Journal of
Plant Ecology

VOLUME 11, NUMBER 3,
PAGES 351–363

JUNE 2018

doi: 10.1093/jpe/rtx015

Advance Access publication
24 February 2017

available online at
academic.oup.com/jpe

Aboveground resilience to species loss but belowground resistance to nitrogen addition in a montane plant community

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Abstract

Aims
Decades of empirical work have demonstrated how dominant plant species and nitrogen fertilization can influence the structure and function of plant communities. More recent studies have examined the interplay between these factors, but few such studies use an explicit trait-based framework. In this study, we use an explicit trait-based approach to identify potential mechanisms for community-level responses and to test ecological niche theory.

Methods
We experimentally manipulated plant communities (control, –dominant species, –random biomass) and nitrogen (N) inputs (control, +organic N, +inorganic N) in a fully factorial design. We predicted that traits related to plants' ability to take up different forms of soil N would differ between dominant and subordinate species, resulting in interactive effects of dominant species loss and N fertilization on plant community structure and function. The study took place in a montane meadow in the Rocky Mountains, Colorado, USA.

Important Findings
After four years, the plant community in removal plots converged toward a species composition whose leaf and root functional traits resembled those of the previously removed dominant species. Ecosystem productivity generally increased with N addition: soil carbon efflux was ~50% greater when either form of N was added, while inorganic N addition increased aboveground biomass production by ~60% relative to controls. The increase in production was mediated by increased average height, leaf mass:area ratio and leaf dry matter content in plant communities to which we added inorganic N. Contrary to our predictions, there were no interactive effects of N fertilization and dominant species loss on plant community structure or ecosystem function. The plant community composition in this study exhibited resistance to soil N addition and, given the functional convergence we observed, was resilient to species loss. Together, our results indicate that the ability of species to compensate functionally for species loss confers resilience and maintains diversity in montane meadow communities.

Keywords: dominant species, fertilization, functional trait, removal experiment, resilience

Received: 26 August 2016, Revised: 14 February 2017,
Accepted: 23 February 2017

INTRODUCTION

The structure of plant communities and the traits of the individual plants in those communities are important predictors of ecosystem function (Lavorel 2013). For example, plants may differ in their ability to access the resource that most limits individual growth, and access to those resources may change over time or with changes in community composition (Farrior *et al.* 2013; Suding *et al.* 2004), in turn leading to changes in ecosystem function and nutrient constraints over time. The species that is the best competitor for the most limiting resource has the potential to achieve the highest abundance within the community (Gilman *et al.* 2010; Tilman 1977), thereby becoming a 'dominant' species (Souza

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et al. 2011). Measuring plant functional traits such as leaf and root morphology, plant size and nutrient content captures variation among plants in life history, competitive ability (Levine and HilleRisLambers 2009), environmental tolerance (Sundqvist *et al.* 2011) and resource uptake strategy (Reich 2014; Violle *et al.* 2007). These differences among individuals determine the outcome of the abiotic (Pavoine *et al.* 2011; Stahl *et al.* 2014) and biotic (Freschet *et al.* 2015) processes that shape abundance distributions of plant communities (Adler *et al.* 2014), in turn leading to variation in ecosystem function (Cornelissen *et al.* 2007; Reichstein *et al.* 2014). In this study, we tested how resource availability and species dominance influence—separately or together—structure and function in plant communities.

Biotic interactions, positive or negative, can influence plant trait expression as well as community structure (Wisz *et al.* 2013). In particular, differences in relative abundance within communities are often attributed to relative fitness differences, or a fitness hierarchy among species (HilleRisLambers *et al.* 2012). Even though the maintenance of diversity in plant communities depends on sufficient stabilizing niche differences among species (Kunstler *et al.* 2012), the net outcome of biotic interactions in communities often results in abundance distributions dominated by a few species at the top of the fitness hierarchy. We know that small changes in the relative biomass of abundant species can have large effects on ecosystem functioning (Grime 1998; Gaston and Fuller 2008). However, we do not yet know whether the response of subordinate plant species to removal of competitively dominant plant species will also alter ecosystem function (Díaz *et al.* 2003; Souza *et al.* 2011; Wardle *et al.* 1999; Wardle and Zackrisson 2005).

When a community of organisms is subjected to change, it can exhibit resistance, the lack of a response in composition or function, or resilience, initial change followed by a return to the previous state after some time (Harrison 1979). The capacity of an ecosystem to resist or be resilient to change is dependent on the traits of the individual organisms (Enright *et al.* 2014; MacGillivray *et al.* 1995). In particular, traits associated with stress tolerance may promote resistance. For example, nutrient stress tolerance predicted resistance to damage from frost and drought in an herbaceous plant community (MacGillivray *et al.* 1995). Conversely, traits associated with rapid growth and resource acquisition may promote resilience. For example, vegetative regrowth was associated with resilience after fire events in shrublands (Enright *et al.* 2014). Furthermore, the insurance hypothesis predicts that high functional redundancy in diverse communities may lead to increased resilience, since the loss of individual species can be compensated for by functionally similar species (Pillar *et al.* 2013).

Variation in root physiological traits and root microbiome may make some species better than others at accessing inorganic nitrogen or at cultivating symbiotic microbes that can break down organic N molecules in the soil. For example, in a European grassland, the specific root length and chemical traits of plant roots predicted the nitrification potential and NH_4^+ affinity of the associated microbial community (Cantarel *et al.* 2015). The variation in root traits and associated microbial communities has the potential to influence community structure and community responses to addition of N in different chemical forms (Harpole and Suding 2011). The resource-ratio theory (Miller *et al.* 2005; Tilman 1980) predicts that the species with traits that confer the ability to most efficiently take up limiting soil resources will have highest abundance in a community. Because species dominance should be related to the ability to most efficiently take up limiting soil resources, we tested the theoretical prediction that the plant community should respond differently to the presence of a dominant species across different levels of nitrogen fertilization. However, if the community response to the dominant species does not depend on soil N addition, it would indicate that the processes that generate community structure do not depend on traits that determine plants' ability to take up soil N, and that the community is resistant to N-induced changes with or without the dominant species.

