north of Boulder, CO where prairie dogs had not been reported over the last century. We simulated historical lower resource conditions using rainout shelters to reduce winter precipitation and adding sugar to reduce nitrogen availability, and measured plant community responses over 2 years.

A year after we set up our experiment, in autumn of 2013, the Colorado Front Range experienced an extreme precipitation event which led to high soil moisture conditions throughout the following winter and spring seasons. Ecological theory predicts that extreme events may facilitate invasive plant success by creating new dispersal opportunities, disturbances, or resource pulses (Diez et al. 2012), and they may be disproportionately important for shaping plant community dynamics (Gutschick and BassiriRad 2003). Because this event delivered a resource pulse (elevated soil moisture and N mineralization) at a time when introduced species would be most likely to benefit, we expected those species to increase in dominance. Indeed, research at nearby study plots found that introduced species did respond with large increases in productivity during the winter and spring seasons after the extreme event, though the magnitude of response was limited by N availability (Concilio et al. 2015). We, therefore, hypothesized that: (H_4) introduced species would gain an added advantage over native species under ambient high N conditions in 2014 compared with 2013 due to high soil water availability provided by the extreme event. In the absence of plant-available soil N, this event would have reduced or minimal effect.

Materials and methods

This study was conducted in a mixed-grass meadow located 15-km northwest of Boulder, CO (40°07′N, 105°18′W; elev 1798 m) on private land. The meadow has never been plowed and has not recently been grazed, but some cattle grazing occurred before 2006. Soils are well-drained, colluvial, sandy loams (USDA 2001). Temperature averages 10.9 °C and the site receives 525 mm of precipitation on average per year, ranging from a low of 277 mm in 1954 to a record high of 867 mm in 2013 (records are from 1893 to 2016; WRCC 2016). The year preceding our experimental treatments, 2012, was a slightly below average precipitation year totaling 398 mm.

The vegetation community is made up of warm- and cool-season native grasses, native forbs, and (mostly cool-season) exotic forbs and grasses. Dominant native grasses include: *Agropyron smithii*, *Buchloe dactyloides, Bouteloua curtipendula, B. gracilis, Hesperostipa comata,* and *Sporobolis cryptandrus*. *Bromus tectorum* comprises most of the introduced grass cover, but *B. brizaeformis, B. inermis*, *B. japonicus*, and *Poa compressa* are also present at the site. The most abundant native forbs include *Ambrosia artimesifolia, Erigeron divergens*, *Liatris punctata, Psoralidium tenuiflorum,* and *Silene antirrhina*. The most abundant introduced forbs include *Alyssum parviflorum*, *Erodium cicutarium*, and *Tragopogon dubius*. One native shrub, *Artemesia frigida,* grows at the site, and several species of cacti, *Opuntia polyacantha* being the most abundant.

To test our hypothesis about how directional shifts in precipitation and N deposition are affecting vegetation and soils in the mixed-grass prairie, we established a manipulative experiment at the meadow site in 2012 with treatments designed to simulate historical conditions. We placed 64 plots, each 3×3 m^2, and randomly assigned each to receive one of four treatment combinations in a full factorial design, including two precipitation treatments (ambient precipitation, decreased winter precipitation) and two nitrogen treatments (ambient nitrogen, low N). Average winter precipitation in the Boulder, CO area, delivered between October and March, from 1970-present was 199 mm, about 22 % higher than the pre-1970 average (163 mm). To simulate historical precipitation conditions, we placed rainout shelters on plots from early October to late March of each year (2012–2013, and 2013–2014). Shelters were modeled after Yahdjian and Sala (2002), and identical to those used in Prevéy and Seastedt (2014) with added gutters to divert water collected on the shelters from flowing onto downhill plots. Prevéy and Seastedt (2014) found that these shelters reduced precipitation by 50 % at our study site. Our winter dry treatment led to reduced volumetric soil moisture throughout the winter and into the spring each year (Fig. 1).

We simulated historically lower soil N conditions using carbon (C) additions. Adding C immobilizes N by stimulating microbial productivity, and reducing N availability to plants (Cherwin et al. 2009; Blumenthal et al. 2003). Each year, we added 500 g C m^{-2} year^{-1} in the form of table sugar to low N plots, distributing the sugar evenly throughout the growing season from March to October every 2–3 weeks. Results from analysis of resin bags indicated that our sugar additions reduced N availability by an average of 63 % compared with ambient levels experienced in control plots ($F = 34.1$, $p < 0.001$; Online Resource 1).

In September of 2013, the Front Range received an extreme rainfall event of 430 mm over a few days and resulted in wetter soils, a characteristic that extended well into the next growing season (Fig. 1). The total amount of precipitation the site received from September to March of 2013/2014 was 639 mm, which was three times greater than the previous winter (194 mm). This represented the largest precipitation event in the region in recorded history. We tested our hypothesis (H_4) about the effect of an extreme event on the plant community by comparing response variables between a normal precipitation year (2013) and an extreme wet year (2014) under low and ambient N conditions.

