

Soil-mediated effects of global change on plant communities depend on plant growth form

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Abstract. Understanding why species respond to climate change is critical for forecasting invasions, diversity, and productivity of communities. Although researchers often predict species' distributions and productivity based on direct physiological responses to environments, theory suggests that striking shifts in community composition could arise if global change alters indirect feedbacks mediated by resources, mutualists, or antagonists. To test whether global change influences plant communities via soil-mediated feedbacks, we grew model communities in soils collected from a seven-year field manipulation of CO₂, warming, and invasion. We evaluated mechanisms underlying variation in the model communities by comparing species' growth in equivalent soil histories with, and without, experimentally reduced soil biota (via sterilization) and nutrient limitation (via fertilization). We show that grasses performed consistently across all soil history scenarios and that soil biota limited grasses more than nutrients. In contrast, forbs were differentially sensitive to soil history scenarios, with the magnitude and direction of responses to soil biota and nutrients dependent upon plant species and global change scenario. The asymmetry in importance of soil history for grasses and forbs is likely explained by differences in life history strategy. We conclude that accounting for species' growth strategies will improve predictions of species sensitivity to altered soil feedbacks in future climates.

Key words: climate change; invasive species; plant functional group; plant growth form; plant–soil feedback; soil nutrients.

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INTRODUCTION

Climate change will alter the outcome of species interactions through initial influences on species physiology (Thomas et al. 2004) and performance of the species in their interaction network (Tylianakis et al. 2008). These initial effects on communities may also promote indirect feedback effects that carry over to influence species

interactions at a later time point (De la Peña et al. 2016, van der Putten et al. 2016). For example, changes in nutrients, antagonists, and mutualists in soil can feed back to influence plant species performance (van Grunsven et al. 2010, van der Putten et al. 2013) and the outcome of plant competition (Chesson 2000, Barot 2004). Such feedbacks could lead to shifts in plant community composition (Meisner et al. 2013) and potentially

loss or gain of biodiversity (Richardson et al. 2000, Suding et al. 2013, Day et al. 2015). Despite the potential importance of global change influences on soil-mediated feedbacks, empirical evidence is scarce (van der Putten et al. 2013), in part, because it can be challenging to tease apart the direct and indirect mechanisms influencing species performance. Desire to forecast, maintain, and restore ecosystem functioning prompts examinations of how indirect effects, such as soil-mediated feedbacks, will influence species growth and the outcome of species interactions in future climates.

Future environments are predicted to have increased atmospheric CO₂ concentrations, warmer temperatures, and more introductions of non-native species (IPCC 2013). By influencing soil nutrients and soil biota, each of these global change factors could alter soil-mediated feedback effects on plant communities (van der Putten et al. 2013, Classen et al. 2015). For example, experimental evidence shows that elevated atmospheric CO₂ often reduces soil inorganic nitrogen (N) concentrations, an effect that has been attributed to increases in microbial N-immobilization (Luo et al. 2004, De Graaff et al. 2006, Dijkstra et al. 2010), which can greatly limit plant growth (Hines et al. 2006). The influences of elevated CO₂ on nutrient availability for plant uptake may be partially offset by climate warming, which can enhance N-mineralization (Bai et al. 2013). However, warming also induces soil desiccation, which can determine whether soil microbial activity results in N-mineralization or N-immobilization (Carrillo et al. 2012), and it can also influence the composition and activity of soil fauna (Hines et al. 2015, Mueller et al. 2016a, McKluney 2017). Notably, soil antagonists and mutualists, which often depend upon abundance of their host plant species (Maron et al. 2011, Bever et al. 2015), show mixed responses to climate (Garrett et al. 2006, Elad and Pertot 2014, Classen et al. 2015). Increases or decreases in abundance of soil biota may parallel or diverge from the influences of global change on resource availability (van der Putten et al. 2016). Consequently, predictions that are based on static measurements of soil nutrients or soil biota alone provide limited evidence about the influence of soil-mediated feedbacks on plant communities. They may over- or underestimate the net effect of

soils on plant communities, depending on how global change drivers affect covariance of soil properties in future. Yet, there have been few comprehensive tests evaluating changes in the relative importance of soil nutrients and soil biota on the growth of plants in communities across a range of global change scenarios.

Responses of plant communities to soil-mediated effects of global change may also depend upon the functional traits of the resident plant species (Meisner et al. 2013, Baxendale et al. 2014). Fast-growing species, for example, may more rapidly obtain nutrients needed for growth, but be poorly defended and more susceptible to increases in antagonists and pathogens than slower growing species with more constitutive defenses (van der Putten 2003, Kulmatiski et al. 2008, Cortois et al. 2016). Such trade-offs in life history strategies have been suggested to explain why stronger negative plant–soil feedbacks consistently limit grasses more than forbs (Kulmatiski et al. 2008). Within different plant growth forms, such as grasses and forbs, growth and defense allocation strategies also vary strongly across species (Herms and Mattson 1992, Kempel et al. 2011, Lind et al. 2013). For example, invasive species that are released from antagonists in their novel ranges may have greater growth advantages in nutrient-rich conditions (Blumenthal et al. 2009). Global changes that enhance resource supply (e.g., climate warming) could then favor fast-growing species when antagonists are rare, but favor better-defended species when antagonists are abundant (van der Putten et al. 2016).

To test whether plant communities are influenced by feedbacks from soil biota and soil nutrients due to global change, we grew model plant communities in soils harvested from a seven-year field manipulation of three factors of global change. Our soil history scenarios included all combinations of elevated atmospheric CO₂, warming, and disturbance–invasion, for a total of eight soil history scenarios. First, we assess plant community biomass in soils from each soil history, which provides a general indication of soil-mediated effects of global change on growth of plants in communities. Subsequently, we evaluate mechanisms underlying soil-mediated effects on plant growth by assessing the proportional change in species performance when soil biota and nutrient limitation are reduced and considering how

these factors covary among species in each environmental context. Examining soil feedbacks at the community level prevents explicit identification of mechanisms driving responses of each species across all soil histories. Yet, this approach allows us to compare which soil history scenarios significantly influence plant communities, and which species and functional groups may be sensitive to soil-mediated effects of global change. Our model communities, composed of eight co-occurring grassland species, allow us to assess the importance of growth form and invasive status (Table 1) for sensitivity to soil-mediated effects. Our focus on grassland plant species is broadly important for understanding maintenance and functioning of plant communities in future, because grasslands currently cover thirty percent of the global land surface (Asner et al. 2004), and grassland productivity is needed to support a diverse array of consumers, including the majority of the world's livestock (Herrero et al. 2013).