While many experimental and observational studies have focused either on the role of competitive interactions in structuring plant communities (Callaway *et al.* 2002; Choler *et al.* 2001; Levine and HilleRisLambers 2009) or on the effects of varying soil resource availability on community and ecosystem processes (Baribault and Kobe 2011; Suding *et al.* 2006), few studies have experimentally tested whether these two processes interact (Farrer and Suding 2016; Gundale *et al.* 2012; Lepš 2004) or used plant traits to predict community-level resistance or resilience to these changes. Here, we examine both the effect of dominant species and partitioning of different forms of N using a factorial experiment in which we crossed the removal of the most abundant plant species, *Festuca thurberi* Vasey (Thurber's fescue), with N addition in two different forms.

In this study, we asked the following questions:

- Do organic and inorganic N fertilization differ in their effects on plant species diversity, community-level functional trait composition, and C storage and turnover in a montane meadow?
- Does the presence of a dominant tussock grass species, *Festuca thurberi*, affect the species diversity and functional trait composition of the remaining plant species in the community, and does this species affect C storage and turnover in the community?
- Are the effects of the dominant grass species on the plant community and on C cycling contingent on soil N addition? Do soil N addition and dominant plant species interact to determine plant species diversity, functional trait composition and C storage and turnover?

METHODS

Site description and natural history

In the summer of 2012, we established 36 permanent 1.5 × 1.5 m plots in Maxfield Meadow, a montane meadow

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in the West Elk Mountains near the Rocky Mountain Biological Laboratory in Gothic, Colorado, USA (38°56′58″N, 107°59′34″W), at 2910 m above sea level. The site has been historically grazed by a low number of cattle and experiences herbivory by pocket gophers (Cantor and Whitham 1989) during summer, and there is regular avalanche activity during winter. The most abundant plant species found in the meadow is *Festuca thurberi*, a large, sturdy perennial tussock grass (Poaceae). *Festuca thurberi* is functionally distinct from all the other common species in this montane meadow community (Fig. 1), with significantly higher leaf mass:area ratio (LMA), higher root mass:length ratio (RML) and lower root N:P ratio. Other abundant species include *Helianthella quinquenervis* (Hook.) A. Gray, *Erigeron speciosus* (Lindl.) DC., *Heliomeris multiflora* Nutt. (Asteraceae) and *Bromopsis inermis* (Leyss.) Holub (Poaceae).

Study design and treatments

We set up a fully factorial experiment ($n = 4$) crossing N addition and dominant species removal; treatments were begun in 2012 and continued through 2016. The three N treatment levels were the addition of 10 g organic N m^{-2} y^{-1} (as 21.7 g urea, $CO(NH_2)_2$), addition of 10 g inorganic N m^{-2} y^{-1} (as 29.4 g ammonium nitrate, NH_4NO_3) and no N addition. In 2013 and 2014, we watered all plots, including controls, as we fertilized them, but in 2015 and 2016 we synchronized fertilization with a rain event. There were three levels of the species removal treatment: fescue removal, random biomass removal and intact control plots. In the fescue removal treatment, we removed all aboveground biomass of the most abundant species (*F. thurberi*) within the 1.5 × 1.5 m plot. The random biomass removal plots control for any potential effects of removing aboveground plant biomass that are not specific to fescue. In the random biomass control plots, percentage fescue cover was recorded before removal, and an equivalent amount of vegetative cover was randomly selected from among all species in the plot, including fescue, and removed. In plots assigned to the intact control treatment, we removed no biomass. After removing and bagging aboveground fescue biomass, we applied a dilute mixture of glyphosate herbicide to the clipped *Festuca* stem bases with a paintbrush to kill the belowground portion of the plant. Glyphosate herbicide was also applied to stem bases of large removed individuals in random removal plots. The removals were effective, and the treatments did not have to be renewed in subsequent years.

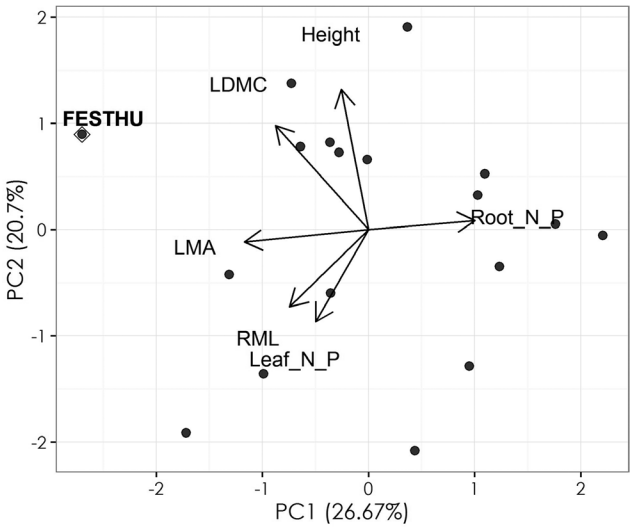

Figure 1: trait ordination of the most abundant plant species in the Maxfield Meadow plant community. Each point represents the mean trait value for a single species in the space defined by the first two principal component axes of the trait ordination, which collectively explain 47.4% of among-species trait variation. Labelled arrows represent the axis loadings for each trait, proportional to the length of the arrow. The location of the dominant species, *Festuca thurberi*, is highlighted with a diamond and labelled FESTHU to show its extreme trait value within the community, especially along axis PCA1.