Prior to treatment initiation in August 2012, we measured species composition with a 1-m^2 point-intercept quadrat in the center of every plot to confirm the lack of pre-treatment differences across plots. Analysis of these

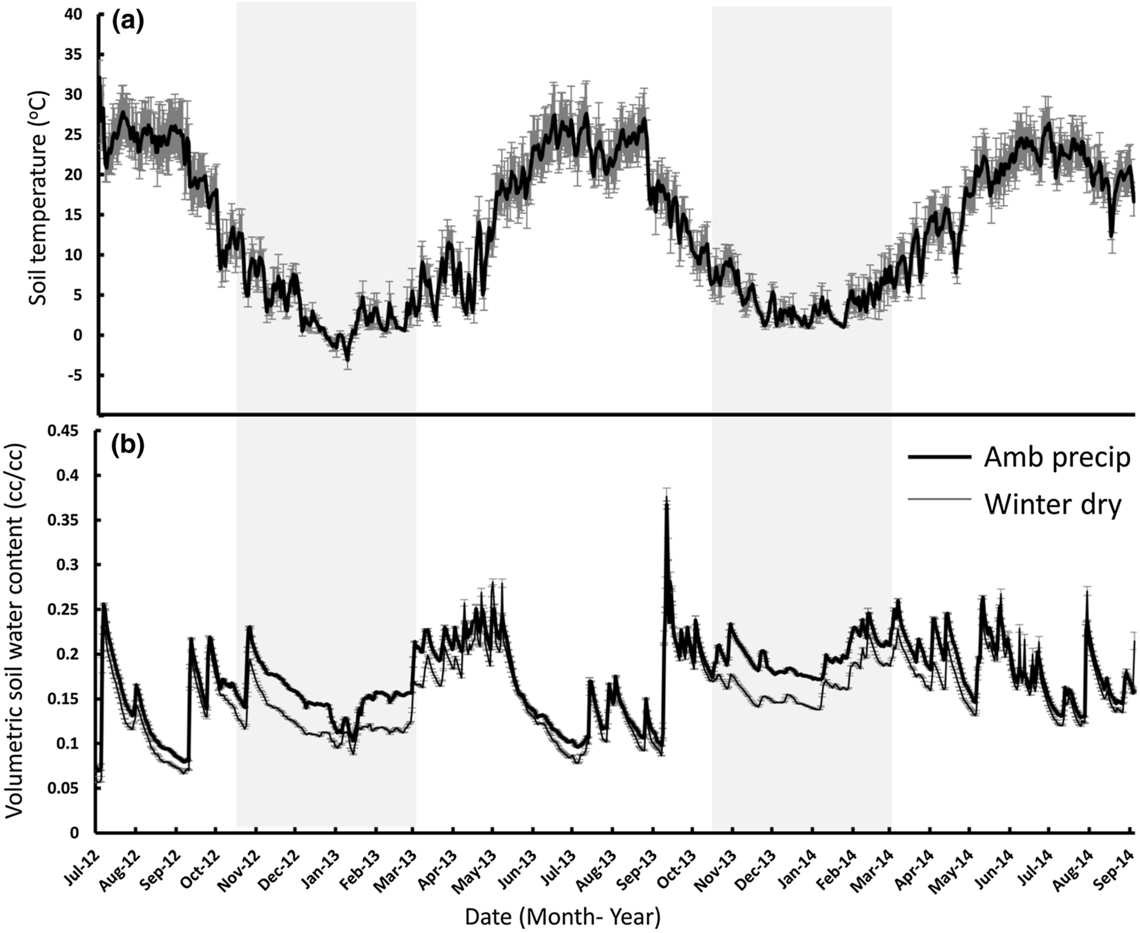


Fig. 1 Soil temperature and moisture collected hourly and averaged daily from 2012 to 2014. Soil temperature is averaged across plots with all precipitation treatments, whereas soil moisture is averaged by ambient precipitation and winter dry precipitation. *Gray* shading represents the time that the rainout shelters were on the winter dry plots

data found no difference in species composition by plots assigned to nitrogen or precipitation manipulations before treatments began (ANOSIM; $p > 0.20$ for all tests). To evaluate treatment responses, we measured species composition and aboveground productivity of both cool- and warm-season species in the spring and summer of 2013 and 2014. All measurements were made within the 2 × 2 m^2 center of each plot (within a 0.5-m buffer on all sides). To measure species composition, we placed a 1-m^2 point-intercept quadrat in the northeast section of the 2 × 2 m^2 central area of each plot and identified and tallied every plant that hit one of the 100 points in the grid. Plants that were in the quadrat but not touching a grid point received a value of 0.5. Percent cover of each species was equal to its number of hits, since there were 100 possible hits per plot. For relative cover, we divided the number of times that each species hit a grid point by the total number of hits for all species in the plot. Measurements were made on June 4–10, 2013 and August 15–21, 2013 and on June 2–9, 2014 and Aug 18–29, 2014. We grouped plants into the following categories for cover analyses: *B. tectorum,* all exotic grasses, native grasses, *E. cicutarium*, all exotic forbs, and native forbs.

We measured aboveground productivity by clipping all live plants within a 20 × 50 cm^2 quadrat placed in one corner of the larger 2 × 2 m^2 measurement area taking care not to clip in the same place twice or in the same location where species composition was measured. Measurements were made in the spring and summer of each year: on May 13–16, 2013 and June 26–29, 2013, and May 22–27, 2014 and July 15–16, 2014. As we clipped, we separated plants into the following groups: *B. tectorum,* other exotic grasses, native grasses, *E. cicutarium*, other exotic forbs, and native forbs. Samples were dried for 48 h at 60 °C and weighed. We calculated relative biomass as the mass of each group divided by total mass for each plot.

We monitored soil moisture and temperature from 2012 to 2014 in a subset of plots to capture the effects of the precipitation treatments on soils. We placed a total of 28 sensors, half in ambient precipitation and half in winter dry plots, at a depth of 10 cm from the soil surface. Temperature and moisture were measured continuously with 5TM sensors (Decagon Devices, Pullman, WA) and recorded hourly on EM50G data loggers (Decagon Devices, Pullman, WA). We downloaded data regularly, and cleaned, compiled, and averaged soil temperature and moisture daily by precipitation treatment from January 2012 to October 2014.