MATERIALS AND METHODS

To test whether plant growth in communities is influenced by soil-mediated effects of three leading factors of global change, we conducted a two-stage experiment. In the first stage, soils were established in a seven-year field experiment, which was conducted from 2007 to 2013 in Cheyenne, Wyoming, USA. The design and functioning of the experiment are described in detail in Morgan et al. (2011). Briefly, we simulated eight global change scenarios using a $2 \times 2 \times 2$ factorial split-plot treatment structure with a randomized complete block design. Whole-plot treatment factors include two levels of atmospheric CO₂

(385 ppm and elevated 600 ppm CO₂) and two temperature (T) regimes (ambient and ambient + 1.5/3.0°C day/night). Every whole-plot treatment was replicated five times resulting in 20 experimental plots. Nested within each whole plot, subplot treatments include two disturbance–invasion treatments (ND): an intact, native plant community (N) dominated by perennial grasses and a disturbed-invaded community (D) created by homogenizing the soil to a depth of 10 cm and sowing a mixture of native and non-native dicots (Reeves et al. 2015). Soil from each plot was sampled in the final year of the experiment on 29–30 August 2013, approximately one month after global change treatments were shut off. Soil samples consisted of 12 bulked cores (4 cm inner diameter, 15 cm deep) taken in each experimental plot. Samples were stored for 2.5 weeks at 3.5°C before shipping to Germany for the next stage of the experiment.

In the second stage of the experiment, soil from each field plot was sieved (2 mm mesh) and divided into three parts, each of which was subjected to a soil conditioning treatment (S) designed to test mechanisms underlying soil-mediated effects of global change on plant communities. The first treatment was an unmanipulated control, which we used to assess the net effect of soil biota and nutrients on plant community biomass in soils from each global change scenario. In a second treatment, we experimentally reduced the influence of soil biota in each soil history scenario by autoclaving soils for 3 h at 121°C. Sterilization by autoclaving can result in a pulsed release of nutrients and toxins that would otherwise be immobilized in microbial biomass and dead soil organic material (Alphei and Scheu

Table 1. Characteristics of competitive strategy of the semiarid grassland plant species used in this study.

Species (Abbreviation)	Invasive status	Growth form	Photosynthetic pathway	Dominance	Life span	Seed mass sown (g)
<i>Bromus tectorum</i> (Brte)	Non-native	Grass	C ₃	Dominant	Annual	0.050
<i>Bromus inermis</i> (Brin)	Non-native	Grass	C ₃	Dominant	Perennial	0.100
<i>Bouteloua gracilis</i> (Bogr)	Native	Grass	C ₃	Dominant	Perennial	0.050
<i>Pascopyrum smithii</i> (Pasm)	Native	Grass	C ₄	Dominant	Perennial	0.150
<i>Centaurea diffusa</i> (Cedi)	Non-native	Forb	C ₃	Subdominant	Annual	0.025
<i>Linaria dalmatica</i> (Lida)	Non-native	Forb	C ₃	Subdominant	Perennial	0.010
<i>Grindelia squarrosa</i> (Grsq)	Native	Forb	C ₃	Subdominant	Biennial	0.100
<i>Artemisia frigida</i> (Arfr)	Native	Forb	C ₃	Subdominant	Perennial	0.015

Note: Dominance is assigned based on overall biomass of the species during the seven-year PHACE field experiment (Zelikova et al. 2014, Mueller et al. 2016b).

1993, Trevors 1996), but nutrient pulses can be reduced by flushing the soil (Jager et al. 1969). Therefore, for three weeks before starting the plant growth experiment, we watered microcosms with 50 mL deionized water every second day to leach surplus nutrients or toxins that resulted from the sterilization procedure (see also Manning et al. 2006, Eisenhauer et al. 2009). In a third treatment, we reduced nutrient limitation in each soil history scenario by applying fertilizer (42 μ L of NPK [7 + 3 + 6]; Plantop, Stein, Germany) once a week. These treatment combinations resulted in 24 treatments total, which were replicated five times (8 soil history scenarios \times 3 soil conditioning treatments \times 5 replicates = 120 experimental units). Each experimental unit consisted of a 9 cm width \times 9 cm height square pot, filled with 400 g soil. To facilitate processing of samples, one replicate of each treatment was randomly assigned to each of five blocks that reflect spatial arrangement of the experimental units in environmental chambers.

To establish model plant communities, we planted seeds of eight species (Table 1) in a defined arrangement that exposed all plants equally to neighbors that were found to be dominant and subdominant species during the seven-year field experiment (Zelikova et al. 2014). The timing and quantity of seeds planted in each pot was based on preliminary germination trials performed in a greenhouse at the USDA Agricultural Research Service, Fort Collins, Colorado, USA (K. E. Mueller, *unpublished data*); that is, to reduce competitive advantages for species with seeds with short germination times, the seeds were planted in stages with species projected to germinate slowest being planted first. Further, if species had lower germination rates in preliminary trials, more seeds were planted (see seed mass sown in Table 1), which increased the potential for germination of all species. To focus on soil history effects on plant growth and biomass, we eliminated the potential influence of differences in germination rates by removing all but one individual of each species before the start of the growth experiment. Plants were grown for five months in climate chambers (15–23.5°C, 9-h night/15-h day). During this time, pot locations were re-randomized within blocks every week to exclude potential influence of position within the chamber. Each pot was watered with deionized water every one to

two days to alleviate water limitation. After five months, the total plant biomass (above- and below-ground) was harvested, sorted by species, placed in paper bags, and dried at 70°C for five days before weighing to the nearest milligram.