Dry mass of removed vegetation did not differ between fescue removal and random removal plots (unpaired *t*-test: $t_{17.6} = 1.235$; $P = 0.233$). In addition, while removal treatments initially decreased vegetative cover, other species replaced *Festuca*. No *Festuca* was observed to have grown back in fescue removal plots. Percent plant cover was not significantly different between removal treatments at the peak of the growing season in 2016, four years after the initiation of the experiment (analysis of variance [ANOVA]: $F_{2,33} = 0.075$; $P = 0.93$).

Plant community structure and function

Community composition and diversity

We measured all response variables within the central 1 × 1 m area of each plot, including plant community composition, soil moisture, soil respiration and leaf area index (LAI). We used percentage aboveground cover of each plant species, estimated visually (to within 1% if ≤10%, and to within 5% if greater), as a proxy for abundance in the plant community composition measurements. We recorded community composition once in June 2012 prior to fescue removal, twice after removal during the growing season of 2012, and twice during the growing seasons of 2013, 2014, 2015 and 2016.

Plant functional trait composition

In 2015, we collected leaf samples from five individuals of each of the 10 most common species at the site, from individuals not in the experimental plots but within 20 m of at least one plot. We also measured the heights of all individuals from which we collected leaves perpendicular to the ground from the base of the stem to the tip of the topmost leaf. We also collected root samples from each individual from which we collected leaves. The plant tissue samples were used to measure LMA, RML and leaf dry matter content (LDMC). As part of a related study, at other sites located within ~5 km of the present study site, we also measured the same traits on individuals from eight of the other species found within the present study plots. We augmented the trait dataset we

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collected directly adjacent to the study plots with the data collected from the individuals from nearby sites, yielding a total of 18 species. Our inferences about functional trait responses of the plant communities within the experimental plots are based on the assumptions that individual variation within species in response to the treatments is negligible: the functional trait responses are calculated from changes in relative cover of the species within the plots, given the average trait values for each species that we measured.

We collected at least three mature and fully expanded leaves from each of the individuals that we sampled for leaf traits. We transported the leaves on moist paper towels and scanned them on a flatbed scanner (Perfection V600, Epson Corporation, Suwa, Japan). We weighed the scanned leaf material, dried it for at least 48 hours at 60°C, and weighed it again. We saved the dried leaf material and pooled it with additional leaves that were collected for chemical analysis (see below).

We took two to four 2.5-cm diameter, 15-cm long soil cores from directly below the base of each individual plant that we sampled for root traits. If individuals were small enough, we uprooted the entire individual to ensure that we obtained roots only from the target individual, but for larger individuals, we assumed that most roots in the core were from the target individual. We extracted as much fine root material as possible from the soil cores, washing the soil over a 2-mm sieve if necessary. We scanned 10 to 20 intact pieces of fine root from each individual on the Epson flatbed scanner after floating the root pieces in a transparent tray of water (Pérez-Harguindeguy *et al.* 2013). We dried the root material for 48 hours at 60°C and weighed it to calculate dry mass. We saved the dried root material and pooled it with additional collected roots for chemical analysis.

To measure total Kjeldahl N and phosphorus (P) content by mass of the dried tissue samples (both leaf and root; Pérez-Harguindeguy *et al.* 2013), we first ground the tissue samples with a mortar and pestle. We weighed at least 20 mg or up to 75 mg, if available, of the ground sample and folded it into a piece of adhesive-free cigarette paper. We digested the sample for 5 h at 350°C in 5 ml H_2SO_4 in a Kjeldatherm digestion block (Gerhardt, Königswinter, Germany); in each digestion run we included a blank with no sample, and one sample of apple leaf standard with known N and P content. After the digests cooled, we added 45 ml deionized water to each one. We used a SmartChem 200 discrete analyser (Unity Scientific, Brookfield, CT, USA) to measure total Kjeldahl N and P, expressed as a proportion of total tissue mass.

We measured the area of the scanned leaf images, and the total length of the scanned root images, with ImageJ software (Schneider *et al.* 2012), using the IJRhizo macro (Pierret *et al.* 2013) to automatically trace all the roots in each image. We calculated LMA for each individual plant by summing the mass and area of each individual dividing the dry mass by the scanned area. LDMC was calculated as the dry leaf mass divided by the leaf mass before drying. We calculated RML for each individual plant by dividing dry root mass by the total root length.

Trait sampling within the study plots

Our destructive and non-destructive trait measurements were taken on individuals growing outside the experimental plots to minimize disruption to the ongoing experiment. However, we also measured a subset of non-destructive aboveground traits on selected individuals within the experimental plots to determine whether individuals showed leaf trait plasticity in response to dominant species removal and N addition. In July 2016, we measured the heights and collected leaves from 5 individuals, sampled randomly irrespective of species, within each plot. We measured LMA and LDMC on these leaves, using the methods described above.

Carbon storage and turnover

We used a LI-6400 gas analyser (Li-Cor Corporation, Lincoln, NE, USA) to measure soil respiration in June and July of 2012, 2013, 2014 and 2015. Permanent PVC soil collars for respiration measurement were placed inside each plot near the edge of the central area. We measured LAI at the peak of the growing season (late July or early August) during 2013, 2014 and 2015. The LAI results presented here from 2015 were taken with an Apogee MQ-200 light sensor (Apogee Instruments, Logan, UT, USA). To confirm that LAI is a good proxy for standing aboveground plant biomass, we collected standing aboveground biomass from six sites in the region, including our study site. We selected these sites to capture most of the regional variation in LAI. At each site, we measured the LAI in 5 randomly selected plots 0.25 m^2 in area, removed all aboveground plant biomass from the plots, dried the biomass for 48 h at 60°C and weighed it. The biomass across sites varied ~7-fold; the mean biomass at a site was very closely correlated to the mean LAI at that site ($R^2 = 0.92$).