To estimate treatment effects on plant-available soil nitrogen, we used ion-exchange resin bags constructed as described in Prevéy and Seastedt (2014). Five grams of resin (Amerlite® MB-150 mixed bed resin) was placed into nylon bags with plastic zip-tie hoops for structural support. Bags were washed in a 0.5-M HCl solution and rinsed with deionized water before being deployed. We buried two bags per plot at a depth of 5 cm in 60 plots at least 0.5 m from the edge of the plot to ensure it received the water and N treatments. From 2012 and 2014, resin bags were deployed seasonally for 2–4 month periods from October 1–March 30 (winter), April 1–June 30 (spring), and July 1–September 30 (summer). After removal, resin bags were extracted in 40 ml of 2-M KCl and kept frozen until they were analyzed. Inorganic nitrogen was analyzed colorimetrically on a Lachat QuickChem 8500 flow injection analyzer.

Data analysis

To test our hypothesis about effects of climate change and nitrogen deposition on plant community change (H_1), we compared biomass and cover of select plant groups by nitrogen and precipitation treatment and by year (comparing a wet year to an average year). Groups included: *B. tectorum* (the most dominant introduced grass), total introduced grasses, *E. cicutarium* (the most dominant introduced forb), total introduced forbs, native grasses, and native forbs. For analysis of percent cover data (not biomass), we further isolated the second and third most dominant introduced forbs at the site, *Alyssum parviflorum* and *Tragopogon dubius*, to test whether each of the dominant cool-season species was responding similarly to changing environmental conditions at the site. We used mixed-effects ANOVAs to test the effects of N and precipitation treatments on biomass, absolute cover, and relative cover (of each group or species). Since the same plots were sampled in both years, year was included as a within-subjects factor. Because year was included in these models, we were able to also test our hypothesis about vegetation response to the extreme precipitation event (H_4) using the same analyses. When treatment effects were significant, we further investigated these differences using two-way ANOVAs within each year followed by post hoc Tukey HSD tests. Tukey tests cannot be performed on repeated measures analyses, since one of the assumptions of the test is that samples are independent. Our data met that requirement when analyzed separately by year. Variables that did not conform to the assumptions of ANOVA were normalized through log or square root transformations before analysis.

We further tested our first hypothesis by analyzing differences in species composition between plots experiencing ambient compared with historically simulated low-resource conditions. We used analysis of similarity (ANOSIM) tests after visualization with nonmetric multidimensional scaling (NMDS) for each season (spring, summer) and year (2013, 2014) separately. Analyses were performed on both raw (absolute abundance) and 4th root transformed data to test for differences in composition weighted for abundant versus rare species, respectively. We generated NMDS graphs with Bray–Curtis dissimilarities using random starts to find a stable solution (metaMDS, vegan package, R statistical software). It was clear from NMDS figures that there were no differences between ambient and winter–dry precipitation treatments, so we performed ANOSIM tests by nitrogen treatment but not precipitation.

To test our hypothesis about the impact of cool-season introduced species in the spring on plant diversity and native species abundance in the spring and summer of the same year (H_2), we used correlation and simple linear regression analyses. Using raw cover data, we calculated the following diversity indices for each plot by season and year: species richness, Shannon's diversity, Fisher's alpha, and Pielou's evenness (vegan package, R). We used Pearson correlation analysis to test relationships between spring cover of the four most dominant introduced species at the site (*B. tectorum, E. cicutarium, A. parviflorum,* and *T. dubius*) with each of the four biodiversity metrics calculated for that same season. Some variables were transformed before correlation analysis (with log or 4th root transformations) to meet normality assumptions of the Pearson test. We used correlation analysis, rather than regression, for relationships within the same season (spring), because we could not rule out the possibility that more diverse parts of the landscape were more resistant to introduced species invasion. However, if we found a negative relationship between introduced species in the spring and summer diversity or abundance, we could be more confident that introduced species abundance was acting as a driver of native species loss. We, therefore, used linear regression analysis to determine whether introduced species cover in the spring had an influence on summer plant diversity. In this case, the dependent variables were diversity indices calculated for the summer season and the independent variables were: dominant introduced forb cover (including *E. cicutarium*, *A. parviflorum*, and *T. dubius*), dominant introduced grass cover (*B. tectorum*), and dominant introduced species cover (including all four species) in the spring. Last, to examine N treatment effects on the calculated diversity indices (H_3), we used mixed ANOVAs, again with year as a within-subjects factor. These analyses were done separately by season (spring, summer), since species composition was different during these two periods.

Results

Effects of precipitation and nitrogen treatments on the plant community

The plant community responded to simulated historical N conditions in the direction that we predicted, with a decrease in the performance of introduced species. Total aboveground spring productivity was reduced in low N treatments by 40 % ($F_{1,60} = 39.5$; $P < 0.001$; Fig. 2a, b). Most of this reduction came from decreased biomass of introduced species, particularly the invasive grass *B. tectorum,* which was reduced by 64 % ($F_{1,60} = 32.2$; $P < 0.001$). Biomass of introduced forbs ($F_{1,60} = 11.8$; $P = 0.0012$), native forbs ($F_{1,60} = 5.57$; $P = 0.021$), and native grasses ($F_{1,60} = 5.63$; $P = 0.021$) were also reduced, but to a lesser extent (by 23–31 %). The winter–dry precipitation treatment alone did not have a significant effect on springtime productivity, but in combination with the low N-treatment, productivity was reduced ($F_{1,60} = 2.98$, $P = 0.089$). This difference was driven by decreased *B. tectorum* biomass under low N-winter dry conditions (precip*N: $F_{1,60} = 5.09$, $P = 0.0277$; $P < 0.001$ for post hoc comparisons); no other species or group responded significantly to reduced precipitation. In the summer, most of the aboveground biomass was made up of native grasses and forbs, and there was little response to N or precipitation treatments (Fig. 2c, d). In the full mixed ANOVA model, we found significant interactions between precipitation and N ($F_{1,56} = 10.4$; $P = 0.0021$) and year and N ($F_{1,56} = 8.04$; $P = 0.0064$) for forb biomass. Follow-up two-way ANOVAs showed that forb biomass was reduced in low N plots in 2014 ($F_{1,58} = 4.76$; $P = 0.0333$), but not 2013. Native grass biomass did not differ by treatment or year.