Statistical analysis

We used factorial mixed models to assess plant growth responses to soils established in global change scenarios. When the response variable was plant community biomass (the sum of all measured species biomasses within a pot), fixed factors included two levels each of the soil history treatments (atmospheric CO₂, temperature, disturbance–invasion) and three levels of the soil conditioning treatment (control, sterilized, and fertilized). Random factors were assigned to account for the split-plot experimental design where the soil conditioning treatments were sampled within disturbance–invasion treatments, which were subplots within the atmospheric CO₂ and temperature treatments applied to experimental rings at the field site.

Because communities biomass can be maintained by changes in performance of particular plant functional groups or species across soil history and soil conditioning treatments, we assessed whether variation in biomass could be attributed to these factors. We started by including plant functional groups (plant growth form and invasive status, see Table 1) as fixed factors in our mixed model. In this test, species identity was included as an independent random factor, and pot was included as the lowest nested random factor to account for non-independence of species growing in the same pot. Subsequently, we tested species identity effects by including species rather than functional groups as a fixed effect, again retaining pot as a nested random factor. When the statistical models indicated that response to treatments depended upon plant functional group or species ($P < 0.05$ for the interaction term), we examined the influence of the soil conditioning and soil history treatments on each functional group or species separately. Biomasses were log-transformed as needed to meet assumptions of homogeneity of variance and normality of residuals.

Next, we more specifically quantified the influence of soil biota and nutrient limitation as mechanisms underlying the influence of soil-mediated effects of global change on plant communities.

When our mixed models indicated that the three soil conditioning treatments influenced a response variable ($P < 0.05$), we calculated the proportional change in species biomass in control compared to experimental soil conditioning treatments (control vs. sterilization, control vs. fertilization, and sterilization vs. fertilization), using log response ratios ($\ln [\text{control}/\text{treatment}] \pm 95\%$ confidence interval (Hedges et al. 1999). This is one of several common methods used for reporting soil feedback effects (Brinkman et al. 2010). We placed treatment in the denominator so that a positive value indicates that the focal mechanism enhanced biomass, a negative value indicates the focal mechanism limited plant biomass, and zero indicates there

was no influence of the focal mechanism on plant biomass. Overall, we calculated 192 species log response ratios based on treatment means (8 soil history treatments \times 3 effect sizes \times 8 species) that summarize 960 species biomass measurements (five replicates of each treatment).

RESULTS

Soil history effects on community production

Plant communities produced similar biomass across the range of soil history scenarios, and the community biomass was influenced by our sterilization and fertilization treatments testing soil biotic and nutrient limitation, respectively (Fig. 1a–c, Table 2). In control soils where plants

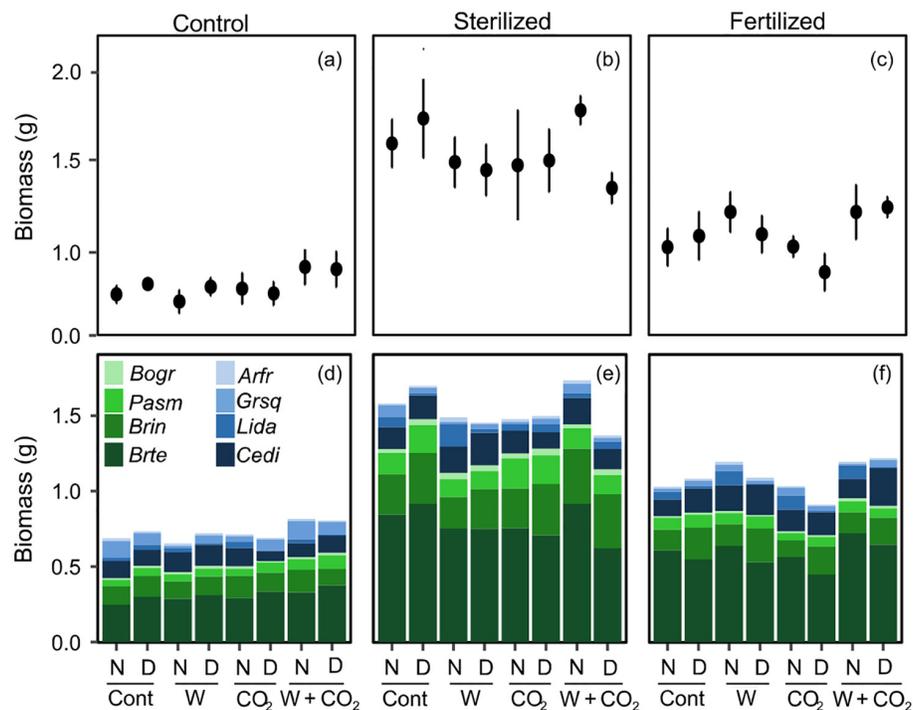


Fig. 1. Biomasses (mean \pm SE, $n = 5$) of model plant communities after five months growing in soils with a history of exposure to a factorial combination of three global change drivers: warming, elevated atmospheric CO₂, and disturbance–invasion (native [N] or disturbed-invaded [D]). Measured biomasses of the whole plant community (a–c) and species-specific contribution to total biomass (d–f) are shown for each of three soil conditioning treatments. Control panels show the net effect of soil biota and nutrient availability on plant biomass in each soil history (a, d). Plant responses to experimental reduction in soil biota and nutrient limitation are shown in sterilized (b, e) and fertilized panels (c, f). Colors indicate plant growth form where grasses are green and forbs are blue. Native species are indicated by lighter shades of each color, and non-native species are shown in the darker shades of each color: non-native grass (*Bromus tectorum*, *Bromus inermis*), native grass (*Bouteloua graciles*, *Pascopyrum smithii*), non-native forbs (*Centaurea diffusa*, *Linaria dalmatica*), and native forbs (*Grindelia squarrosa*, *Artemisia frigida*). Plant species names are abbreviated using the first two letters of the genus name and the epithet.