Data processing and analysis

All analyses were conducted in R 3.3.1 (R Core Team 2016), with packages listed where appropriate. We excluded *Festuca* from the diversity metric calculation because it was physically removed from some of the plots, and we were interested in assessing the diversity of the remaining community. However, for the functional diversity, community-weighted trait mean, and community-weighted trait variance calculations, *Festuca* was included to investigate how the entire community's function changed with the removal of *Festuca* and whether communities where *Festuca* was removed would converge functionally on intact communities. The analysis of trait convergence through time is based on community data collected from 2012 to 2016.

Calculation of diversity metrics

We calculated species diversity metrics for each treatment combination (Jost 2007). We converted Shannon's alpha diversity (H′) to first-order effective species number (d_1) using

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the formula $d = \exp(H')$. For a particular community, the effective species number is the number of species in a community of maximum evenness that would be required to attain an equivalent value of Shannon's diversity. We excluded *Festuca* from the calculations of effective species number.

We also calculated functional diversity in each plot by taking the mean trait value for all species for which we have trait data (19 species, comprising all dominant and most subordinate species, with a median of 93% of the plant cover in each plot, and over 80% in all but one plot). For each of these species, we used the trait values of LMA, RML, LDMC, leaf N:P ratio, root N:P ratio and plant height. We calculated the pairwise Gower distance between each pair of species and used these distances to estimate an index of functional dispersion (FDisp) for each plot. For this calculation, we used the *gowdis* and *fdisp* functions in the *FD* package in R.

Calculation of community-weighted trait means

We calculated community-weighted means (CWMs) and community-weighted variances (CWV) for LMA, RML, LDMC, leaf N:P ratio, root N:P ratio and plant height for each of the 36 experimental plots. In addition, we ran a principal components analysis on the six traits using the *prcomp* function in R (Fig. 1), and calculated CWM and CWV for the first principal component axis. CWMs are calculated by taking the mean trait value for the 10 species for which we have trait data and calculating a mean trait value for each of the 36 plots weighted by the relative cover of each plant species; variance is calculated in a similar way. We calculated CWM and CWV both with and without *Festuca*, to distinguish changes caused by the loss of the species from changes caused by the differential response of species with different functional traits.

Statistical analysis

We assessed the effect of the fertilization treatments, the removal treatments, and their interaction on taxonomic diversity, functional diversity and functional trait means with a linear model (ANOVA). For the analyses of LAI and soil respiration, we fit a repeated-measures mixed-effects model to the peak-season response variables from 2013, 2014 and 2015 to incorporate interannual variation into the responses. In the repeated-measures models, we included year as an additional fixed effect with a random intercept for each study plot. Finally, we asked whether treatment-induced changes in LAI and soil respiration were mediated by changes in community-weighted trait means in treatment plots relative to the control; we tested this by fitting an additional repeated-measures mixed-effects model, regressing change in LAI or soil respiration on change in trait mean. We visually examined all residual plots for normality to ensure that parametric analysis of untransformed data was appropriate. For all models, including both ANOVAs and mixed models, we fit the full model with both main effects and their interactions, then fit all possible subsets of that model and compared their AICc scores using the *dredge* function from the *MuMIn* package. Models with an AICc value within two of the lowest value were considered to be the best models. We fit the mixed models with the *lmer* function in the *lme4* package. We used a bootstrap procedure with 999 iterations to find 95% confidence intervals around parameter estimates (*confint.merMod* and *confint.lm* methods), and used the *r.squaredGLMM* function in the *MuMIn* package to find the proportion of variation explained by the fixed effect. As a *post hoc* test for differences among treatment means, we calculated the least-square means for each treatment combination and marginal least-square means for each single treatment, along with their standard errors and 95% confidence intervals using the *lsmeans* function from the *lsmeans* package. To determine whether variation in community structure was explained by the treatments, we ran 9999 iterations of a permutational ANOVA (PERMANOVA; Anderson 2001) for both the early-season and peak-season time points, excluding *Festuca*. This test, implemented in the *adonis* function in the *vegan* R package, partitions variance in ecological community datasets similarly to a multivariate ANOVA.

In addition to comparing means across treatment groups for the 2016 growing season, we also investigated whether the plant community in plots where *Festuca* was removed converged functionally over time toward intact control plots where no species was removed. We used the plot-level values of the six trait CWMs of each removal treatment group (intact control, *Festuca* removal and random biomass removal), pooled across all fertilization treatments, for the peak growing seasons in each of the five years since treatments were established (2012–2016), as well as the first principal components axis. Within each year, we subtracted the median CWM value of the intact control group from the plot-level CWM values of the *Festuca* removal group and from the random removal group. For each of the two removal groups, we regressed the difference relative to the control against the number of years since treatments were established in a mixed-model framework with plot as a random effect. A difference between CWMs trending toward zero over time would indicate that the mean trait value of the community without *Festuca* is converging on the mean trait value of the community with *Festuca*, presumably because other species are increasing in relative abundance to fill the niche space left by the removal of *Festuca*. We fit the mixed model and then found the confidence interval around parameter estimates as described above.

Finally, we determined whether any species exhibited plasticity in height or leaf traits in response to the treatments by fitting a linear mixed-effects model to the individual height and leaf trait measurements collected in 2016 within the plots, treating the removal treatment, the fertilization treatment, and their interaction as fixed effects, and species identity as a random effect. As above, we used a bootstrap procedure with 999 iterations to find 95% confidence intervals around parameter estimates from the mixed models.