Cover responses to treatment mirrored those of biomass (Online Resource 2). Introduced grass cover, dominated by *B. tectorum*, responded most strongly to treatments, while native grass cover did not show any significant treatment responses. Introduced forb cover was reduced under low N conditions in the spring. Precipitation and N treatments were interactive in their effect on introduced grasses in both years, and on introduced forbs in 2013 (Fig. 3). When we compared responses of the four most dominant introduced species to N and precipitation treatments, we found variation by both year and species (Table 1). In general, most showed a stronger response to the N than precipitation treatment. The exotic forb *A. parviflorum* was the only species that was significantly affected by precipitation alone, whereas *E. cicutarium* and *T. dubius* were least effected by treatments.

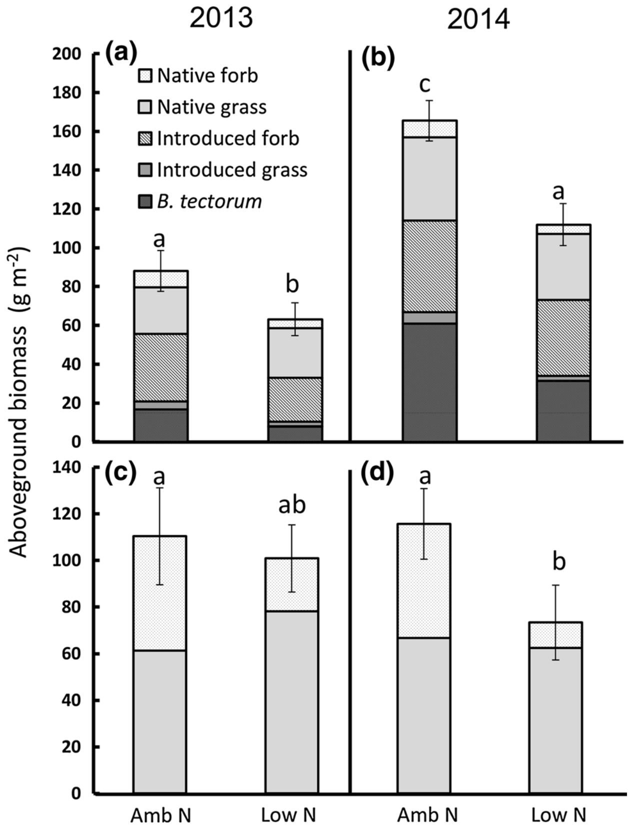


Fig. 2 Biomass of native and introduced grasses and forbs and the introduced grass *B. tectorum* in the **a**, **b** spring and **c**, **d** summer of 2013 (*left panels*) and 2014 (*right panels*) in ambient N or low N treatments. Data are from ambient precipitation plots only. *Error bars* are the standard error of the mean aboveground biomass of all groups combined. Significantly different means between year and treatment are represented with *different lowercase letters* within each season (Tukey HSD)

None of the diversity indices that we measured differed by precipitation or N treatment alone, but interactions between N and year were significant for all four indices in the spring ($P < 0.05$ in all cases). With follow-up ANOVAs, we found that there were differences in diversity by treatment, but they were not consistent across the two years. In spring 2013, species richness was higher under ambient than low N conditions ($F_{1,60} = 4.65$, $P = 0.035$). In 2014, however, the low N plots were more diverse (Fisher's alpha: $F_{1,60} = 4.62$, $P = 0.036$; Pielou's evenness: $F_{1,60} = 4.66$, $P = 0.035$). None of the diversity metrics differed by treatment during the summer.

Finally, we analyzed differences in community composition by N treatment using ANOSIM on raw cover data and 4th root transformed data. Although results were significant for the spring of 2013 and 2014 using both datasets,