Table 2. Mixed-model results showing the influence of soil conditioning treatments (S: control, sterilized, fertilized) and soil history with global change scenarios (ND: native or disturbed-introduced plant community), temperature (T: ambient or warmed), and atmospheric CO₂ (CO₂: ambient or elevated) on biomass model plant communities composed of eight North American grassland plant species.

Source of variation	df	F	P
Soil conditioning (S)	2, 64	61.35	<0.0001
Native/disturbed-invaded (ND)	1, 16	0.23	0.64
CO ₂	1, 16	0.00	0.95
Temperature (T)	1, 16	0.70	0.42
S × ND	2, 64	0.18	0.83
S × CO ₂	2, 64	0.20	0.82
S × T	2, 64	1.06	0.26
ND × CO ₂	1, 16	0.75	0.40
ND × T	1, 16	0.56	0.47
CO ₂ × T	1, 16	2.01	0.18
S × ND × CO ₂	2, 64	0.22	0.81
S × ND × T	2, 64	0.60	0.55
S × CO ₂ × T	2, 64	0.07	0.93
ND × CO ₂ × T	1, 16	0.01	0.94
S × ND × CO ₂ × T	2, 64	0.42	0.66

Note: Significant tests ($P < 0.05$) are shown in boldface.

were confronted with the unmanipulated influence of soil biota and nutrient limitation established in the eight soil history scenarios, plant communities produced 0.72 ± 0.02 g (Fig. 1a). When we experimentally reduced soil biota via sterilization, plant communities produced 2.1 ± 0.03 times more biomass (Fig. 1b). Reducing nutrient limitation by adding fertilizer resulted in a 1.6 ± 0.03 -fold increase in community biomass (Fig. 1c). Consequently, the negative influence of soil biota on plant community biomass was 1.4 ± 0.4 times stronger than that of nutrient limitation (Fig. 1b, c).

Soil history effects on grasses

When we considered the contribution of species to the community biomass, we found that plant production depended on species-specific differences (Fig. 1d–f; Appendix S1: Tables S1–S3) that could only partially be attributed to plant growth form and invasive status (Fig. 1d–f; Appendix S1: Tables S4, S5). Grasses were dominant overall, and they established a consistent hierarchy of biomass production across the range of soil history scenarios in control soils (Figs. 1, 2; no significant effect of soil history on production of grass species

considered individually [Table 3] or by invasive status [Appendix S1: Table S5] in control soils). The non-native annual grass species *Bromus tectorum* followed by its non-native perennial congener *Bromus inermis* produced the most biomass, characterizing them as the dominant species in our model communities (Fig. 1d). Native grasses produced 83.2% less biomass than non-native grasses, and among the two native grasses, *Pascopyrum smithii* produced 4.0 ± 0.3 times more than *Bouteloua gracilis* (Fig. 1d).

When we reduced soil biota via sterilization, grass species produced 2.3–2.5 times more biomass (Fig. 1e), showing a consistent negative effect of soil biota on all four grass species' biomasses (Fig. 3a–d). Additionally, one grass species (*P. smithii*) showed sensitivity to soils with a history of warming when soils were sterilized (Fig. 2h; Appendix S1: Table S2; $S \times T$: $F_{2,64} = 7.65$, $P = 0.001$; Table 3), although decreased production in response to history of warming was never strong enough to change its rank among the four grasses in our model communities.

Fertilization usually enhanced biomass of grass species in our model communities, although the magnitude and consistency of this effect depended on species (Figs. 1f, 2c, f, i, l). Nutrient addition benefited the non-native grass *B. tectorum* equally across all soil history scenarios (Figs. 2c, 3i, Table 3). The invasive grass *B. inermis* benefited more from nutrient addition in soils with a history of disturbance–invasion (D) compared to in soils from undisturbed–native (N) communities (Fig. 2f, Table 3). History of disturbance also influenced the native grass *B. gracilis* in fertilized soils, but the presence and direction of the effect depended upon soil history of warming (Fig. 2l; significant $T \times ND$ effect, Table 3). In fertilized soils, *P. smithii* showed non-significant trends toward reduced performance in soils with a history of elevated CO₂ (Figs. 2i, 3k, Table 3). Due to some variation in the magnitude and consistency of nutrient limitation of grasses (Fig. 3i–l), the negative influence of soil biota was always comparatively stronger than the influence of nutrient limitation in all soil history scenarios (Fig. 2q–t).

Soil history effects on forbs

Forb species were subdominant to grasses, producing 43% less biomass than grasses in control soils (Fig. 1d). Forb species did not establish