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RESULTS

Plant community structure and function

Community composition and diversity

Species richness ranged between 8 and 16 species in the 1 × 1 m plots, with no significant difference in richness among treatments. There was no significant difference in species diversity among any of the treatments in 2016 (null model was selected by AICc). In addition, community structure, as measured by turnover in species identity, did not respond either to fertilization or removal (PERMANOVA; fertilization, $P > 0.1$; removal, $P > 0.1$). In contrast, functional diversity (FDisp) was 16% lower in *Festuca* removal plots relative to intact control plots ($P = 1.1 \times 10^{-5}$, $R^2 = 0.454$, ΔAICc of best model = −16.87 less than null model; Fig. 2). However, functional diversity was not significantly lower in random biomass removal plots compared to intact control plots. There was no interactive effect of the treatments on species diversity or functional diversity.

Plant functional trait composition

The functional composition of plant communities in 2016 differed across removal treatments as well as fertilization treatments, for some traits. Dominant species removal was associated with a decrease in the CWM of LMA (ΔAICc = −2.38; see online supplementary Fig. S1a) and RML (ΔAICc = −11.56; see online supplementary Fig. S2a). These differences exist because *Festuca* has higher LMA and RML than most other species in this system. Plant height was greater in plots with added organic N (ΔAICc = 1.81; see online supplementary Fig. S3a). Neither removal nor N addition treatment was associated with any change in the CWM of LDMC (see online supplementary Fig. S4a), leaf N:P ratio (see online supplementary Fig. S5a), or root N:P ratio (see online supplementary Fig. S6a). Removing *Festuca* caused the plant community to have a 15% lower LMA ($P = 0.01$; $R^2 = 0.184$) and 23% lower mean RML ($P = 0.0002$; $R^2 = 0.368$), and organic N fertilization was associated with a 23% increase in mean height ($P = 0.02$; $R^2 = 0.171$). In all cases, the coefficient associated with random biomass removal was not significantly different from zero. Again, there was no interactive effect of treatments on functional trait means. When *Festuca* was excluded from this analysis, species removal was not retained as a predictor in any model, indicating that there were no net changes in traits of the subordinate community as a result of removal after four years, although fertilization effects on trait means were qualitatively similar with or without *Festuca*.

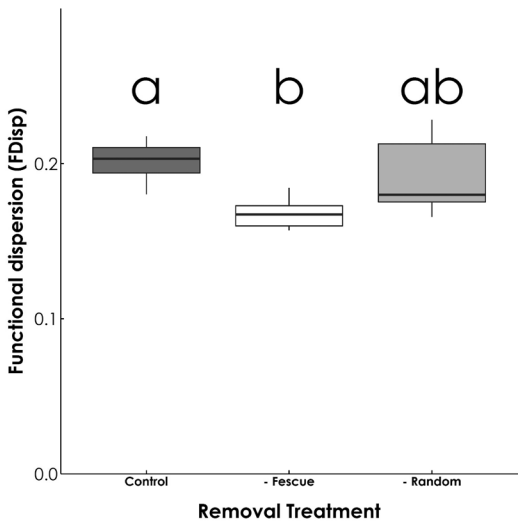

Figure 2: boxplots of functional dispersion (on *y*-axis; in PCoA axis units) by removal treatment (*x*-axis) in July 2015. The intact-community control is shown in dark grey, fescue removal treatment in white and random removal treatment in light grey. The central line of each boxplot is the median value for experimental plots in each treatment group, the bottom and top hinges are the 25% and 75% quantile values, respectively, and the whiskers extend 1.5× the width of the interquartile range. All points outside this range are plotted as outliers. Different letters indicate removal treatments that significantly differ from one another (*post hoc* comparison of least-square means across all levels of fertilization treatment). The fescue removal treatment has significantly lower functional dispersion than the control.

Paralleling the overall decrease in FDisp, the variance in RML also decreased in the absence of *Festuca*. CWV of RML decreased by 53% ($P = 0.02$; $R^2 = 0.172$; see online supplementary Fig. S2b); this translated to a significant 54% decrease in the CWV of the first principal component trait axis ($P = 4 \times 10^{-7}$; $R^2 = 0.569$). Organic N fertilization increased the variance of plant height by 127% ($P = 0.003$; $R^2 = 0.243$; see online supplementary Fig. S3b), and inorganic N fertilization increased the variance of root N:P ratio by 31% ($P = 0.04$; $R^2 = 0.146$; see online supplementary Fig. S6b). Again, removal effects were much weaker when *Festuca* was excluded from analysis, but fertilization effects were qualitatively similar.

Trait convergence

The lack of difference in community-weighted traits between control and removal plots may be because the remaining plant community had converged toward the trait value of *Festuca* in removal plots. The CWM of the principal trait axis in *Festuca* removal plots increased relative to control plots from 2012, just after *Festuca* removal, to 2016, four years after removal (Fig. 3; 95% confidence interval of slope [0.062, 0.159]; $R^2_{\text{marginal}} = 0.10$), indicating that the community trait value in *Festuca* removal plots was converging on the pre-removal value. No significant trend in the CWM of random biomass removal plots was observed (Fig. 3). This change was driven by significant increases over time in LDMC, RML, and height, and a significant decrease in root N:P ratio (see online supplementary Fig. S7), all of which indicate that the community trait means of the removal plots were becoming increasingly *Festuca*-like over time. In particular, the species most similar to *Festuca* along the first principal component axis increased in abundance, including *Heliomeris multiflora* and *Poa pratensis*, while dissimilar species like *Elymus glaucus*, *Bromopsis inermis* and *Erigeron speciosus* decreased in abundance. In contrast, *Helianthella quinquenervis* increased in abundance with