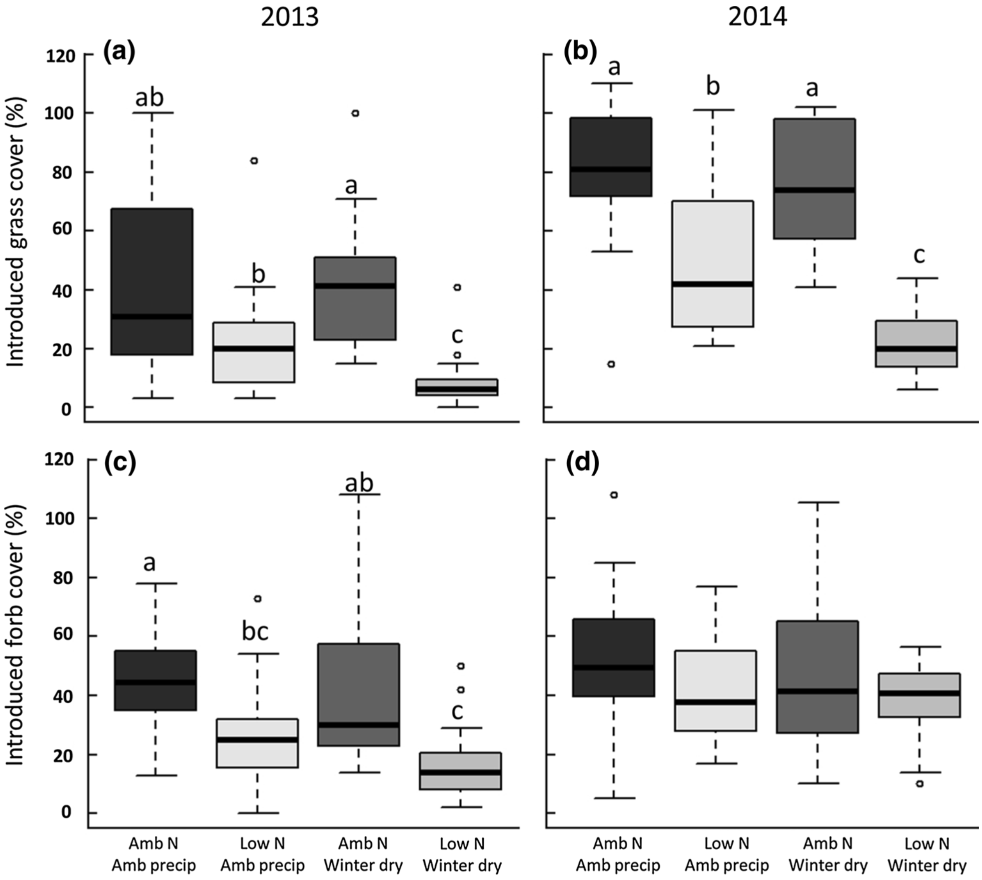


Fig. 3 **a**, **b** Introduced grass and **c**, **d** forb cover in response to N and precipitation treatments in the spring of 2013 (*left panels*) and 2014 (*right panels*). *Points above* and *below the box-and-whisker plots* represent outlier values. *Different letters* represent significantly different means within each panel. There were no significant differences in introduced forbs in the summer ($\alpha = 0.05$)

only 8–19 % of the variation in species composition could be explained by N treatment (Table 2). More variation was explained using untransformed than transformed data. During the summer, the N treatment only explained 6 % of the variation in the data in 2014 and was an insignificant predictor in 2013.

Plant community differences between years

The extreme precipitation event that occurred at the site in the autumn of 2013 increased soil moisture availability in spring of 2014 (Fig. 1), and caused excessive N mobilization—with rates of capture per unit time period more than three times that of any other sampling period (Online Resource 1). In response, total aboveground productivity in the spring of 2014 was 84 % higher than in 2013 ($F_{1,60} = 124.2$, $P < 0.001$). This was largely due to greater productivity of introduced species, particularly *B. tectorum*, which increased by 270 % ($F_{1,60} = 128.8$; $P < 0.001$)—nearly an order of magnitude more than any other species. Cover of the four dominant introduced species collectively increased by more than 60 % from 2013 to 2014 ($F_{1,60} = 121.8$; $P < 0.001$). We also found increased species richness throughout the site from spring 2013 to 2014 ($F_{1,60} = 12.4$, $P < 0.001$). This was due to more native forb species appearing in our plots in 2014 compared with 2013. Diversity showed positive responses to the extreme precipitation event during the summer season as well: species richness ($F_{1,60} = 29.7$, $P < 0.001$), Shannon diversity ($F_{1,60} = 2.88$, $P < 0.001$), and Fisher's alpha ($F_{1,60} = 8.60$, $P = 0.0048$) were higher in 2014 than 2013. However, summer productivity was reduced in 2014 compared with 2013 ($F_{1,60} = 8.11$, $P = 0.0061$).

Effect of introduced species on native species abundance and biodiversity

We found that the two most dominant introduced species at the site, *B. tectorum* and *Erodium cicutarium*, were generally negatively related to spring diversity, but relationships were inconsistent by year and species (Fig. 4). In contrast, the introduced forbs *Alyssum parviflorum* and *Tragopogon dubius* had positive or insignificant relationships with diversity. *A. parviflorum* was positively related to Shannon diversity ($r = 0.44$, $P = 0.0003$) and species richness ($r = 0.50$, $P < 0.001$) and *T. dubius* was positively related to Pielou's evenness ($r = 0.25$, $P = 0.043$) in 2013. In 2014, *T. dubius* was again positively related to Pielou's evenness ($r = 0.38$, $P = 0.0021$), but there was no significant relationship between *A. parviflorum* and diversity.

Table 1 Mean percent cover (±SEM) of each of four dominant introduced species under ambient (Amb N) and low nitrogen (Low N) conditions, ambient (Amb precip) and reduced winter precipitation (Winter dry), and during an average year (2103) and a wet year (2014)