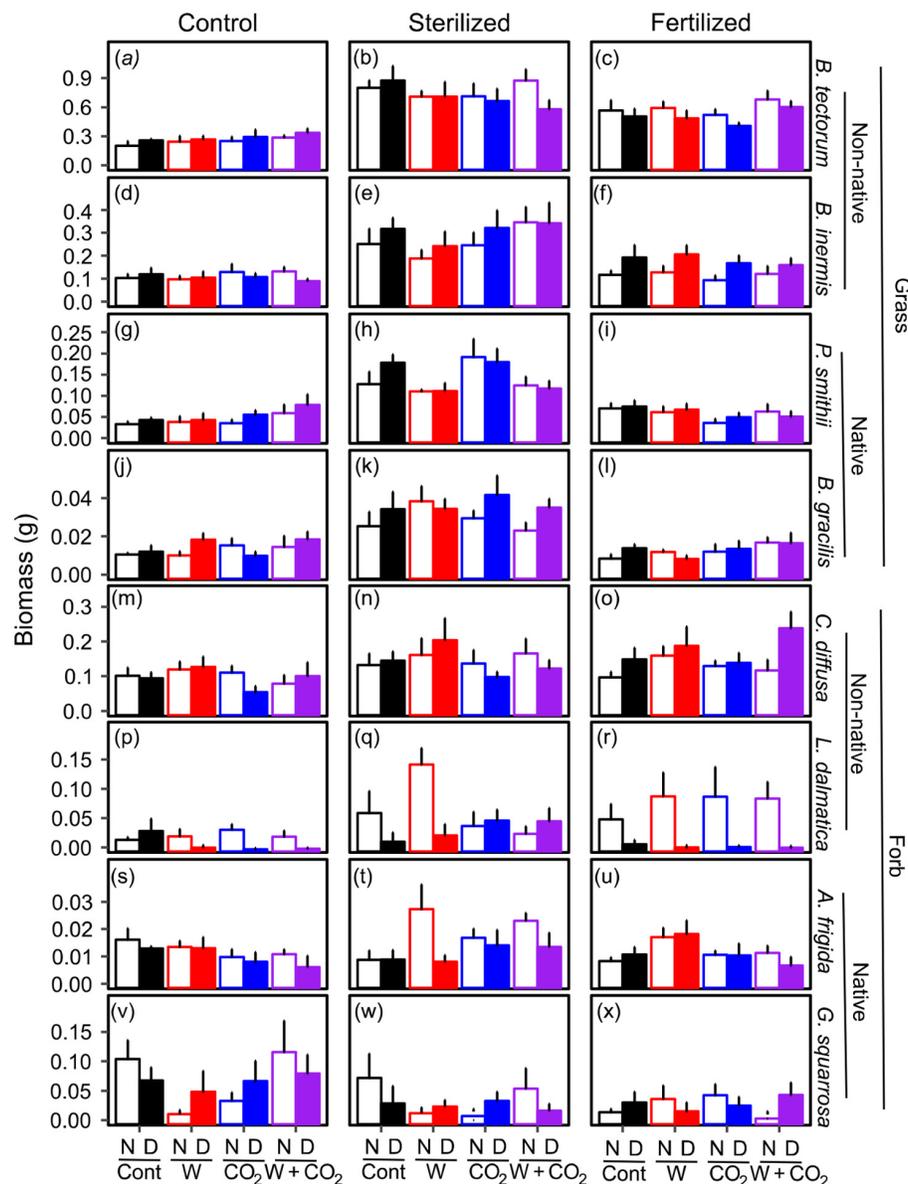


Fig. 2. Biomass (mean \pm SE, $n = 5$) of plant species growing in model communities established in soils with a history of exposure to a factorial combination of three soil conditioning treatments (control, sterilized, fertilized) and three global change drivers. Colors indicate soil history of global change: black, control; red, warming; blue, elevated CO_2 ; and purple, warming + elevated CO_2 . Open bars indicate native soil, and solid bars indicate disturbed-invaded soil.

a consistent dominance hierarchy nor did non-native forb species consistently produce more biomasses than native forb species (Fig. 1d; Appendix S1: Tables S2–S5). Instead, the relative performance of focal species depended upon soil history (Fig. 2m, p, s, v, Table 4). The non-native

Centaurea diffusa showed non-significant trends toward being influenced by CO_2 , but was usually one of the largest forbs (Fig. 1d, Table 3). In four out of eight soil history scenarios, however, its biomass was rivaled by *Grindelia squarrosa*, a native forb that had highly variable production

Table 3. Mixed-model results showing the influence of soil history with global change scenarios (ND: native or disturbed-invaded plant community), temperature (T: ambient or warmed), and atmospheric CO₂ (CO₂: ambient or elevated) on grass species biomass in three soil conditioning treatments (control, sterilized, fertilized).

Source of variation	df	Control		Sterilized		Fertilized	
		F	P	F	P	F	P
<i>B. gracilis</i>							
ND	1, 16	1.02	0.32	3.62	0.08	0.03	0.86
T	1, 16	0.00	1.00	0.11	0.74	0.52	0.48
CO ₂	1, 16	1.28	0.27	0.00	0.95	1.17	0.30
ND × T	1, 16	0.12	0.73	0.16	0.70	4.35	0.05
ND × CO ₂	1, 16	0.62	0.44	1.14	0.30	0.05	0.82
T × CO ₂	1, 16	0.45	0.51	1.88	0.19	1.12	0.31
ND × T × CO ₂	1, 16	0.17	0.68	1.39	0.25	1.42	0.25
<i>P. smithii</i>							
ND	1, 16	0.76	0.39	0.40	0.54	0.22	0.64
T	1, 16	1.15	0.29	5.96	0.03	0.02	0.89
CO ₂	1, 16	0.17	0.68	0.76	0.40	3.24	0.09
ND × T	1, 16	3.91	0.06	1.07	0.32	0.60	0.45
ND × CO ₂	1, 16	0.44	0.51	0.78	0.39	0.00	0.99
T × CO ₂	1, 16	0.00	0.97	0.19	0.67	0.79	0.39
ND × T × CO ₂	1, 16	0.11	0.74	0.77	0.39	0.92	0.35
<i>B. inermis</i>							
ND	1, 16	0.57	0.46	0.04	0.84	10.70	>0.005
T	1, 16	0.12	0.74	0.35	0.56	0.17	0.69
CO ₂	1, 16	0.19	0.67	0.65	0.43	1.00	0.33
ND × T	1, 16	0.75	0.40	1.14	0.29	0.04	0.84
ND × CO ₂	1, 16	1.40	0.25	0.15	0.70	0.01	0.93
T × CO ₂	1, 16	0.06	0.81	0.77	0.39	0.00	0.97
ND × T × CO ₂	1, 16	0.13	0.73	0.07	0.80	0.27	0.61
<i>B. tectorum</i>							
ND	1, 16	2.81	0.11	1.35	0.26	2.83	0.11
T	1, 16	0.75	0.40	0.17	0.69	2.50	0.13
CO ₂	1, 16	1.27	0.28	0.90	0.36	0.14	0.72
ND × T	1, 16	0.05	0.83	0.89	0.36	0.00	0.96
ND × CO ₂	1, 16	0.25	0.63	1.17	0.29	0.00	0.95
T × CO ₂	1, 16	0.19	0.67	0.74	0.40	1.80	0.20
ND × T × CO ₂	1, 16	0.06	0.82	0.28	0.60	0.59	0.45

Notes: Each grass species was planted in a model community composed of eight North American grassland plant species (Table 1). Significant tests ($P < 0.05$) are shown in boldface.