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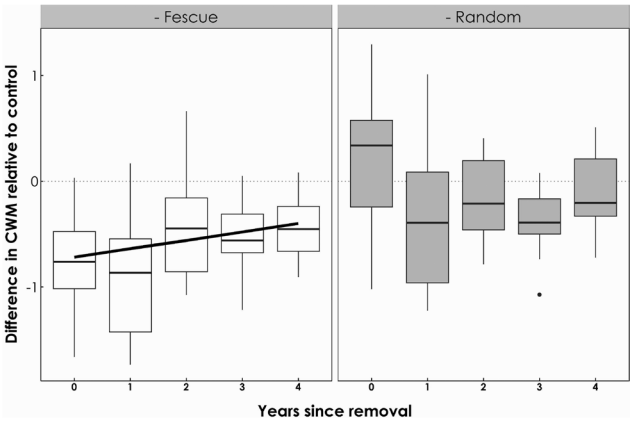

Figure 3: trait convergence since dominant species removal. Differences between removal and control treatments along the first principal components axis, encompassing 27% of trait variation, are shown on the *y*-axis. For each year and removal treatment, a box-and-whisker plot (with dimensions as in Fig. 2) shows the distribution of differences between the removal treatment and the median value of the control treatments. The solid line on the fescue removal panel shows a significant convergent trend toward the weighted-mean trait value of undisturbed control plots; no such trend was observed in random biomass removal plots.

Festuca removal but is relatively functionally dissimilar to *Festuca*. Despite this anomaly, overall the species most similar to *Festuca* increased in abundance. There were no trends over time within fertilization treatments, and no significantly convergent trends within the random biomass removal treatment (see online supplementary Fig. S7).

Finally, we found no within-species plastic response in LMA (Fig. 4a and b) or LDMC to any of the treatments; 95% confidence intervals overlapped zero in both cases. However, we did observe a small but significant increase in height of individuals in the inorganic N fertilization treatment ($R^2_{marginal}$ = 0.04; Fig. 4c and d), corresponding to an average increase of about 10 cm per individual (95% confidence interval [2.5, 17.6]). Other than increased height due to N fertilization, these results indicate that there was negligible within-species trait variation due to treatments, and that the responses due to varying species abundance across treatments describe the functional response of the community to our treatments.

Carbon storage and turnover

Leaf area index

From 2013 to 2015, LAI, a reliable proxy for standing aboveground biomass in our study system (see Methods above),

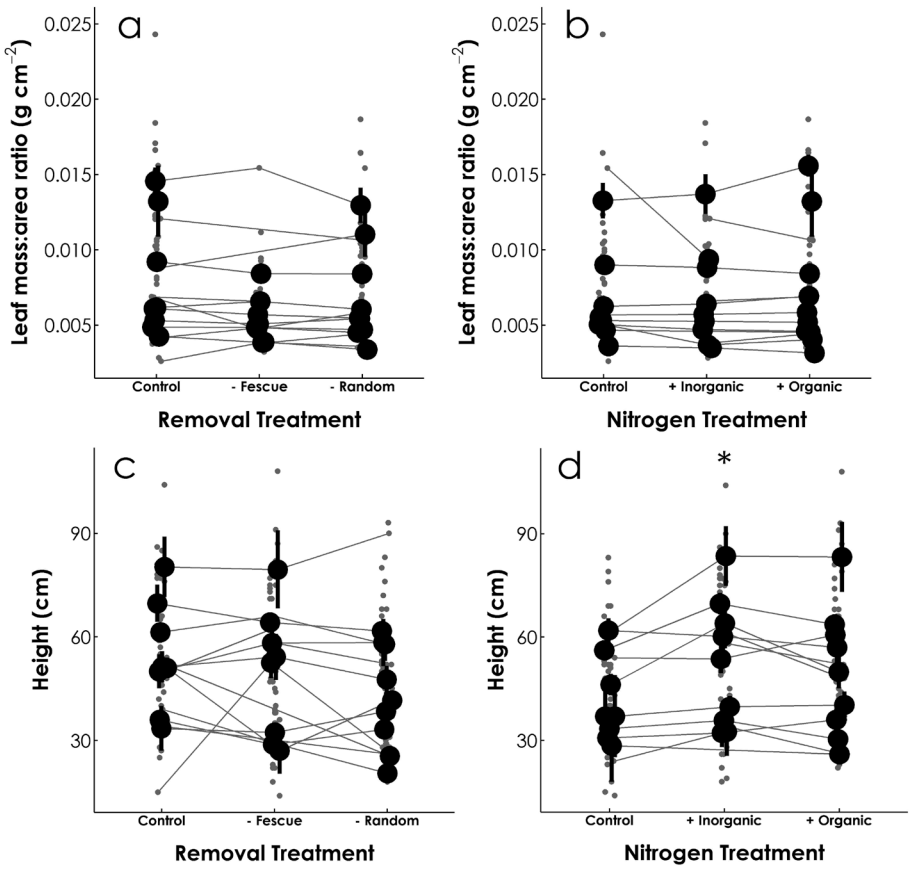

Figure 4: leaf mass:area ratio (**a**: removal treatments; **b**: fertilization treatments) and height (**c**: removal treatments; **d**: fertilization treatments) of individuals within treatment plots. Grey points represent individual measurements, and dark points and bars represent means and standard errors within each species. Grey lines connect species means between treatments. The asterisk in panel d indicates significantly taller plants in the inorganic N fertilization plots.