Treatment	*B. tectorum*	*E. cicutarium*	*A. parviflorum*	*T. dubius*
2013				
Amb N				
Amb precip	31.5 ± 8.1	18.2 ± 3.7	15.1 ± 2.0	2.4 ± 0.5
Winter dry	33.8 ± 6.8	22.6 ± 5.1	8.1 ± 17	2.0 ± 0.6
Low N				
Amb precip	14.9 ± 5.1	15.7 ± 2.7	2.3 ± 0.7	1.3 ± 0.3
Winter dry	5.3 ± 1.3	9.2 ± 2.5	0.88 ± 0.4	2.2 ± 0.7
2014				
Amb N				
Amb precip	53.2 ± 7.7	16.3 ± 3.2	16.7 ± 2.2	12.1 ± 1.8
Winter dry	55.5 ± 7.3	15.9 ± 2.6	11.8 ± 1.8	11.8 ± 3.1
Low N				
Amb precip	29.6 ± 6.4	17.0 ± 2.2	8.9 ± 1.4	8.3 ± 1.4
Winter dry	14.1 ± 2.1	12.9 ± 1.6	5.2 ± 1.1	13.1 ± 1.7
Results from mixed ANOVAs				
Nitrogen	**$F = 23.6, P < 0.0001$**	$F = 2.45, P = 0.123$	**$F = 42.1, P < 0.0001$**	$F = 0.302, P = 0.585$
Precipitation	$F = 0.682, P = 0.412$	$F = 1.25, P = 0.267$	**$F = 9.54, P = 0.0030$**	$F = 0.513, P = 0.477$
Year	**$F = 90.4, P < 0.0001$**	$F = 1.09, P = 0.742$	**$F = 47.6, P < 0.0001$**	**$F = 169.7, P < 0.0001$**
Nitrogen *precip	$F = 3.02, P = 0.087$	$F = 2.63, P = 0.110$	$F = 0.582, P = 0.449$	$F = 3.18, P = 0.079$
Nitrogen *year	$F = 0.024, P = 0.626$	$F = 3.37, P = 0.071$	**$F = 11.2, P = 0.0014$**	$F = 0.072, P = 0.789$
Precip * year	$F = 0.029, P = 0.595$	$F = 0.070, P = 0.792$	$F = 0.070, P = 0.792$	$F = 0.640, P = 0.427$
Nitrogen *precip *year	$F = 0.0023, P = 0.962$	$F = 5.68, P = 0.454$	$F = 2.75, P = 0.102$	$F = 1.69, P = 0.199$

Results from mixed ANOVA tests ($df = 1, 60$; $n = 64$) comparing each species' cover by treatment (precipitation, nitrogen) and year

Significant results are bolded ($\alpha = 0.05$)

Table 2 Results from analysis of similarity (ANOSIM) of absolute cover (untransformed) and 4th root transformed cover on pre-treatment (2012) and post-treatment species composition data (2013–2014) using Bray–Curtis dissimilarities, including fit (*R*) and significance (*P*)

	Transformed		Untransformed	
	R	*P*	*R*	*P*
2012 August	0.013	0.195	0.004	0.321
2013 June	**0.094**	**0.001**	**0.159**	**0.001**
2013 August	0.007	0.297	0.021	0.135
2014 June	**0.098**	**0.002**	**0.187**	**0.001**
2014 August	**0.065**	**0.005**	**0.061**	**0.005**

Tests are for differences by nitrogen treatment (ambient N vs. low N)

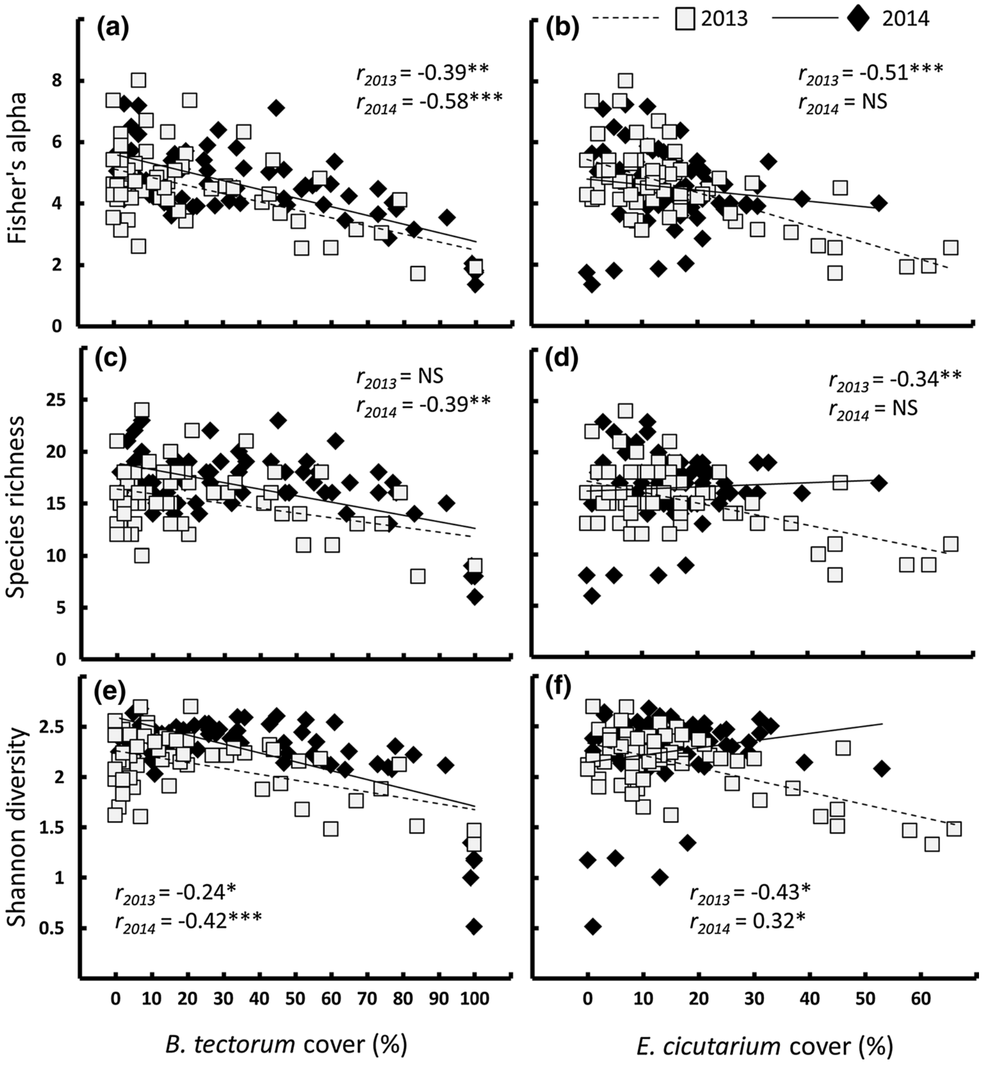
Significant results are bolded ($\alpha = 0.05$)

We evaluated the effect of introduced species cover in the spring on diversity and abundance of warm season species in the summer of the same year. In 2013, cover of dominant forbs and grasses at the site in the spring was relatively strong predictors of diversity and cover of native species during the summer season (Online Resource 3). However, those relationships were either non-significant or introduced species explained very little of the variation of the same diversity indices in 2014.