(Fig. 2v, Table 4). The non-native species, *Linaria dalmatica* (Fig. 2p), and the native species, *Artemisia frigida* (Fig. 2s), produced the least biomass of the forbs, and they both performed better in native-undisturbed soils (Table 4; Appendix S1: Table S3).

When soil biota were reduced, *C. diffusa* became the largest forb in seven out of eight soil history scenarios (Fig. 1d), showing that soil biota had consistent, but weak, negative effects on performance of largest forb (Fig. 3e). With comparatively stronger but more variable growth responses, the remaining forb species did

not benefit from experimental reduction in soil biota as consistently (Figs. 2q, t, w, 3f–h), and only *L. dalmatica* was sensitive to soil history in sterilized soils (Table 4; significant ND × CO₂ effect). Consequently, the influence of soil biota on *L. dalmatica* performance in communities ranged from neutral to strongly negative (Fig. 3f). Depending on soil history, the native forb, *A. frigida* (Fig. 3g), performed better, worse, or did not change when soil biota were reduced, whereas *G. squarrosa* (Fig. 3h) was the only species that regularly performed better in communities when soil biota were reduced.

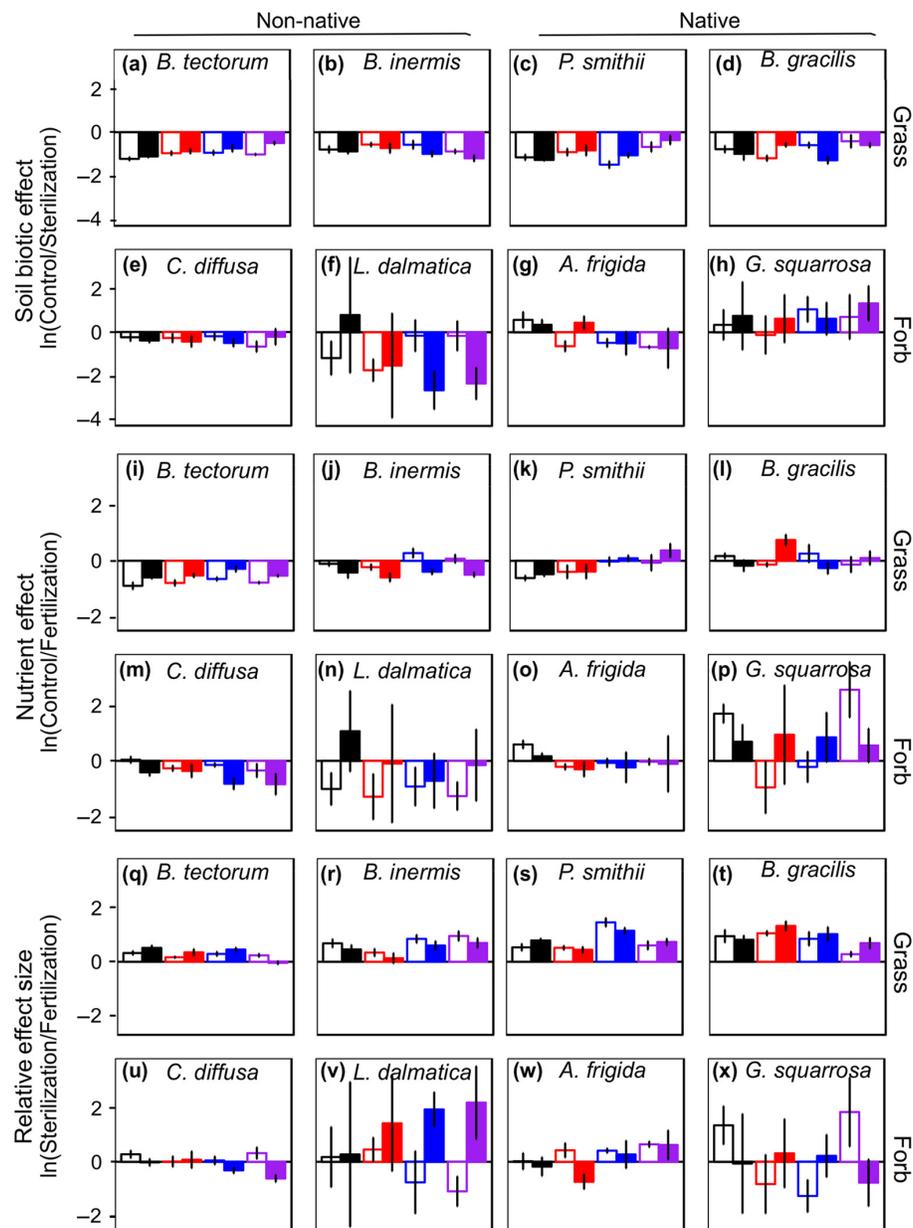


Fig. 3. The influence of soil biota and nutrient limitation on performance of plant species in model communities. Bars show proportional changes in plant species biomass (log response ratio) in unmanipulated soils from each soil history ($\text{CO}_2 \times \text{warming} \times \text{disturbance-invasion}$) compared to biomass in the same soil history where soil biota or nutrient limitation was experimentally reduced. Colors indicate soil history of global change: black, control; red, warming; blue, elevated CO_2 ; and purple, warming + elevated CO_2 . Open bars indicate native soil, and solid bars indicate disturbed-invaded soil.

Nutrient availability had similarly variable effects on forbs (Fig. 1f). For example, nutrient availability limited *L. dalmatica* performance in native soils, but had no effect on its performance

in soils with a history of disturbance/invasion (Figs. 2r, 3n, Table 4; Appendix S1: Table S3). Compared to production in control soils, the performance of native forbs *G. squarrosa* and

Table 4. Mixed-model results showing the influence of soil history with global change scenarios (ND: native or disturbed-invaded plant community), temperature (T: ambient or warmed), and atmospheric CO₂ (CO₂: ambient or elevated) on forb species biomass in three soil conditioning treatments (control, sterilized, fertilized).