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did not differ among-species removal treatments, nor did species removal treatments interact with fertilization treatments to affect LAI (Fig. 5). However, inorganic N fertilization, but not organic N fertilization, caused a significant increase in LAI (ΔAICc of model including fertilization and year = −2.8; R^2 = 0.417; Fig. 5). Averaged across all levels of removal treatment in 2015, the least-square mean of LAI in unfertilized control plots was 2.38, with 95% CI [1.69, 3.07], compared to 3.75 [3.05, 4.44] with ammonium nitrate fertilization and 2.38 [1.68, 3.07] with urea fertilization. The increase in LAI resulting from ammonium nitrate fertilization may have been mediated by a treatment-induced increase in the relative abundance of taller, thicker-leaved plants: N addition plots with higher increases in community-weighted average of the first trait PCA axis relative to control plots also had higher increases in LAI relative to the control mean (ΔAICc = −4.7; R^2 of fixed effect = 0.178; see online supplementary Fig. S8).

Soil respiration

Soil carbon efflux did not change significantly with the addition of both organic N and inorganic N (Fig. 6). However, when analysing 2015 response data alone, in the early part of the growing season shortly after the N addition event soil respiration increased by 68% (P = 0.005) with ammonium nitrate addition relative to the control, and by 57% with urea addition relative to the control (P = 0.02; R^2 = 0.369). However, soil respiration did not vary with the presence or absence of *Festuca* after four growing seasons of removal, despite a moderate but non-significant pulse in the respiration rate shortly after removal in the *Festuca* removal plots but not the random biomass removal plots.

DISCUSSION

The plant community in this study exhibited resilience to dominant species loss in that species with traits similar to the dominant species increased in abundance over time. Furthermore, the community exhibited resistance in that its structure was unaffected by N addition. Both species and functional diversity of the plant community were largely resistant to change in response to species loss and N addition, although functional diversity decreased somewhat in response to dominant species loss. The remaining plant community demonstrated resilience to change—the increase in relative abundance of some species compensated for the loss of *Festuca* by increasing the relative dominance of species with higher RML, LDMC, and height and lower root N:P ratio, as evidenced by the significant change in the CWM of these traits over time since the initial removal event in 2012. Organic nitrogen fertilization promoted taller species and increased the variance of plant height, inorganic nitrogen fertilization promoted aboveground biomass production and increased the height of individuals growing within the treatment plots, and both forms of nitrogen separately increased soil respiration during the early part of the growing season.

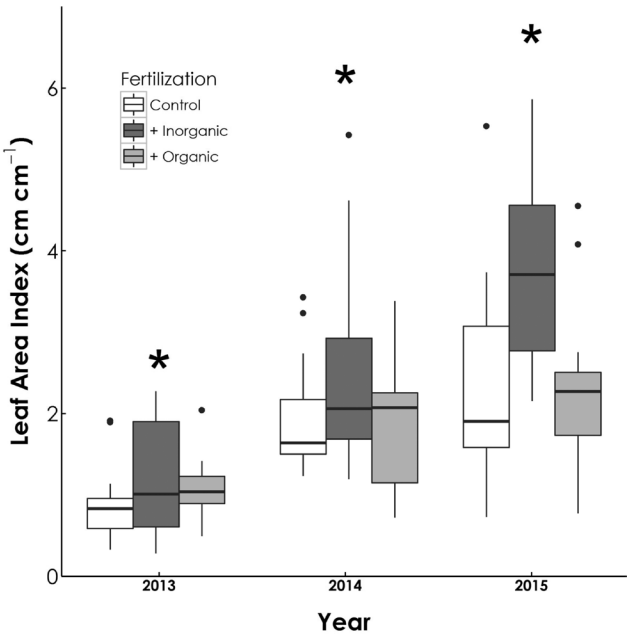

Figure 5: boxplots of leaf area index (*y*-axis) by fertilization treatment (*x*-axis) in July 2013, 2014 and 2015. Leaf area index is an easily measured variable closely correlated with standing aboveground plant biomass. The unfertilized control is shown in white, inorganic N fertilization in light grey and organic N fertilization in dark grey (boxplot dimensions as in Fig. 2). Here, asterisks indicate that the inorganic N fertilization treatment plots had significantly higher leaf area index in each year.

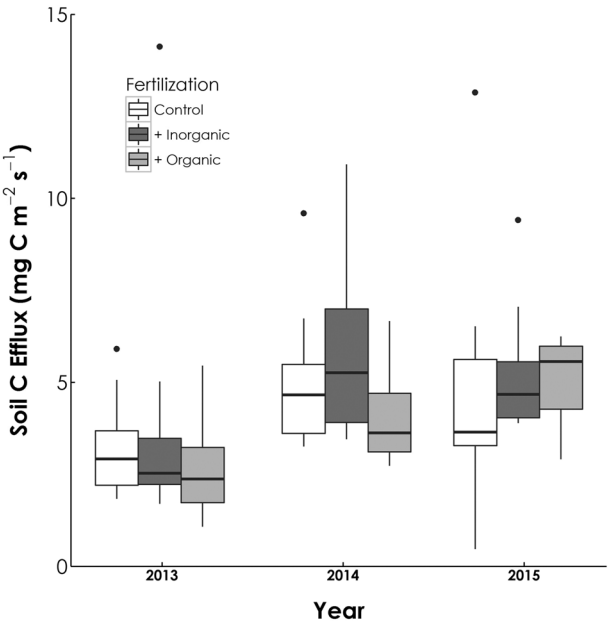

Figure 6: boxplots of soil C efflux (*y*-axis) by fertilization treatment (*x*-axis) in July 2013, 2014 and 2015. The unfertilized control is shown in white, inorganic N fertilization in light grey and organic N fertilization in dark grey (boxplot dimensions as in Fig. 2). There are no differences among fertilization treatments.