Discussion

Global change-mediated shifts in climate and nutrients can result in no analog conditions which support novel plant communities comprised of the species present that are best adapted to survive in these new conditions. In support of our hypotheses, we have shown that directional shifts in the Colorado Front Range are indeed facilitating changes in the plant community. Wetter winters coupled with increased nitrogen deposition provide excess resources at a time when cool-season introduced species are active, and are, therefore, able to increase in dominance, resulting in novel communities. In turn, we found that at least some of these species appear to be negatively impacting diversity and cover of native species during the following summer season. However, overall impacts of changing precipitation and soil nitrogen conditions on plant diversity were generally positive (or at least not clearly and consistently

Fig. 4 Relationships between the percent cover of the two dominant introduced species (*B. tectorum* and *Erodium cicutarium*) and diversity indices: **a**, **b** Fisher's alpha; **c**, **d** species richness; **e**, **f** Shannon diversity in spring 2013 (*solid line, diamonds*) and 2014 (*dashed line, squares*). Results from Pearson correlations are reported and *asterisks* represent their significance (*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$, *NS* not significant)



negative, as we predicted). This suggests a scenario in which introduced species initially add to the regional flora without immediate negative effects, but can cause losses in diversity when and where they become dominant. The extreme precipitation event acted to amplify the shifts in plant community composition that were already occurring: the same introduced species that benefit from wetter winters and higher rates of N deposition increased in dominance after the extreme event. Interestingly, we found that native grasses were largely unaffected by both shifting means and extremes, indicating some degree of resistance of native mixed-grass species to global change.

This grassland system recovered quickly from chronic N and changing precipitation conditions. With just 1 year of treatments simulating historic conditions, the plant community began to resemble the historic species assemblage. Although many of the introduced species at the site have occurred in North America for a half century or more, most have just recently become more locally abundant in the Colorado Front Range. Loss of the native seed bank has not occurred, and although it is possible that introduced species are causing changes to soil nutrient cycling or other ecosystem properties, our results suggest that those changes have not been so great as to inhibit native species germination and growth.

We found that native grasses at our site were relatively resistant to changes in shifting resource conditions. The lack of response to nitrogen reduction was somewhat expected, as numerous studies have found native perennial grasses to be favored over introduced exotic species with carbon addition (e.g., Paschke et al. 2000; Blumenthal et al. 2003; Prober et al. 2005). However, we expected that native grass productivity would be affected by inter-annual and treatment differences in precipitation. It is well known that precipitation is an important driver of regional variation in grassland productivity (Sala et al. 1988), and many researchers have found that grasslands can be highly sensitive to changes in magnitude and variability of rainfall from year to year (e.g., Knapp et al. 2001; Lauenroth and Sala 1992). However, others have also found little variation in aboveground grassland productivity in response to rainfall or drought simulations (e.g., Heitschmidt et al. 1999; Frank 2007; Cherwin and Knapp 2011). Like our study, many manipulative climate change experiments in grasslands have been relatively short term and some of the dominant species of these systems are slow to respond to change. One 11-year study found that only after 7 years, the dominant mixed-grass prairie species, *Bouteloua gracilis*, show any response to drought manipulations (Evans et al. 2011), suggesting that native grass decline may occur in the Front Range with on-going change. In contrast to native grasses, we found that native forbs responded negatively to N reduction after just two seasons of treatments. This response was expected, since Front Range species of this group generally favor higher N soils (e.g., Cherwin et al. 2009), and this group has increased in relative cover in other nearby grasslands not impacted by prairie dogs (Beals et al. 2014).

The introduced grass, *B. tectorum,* responded most strongly to changes in resource conditions (both with experimental treatments and the extreme event). This result was consistent with past research, which has shown that *B. tectorum* exhibits "boom and bust" years and can respond rather dramatically to increases in precipitation (Kay 1966; Wei-Ming et al. 2011; Lowe et al. 2003), shifts in precipitation timing and magnitude (Bates et al. 2006; Concilio et al. 2013; Prevéy and Seastedt 2014), and increases in nitrogen availability (Kay 1966; Wei-Ming et al. 2011; Lowe et al. 2003; Concilio et al. 2015). Most research on *B. tectorum* invasion in the USA has been conducted in sagebrush steppe ecosystems of the Intermountain West, where it has come to dominate hundreds of thousands of hectares (Knapp 1996). This region is characterized by cold, wet winters, and hot, dry summers, similar to the climate of *B. tectorum*'s native range (Mack 1981). As a cool-season species, *B. tectorum* can take up soil water and nutrients at a time of year when most native plants in the Intermountain West are still dormant, giving it a competitive advantage and facilitating its spread (Melgoza et al. 1990; Booth et al. 2003). In contrast, precipitation is distributed more evenly throughout the year in eastern Colorado, and *B. tectorum* has historically been much less abundant. Our results provide evidence that the documented increase in *B. tectorum* in the Rocky Mountains and surrounding foothills (e.g., Bromberg et al. 2011; Mealor et al. 2012; Beals et al. 2014) has been facilitated, at least in part, by the concurrent increase in winter precipitation. Notably, *B. tectorum* showed the greatest decreases when both water and nitrogen (N) were reduced, indicating some degree of co-limitation and providing support for our hypothesis that it is the combination of these global change drivers that is facilitating documented changes in the plant community.