Source of variation	df	Control		Sterilized		Fertilized	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>A. frigida</i>							
ND	1, 16	3.08	0.10	2.52	0.12	1.32	0.27
T	1, 16	0.18	0.68	1.03	0.32	0.51	0.49
CO ₂	1, 16	6.41	0.02	2.31	0.14	3.32	0.09
ND × T	1, 16	0.87	0.36	0.72	0.40	0.57	0.46
ND × CO ₂	1, 16	1.68	0.21	0.13	0.73	2.52	0.13
T × CO ₂	1, 16	0.00	0.99	0.11	0.75	3.01	0.10
ND × T × CO ₂	1, 16	0.64	0.43	0.29	0.59	0.11	0.74
<i>G. squarrosa</i>							
ND	1, 16	0.47	0.50	0.03	0.88	0.07	0.79
T	1, 16	1.26	0.28	0.10	0.75	0.77	0.39
CO ₂	1, 16	0.47	0.50	0.00	0.95	0.05	0.83
ND × T	1, 16	0.74	0.40	0.11	0.74	0.03	0.87
ND × CO ₂	1, 16	0.18	0.67	0.32	0.58	0.41	0.53
T × CO ₂	1, 16	5.58	0.03	0.11	0.74	0.10	0.75
ND × T × CO ₂	1, 16	5.75	0.03	1.64	0.22	2.18	0.16
<i>C. diffusa</i>							
ND	1, 16	0.78	0.38	0.03	0.88	1.75	0.20
T	1, 16	0.30	0.59	0.78	0.39	1.26	0.27
CO ₂	1, 16	3.23	0.08	0.55	0.47	0.24	0.63
ND × T	1, 16	1.21	0.28	0.00	0.96	0.16	0.69
ND × CO ₂	1, 16	0.88	0.36	1.66	0.22	0.48	0.49
T × CO ₂	1, 16	0.24	0.63	0.00	0.99	0.03	0.87
ND × T × CO ₂	1, 16	0.78	0.38	0.00	0.98	2.62	0.12
<i>L. dalmatica</i>							
ND	1, 16	25.19	<0.0001	2.68	0.11	22.32	<0.0001
T	1, 16	2.55	0.13	0.71	0.41	0.02	0.90
CO ₂	1, 16	0.33	0.57	0.08	0.78	0.12	0.73
ND × T	1, 16	0.37	0.55	0.48	0.50	0.32	0.58
ND × CO ₂	1, 16	6.59	0.02	5.25	0.03	0.17	0.69
T × CO ₂	1, 16	1.84	0.19	2.33	0.14	0.10	0.75
ND × T × CO ₂	1, 16	6.19	0.02	0.26	0.61	0.04	0.85

Notes: Each forb species was planted in a model community composed of eight North American grassland plant species (Table 1). Significant tests ($P < 0.05$) are shown in boldface, and marginally significant tests ($P < 0.10$) are shown in italics.

A. frigida was enhanced, diminished, or not changed by nutrient availability depending on the soil history scenario (Fig. 3o, p). Consequently, the relative influence of soil biota and nutrients on native forb performance was also variable within and between soil history scenarios (Fig. 3u, v).

DISCUSSION

We found support for soil-mediated effects on plants, but little indication that elevated CO₂, warming, or disturbance–invasion would alter the influence of soil-mediated effects on community production. Our results show that total community

biomass was limited by soil biota and soil nutrients, and the magnitude of these effects was dependent upon plant growth form (grass vs. forb) and invasive status (native vs. non-native). However, only changes in relative biomass of forbs, which contributed little to total community production, were sensitive to soil history of global change in control soils. Across soil histories, increased production of small forb species was balanced by declines in other species, giving only minimal support to the idea that conservation of biodiversity is important to maintain ecosystem functioning across multiple environmental contexts (Isbell et al. 2011). The overall paucity of global change effects

on species in this study suggests that other mechanisms, such as changes in physiology, phenology, or transient effects on soil water and N, explain CO₂ and warming effects on plant communities in the field (Blumenthal et al. 2013, 2016, Reyes-Fox et al. 2014, Mueller et al. 2016b).

The soil-mediated effects on community biomass that we were able to detect were mostly driven by biomass of grasses. Grasses constituted 50–80% of the community biomass in the field (Zelikova et al. 2014, Mueller et al. 2016b), and grasses produced the most biomass in all soil history scenarios in our model communities. Our results show that grasses were consistently limited by soil biota. That the negative effects of soil biota on these productive species were generally not sensitive to soil history scenarios, however, hints that changes in soil biota may contribute little to global change effects on grass production observed in the field (Blumenthal et al. 2013, 2016, Zelikova et al. 2014, Mueller et al. 2016b). The responses of the grasses to nutrients, however, suggest that this may not be the whole story. We found that most grass species were limited by nutrient availability, but one species, *Bromus tectorum*, benefitted most consistently from nutrient addition. This fast-growing non-native grass may preempt nutrient use by slower growing competitors, or more efficiently use the most abundant forms of nitrogen in soil and established their dominance by relegating inferior species to uptake less abundant N forms (McKane et al. 2002, Abraham et al. 2009). Warming and disturbance–invasion usually enhanced N-availability and elevated atmospheric CO₂ usually reduced N-availability of soils in the field (Carrillo et al. 2012, Dijkstra et al. 2012, Mueller et al. 2016b), so we were surprised to observe that production was not more divergent across the range of soil history scenarios we tested in control soils. Because we did observe that grasses (*Bromus inermis* and *Bouteloua gracilis*) were influenced by soil-mediated effects of global change when nutrients were directly added, we suggest that our ability to detect soil-mediated effects of global change on community production in control soils may be influenced by nutrient availability.

To better understand the implications of our results requires consideration of whether soil-mediated feedbacks that could occur in the field were reflected in the biomass of the model plant

communities. Our field-harvested soils collected at the end of the seven-year field experiment could influence plants through cumulative effects of global change on soil biota or capacity for nutrient supply. Other effects of global changes on soils, however, such as differences in soil water or more transient effects on nutrient availability, were likely not captured in this study. For example, precipitation and soil moisture can mediate effects of CO₂ and warming on both plants and soil nitrate availability in the field (Morgan et al. 2011, Hovenden et al. 2014). We watered our model communities weekly, making it likely that our experiment does not capture water-mediated effects of global change. We also collected our soils in a year with high precipitation, when effects of elevated atmospheric CO₂ on soil nitrate and plant growth were relatively small (Mueller et al. 2016b). By capturing a subset of environmental conditions in this experiment, our soils with a seven-year history of eight global change combinations allowed us to separately evaluate persistent effects of soil biota and nutrient limitation and learn that these were less important for community production than other aspects of global change.

We did find evidence that forb species were sensitive to the soil-mediated effects of global change that we captured in this study. *Centaurea diffusa*, which was consistently one of the largest forbs, showed tendency toward being sensitive to CO₂. This response matches CO₂ effects observed for this species in the field (Reeves et al. 2015), but suggests that responses observed in this study were rather weak and context dependent. Notably, reducing soil biota did not promote *C. diffusa* growth as much as it helped other plants, suggesting that soil biota have an overall weaker negative effect on *C. diffusa* compared to the other species. This hints that if soil-mediated effects are important for *C. diffusa* invasion in warmed or elevated CO₂ soil conditions, the extent to which effects are realized could depend upon the composition of the local community.

The remaining forbs were influenced by prior exposure of soils to disturbance–invasion, either directly or interactively with other factors of global change. The most striking differences in growth were seen for *Linaria dalmatica*, which changed from being more nutrient-limited in native soils to more limited by soil biota in

disturbed-invaded soils. The non-native *L. dalmatica* was seeded into disturbed-invaded soils in the field. Therefore, it is possible that in disturbed-invaded soils *L. dalmatica* accumulated host-specific pathogens that did not influence its performance in soils from native plant communities. If so, a temporary escape from negative plant–soil feedbacks might contribute to *L. dalmatica*'s initial success in habitats with native species, but not to its persistence in disturbed patches where it has already invaded.

The native forbs *Grindelia squarrosa* and *Artemisia frigida* frequently performed worse when soil biota were reduced, suggesting either that they depend upon mutualists and beneficial soil organisms that were absent when soil biota were reduced or that they were more strongly inhibited by dominant grasses. Biennial forbs like *G. squarrosa* often invest more resources in root biomass in their first year of growth, and reduced root production could explain why this species was smaller when fertilizer was added. Overall, the native forb species were the most sensitive to soil history treatments, with the magnitude and direction of soil biotic- and nutrient-mediated effects depending on the soil history scenario. Monitoring native forbs in ecological assessments and restorations may provide some warnings of when grasslands are influenced by soil-mediated effects of global change.

Considered together, our results showing community variation in nutrient and soil biotic limitation indicate that mechanisms influencing plant growth may depend on soil history, although this result stems predominantly from responses of forbs rather than grasses. Previous studies have used similar effect sizes as orthogonal axes to test how species in communities differ in their sensitivity to biota (herbivores) and nutrients (Viola et al. 2010). They expected, but did not find, that responses to biota and nutrients would reflect a growth–defense trade-off that was important for the structure and dynamics of plant communities. Lack of support for growth–defense life history trade-offs in their study could be because they did not consider the multiple roles of soil biota (decomposers, pathogens, mutualists) that may also accompany changes in soil nutrients (Suding et al. 2013, Farrer and Suding 2016). We observed that across soil history conditions, forb species simultaneous responses

to both soil biota and nutrient limitation likely reflect the combined effect of many components in the soil community, some of which enhance plant performance while others reduce plant performance. Therefore, despite previous reports showing that elevated CO₂ and warming influence N-mineralization (Nie et al. 2013) and nutrient concentrations (Dijkstra et al. 2012) at our field site, our results suggest that nutrient limitation is not the sole factor influencing changes in soil-mediated effects of global change. Instead, the combined influences of plant–plant and plant–soil biota competition, as well as plant–soil feedbacks, seemed to influence the growth of forb species in our model communities.

Like all experiments, our results should be interpreted with some limitations in mind. The composition of our model communities likely constrains inferences about plant performance that can be drawn from our results. Our model communities always included *B. tectorum* and *B. inermis*, and these two species might have suppressed growth of the native grasses, masking their susceptibility to soil-mediated effects of global change that may occur in the field. For example, *B. gracilis* performs better when surrounded by other *B. gracilis* compared to when it competes with *B. tectorum* (Milchunas and Lauenroth 1995, Lowe et al. 2003), but we do not consider differences resulting from changes in competitive environment by varying different species combinations here. Nonetheless, our findings contribute to the growing body of work identifying soil-mediated effects as an important mechanism influencing plant community dynamics (Classen et al. 2015, van der Putten et al. 2016).

In conclusion, combinations of warming, elevated atmospheric CO₂, and disturbance–invasion have substantially altered water and nutrient availability, soil biota, plant productivity, and the abundance of C₃ grasses, forbs, and invasive species in the field experiment from which we sampled soils for use in our model plant communities (Dijkstra et al. 2010, Blumenthal et al. 2013, 2016, Mueller et al. 2016b). Yet, we found surprisingly few effects of soil history on community biomass in our laboratory experiment, suggesting that soil-mediated feedbacks may be transient, context depended, and reversible if global change factors no longer actively stimulate communities (Rousk et al. 2013). We did find that soil-mediated

feedbacks influence plant biomass production in an important and generalizable way. We show that soil biota consistently limited dominant grasses across all soil legacy scenarios, a particularly pronounced result that is consistent with those of a meta-analysis of 329 experiments showing that grasses generally have stronger negative plant–soil feedbacks than forbs (Kulmatiski et al. 2008). In contrast, the direction and magnitude of soil history effects on the performance of subdominant forb species were much more sensitive to soil history scenarios, identifying them as important indicator species. Considered together with robust field experiments (Morgan et al. 2011), and increases in broadscale efforts to monitor biodiversity (Pereira et al. 2013, Eugene and Loescher 2016), these findings contribute to work designed to quantify and predict mechanisms regulating the production and stability of plant communities in future.

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