As we predicted, the extreme precipitation event acted to increase introduced species cover and productivity at the site. Contrary to our hypotheses, this occurred in both the ambient and low-N plots. Our results from resin bag measurements indicated that substantial inorganic N leached through the top 5 cm of soil during the extreme event. Once soils returned to levels at or below field capacity (i.e., holding the moisture in situ), substantial decomposition and mineralization may have occurred. This N would have been available first to cool-season species in the spring. The fact that productivity of warm-season species was not elevated in the summer of 2014 over 2013 suggests that plants experienced the extreme event as a temporary resource pulse, with little long-term effects. N availability returned to pre-event levels during the following sampling period, indicating that the event may have had a little long-term effect on N dynamics. Interestingly, even though introduced species became more dominant, we measured no loss in absolute cover of native species and species richness actually increased after the extreme event. We identified several new species that we had not previously seen growing at the site. Seeds from upslope may have washed into the meadow, the event may have provided sufficient water to germinate high-moisture requiring seeds that were dormant in the soil seed bank, or both of these activities may have occurred.

We predicted that cool-season introduced species would have similar responses to global change drivers and impacts on the system, but found that they did not act as a unified group. Unlike grasses, introduced forbs did not respond strongly to treatments, and their responses varied by species and year. Of the dominant forbs, only *Alyssum parviflorum* was significantly reduced in the winter–dry precipitation treatment. Unlike the shallow-rooted *Alyssum*, most of the introduced forbs at the site are biennials and may have developed long taproots that allow them to access deeper soil water under drier conditions. The most dominant forb at the site, *Erodium cicutarium*, is an annual species, but it evolved under arid conditions and is known to be relatively drought resistant (Paláez et al. 1995; Cox and Conran 1996; Busso et al. 1998). Consistent with our results, both Paláez et al. (1995) and Cox and Conran (1996) found little to no difference in *E. cicutarium* growth under drought compared with ambient conditions in arid regions of Argentina and Australia, respectively. Introduced forb response to nitrogen reduction was also weaker than the response of *B. tectorum*. This was consistent with results from a meta-analysis by Xia and Wan (2008), which found that grasses generally respond to nitrogen additions with greater productivity increases compared with forbs, and annuals are generally more responsive than perennial herbaceous species. Indeed, we found that the annual forbs *E. cicutarium* and *A. parviflorum* responded to changes in nitrogen more so than did the biennial aster, *T. dubius,* which likely grew a deeper tap root that buffered its response to changes in soil resources.

Impacts of introduced species on biodiversity varied based on species and year, indicating the presence of climate-mediated species interactions. *B. tectorum* cover was negatively related to springtime species diversity, consistent with findings by Prevéy and Seastedt (2014), but the relationship was stronger in 2014 than 2013. This was accompanied by an increase in cover and dominance across the site after the extreme event, suggesting that *B. tectorum* abundance may have increased to the degree that it was causing a decline in rare species in some plots by preempting resources. In addition, our results show an apparent threshold of ~95 % *B. tectorum* cover, above which biodiversity indices plummeted. This occurred in 2014, but not 2013. In contrast, *E. cicutarium* showed the opposite effect—a strong negative relationship to biodiversity in spring 2013 and little to no significant relationship in spring 2014. The effects of introduced cool-season species on diversity and cover of summer-active native plants were consistently negative in 2013. Where these winter-active species are most dominant, they are likely depleting soil nutrients and moisture down to low levels, so that even after their senescence, they may affect summer-active species (Prevéy and Seastedt 2014). In 2014, however, all relationships were weak or non-significant—perhaps because soil moisture was not limiting after the extreme precipitation event. Our results suggest negative interactions among the recently introduced and historically present species, but we have not detected notable losses to biodiversity at the site. Thus, although species assemblages are changing and introduced species are becoming more abundant, significant losses in biodiversity and other ecosystem services may require some disturbance or threshold being passed. This has occurred in nearby grasslands occupied by prairie dogs and may occur, for example, when *B. tectorum* cover increases over 95 %.

In summary, the Colorado Front Range mixed-grass prairie has been experiencing directional shifts in climatic and edaphic conditions via changing seasonality of precipitation and increased anthropogenic nitrogen deposition (Baron et al. 2000; Prevéy 2014). By simulating historical winter-dry, low-nitrogen conditions, we found that modern global changes are very likely to have facilitated the spread some introduced species at the site: the shallow rooted cool-season annual species *B. tectorum* and *A. parviflorum.* These results are noteworthy considering that most research on nitrogen deposition and invasive species has tested potential future changes using fertilization experiments, whereas our research provides causal evidence linking changes in environmental conditions to effects on plant community composition which have already occurred. Consistent with past research, we found that native C_4 grasses were relatively resistant to changes in resource availability. Likewise, we found no evidence that species richness was affected by changing environmental conditions at this site, though we did find negative interactions between some recently introduced and historically present species that appear to be climate-mediated. In sum, on-going shifts in nitrogen deposition and precipitation seasonality are likely to favor some introduced species at the expense of native grasses and forbs with uncertain long-term effects on biodiversity and ecosystem functioning.

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Author contribution statement TRS and JBN conceived and designed the experiments. ALC, SE, and KC performed the experiments. ALC analyzed the data and SE drew the figures. ALC, JBN, and TRS wrote the manuscript; other authors provided editorial advice.

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