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Changes in plant traits with *Festuca* removal show compensation

Neither CWM nor variance of any trait differed among removal treatments in 2016, other than the obvious change resulting from physically removing *Festuca*. The relatively high LMA, RML and leaf N:P ratio of *Festuca* suggests that its high abundance is associated with high investment into structural tissue that is durable and can withstand stress (Wright *et al.* 2004), at the expense of achieving high short-term rates of carbon (C) gain in leaves (Poorter *et al.* 2009) or soil resource uptake in roots (Bardgett *et al.* 2014; Freschet *et al.* 2010). However, plant species with relatively high RML, LDMC, and height, and low root N:P ratio became more abundant in response to removal of *Festuca*, as shown by the increases over time in CWMs for those traits relative to the control. This likely illustrates a compensatory response by those subordinate species whose leaf and root traits were most similar to *Festuca* (McLaren and Turkington 2010). The response we observed suggests that it may be possible to predict which species might compensate for species loss based on trait similarity. The plant community that remained after *Festuca* removal demonstrated resilience by replacing both its aboveground biomass and its functional role (Craine *et al.* 2011; Smith and Knapp 2003).

High LMA and high RML indicate, for leaves and roots respectively, a tradeoff in favour of stress tolerance and durability over resource acquisition potential (Lind *et al.* 2013). This compensatory response may explain the lack of response in ecosystem process rates related to soil C cycling, as both the biomass and function of *Festuca* were replaced by other species. It is likely that there is a combination of traits that optimizes competitive ability within this plant community; we would expect the most abundant plant species to exhibit traits closest to that optimum (Gilman *et al.* 2010). When that species is lost from the community, the remaining species that are closer to the optimum value will increase in relative abundance. In this case, the high LMA and RML of *Festuca* may represent one of several possible optimal trait combinations. However, full convergence will probably not occur if the dominant species is prevented from regenerating, since there are no species with such extreme values of LMA and RML in this particular local community. The timeframe of this experiment was short relative to the lifespan of the plants in this system. For example, many *Helianthella* individuals that have been tracked since 1973 in an observational study adjacent to our study site are still living (Inouye 2008). Therefore, this study may not capture the magnitude or direction of long-term change caused by species turnover (Sandel *et al.* 2010). Over the long term, recruitment from other locations might cause the mean trait value of the community to return closer to the optimum value.

Nitrogen addition had moderate effects on carbon cycling processes belowground

We found that inorganic N addition, but not organic N addition, increased aboveground plant biomass as measured by LAI, indicating that the plant community is at least partially limited by soil N. Organic N addition may have had similar effects on aboveground productivity, as it was associated with greater variance in height and taller individuals, but there was no significant difference in aboveground biomass. The increase in biomass with inorganic N addition is unsurprising given that N fertilization tends to increase shoot:root biomass allocation ratio in natural communities (Li *et al.* 2011). Interestingly, the increase in aboveground leaf biomass induced by inorganic N addition was mediated by increases in the relative abundance of taller plant species with higher LMA and LDMC. This relationship suggests that abiotically induced changes in biomass production are partially mediated by changes in community-averaged plant traits.

Rates of soil respiration increased after adding either organic or inorganic forms of N, but this effect dissipated after several weeks each year—when considering all years jointly there was no effect of N addition on soil respiration. Soil C dynamics may be regulated by factors not associated with plant composition or biomass: N effects belowground may have been independent from aboveground shifts in the plant community, paralleling experimental results from other systems (Wardle *et al.* 2013). Neither form of N addition had any significant impact on the species composition of the plant community nor on functional trait composition. This striking lack of community response, especially in a region where the rate of anthropogenic N deposition is among the lowest in North America (Schwede and Lear 2014), may arise because there is no significant variation among the plant species in their ability to take up N. Therefore, no individual species was able to benefit disproportionately from N addition.

We had initially hypothesized that organic and inorganic N would have positive effects on different plant species because plant community diversity may be maintained by partitioning of different sources of soil N (Chesson *et al.* 2004; McKane *et al.* 2002). However, the only difference observed in different forms of N fertilization was a greater blanket increase in aboveground biomass when inorganic N was added. One plausible set of explanations is that most plants in this system can take up inorganic N from the soil more readily, and that partitioning of soil N pools is not an important mechanism helping to maintain diversity in this plant community. Another possible explanation for the greater fertilization effect of ammonium nitrate relative to urea is that the urea tends to be rapidly nitrified and leached from the soil as nitrate ions. Therefore, the fertilization effect may primarily be due to ammonium fertilization. Most research on organic N uptake by plants has looked at the capacity of plants or associated symbionts to take up free amino acids or peptides from the soil (Näsholm *et al.* 2009), so the urea fertilization treatment may not have adequately simulated organic N uptake. Interestingly, we observed no leaf trait plasticity, and little change in species abundance that could be predicted by traits, in response to N addition, although other short-term N addition treatments in similar systems have resulted in

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altered trait expression (La Pierre and Smith 2015) and in altered species composition (Yu *et al.* 2015). The plants in this community may have been selected for high N homeostasis, enabling them to decouple their internal chemistry from local fluctuations in soil N availability, which has been related to stress tolerance, temporal stability and dominance in similar systems (Yu *et al.* 2011, 2015).

Lack of interaction may be due to legacy effects

The effect of *Festuca* removal did not depend on N addition, or vice versa; that is, there were no interaction effects retained as predictors for any of the variables we measured. Thus, we did not find support for the prediction generated by resource-ratio theory (Miller *et al.* 2005; Tilman 1980) that the relationship between dominant and subordinate species is contingent on levels of soil resource availability. Perhaps there has been insufficient time for the loss of *Festuca* to have changed abiotic conditions in the plots or to have altered the microbial community. In addition, the sample size may have been inadequate to detect interaction effects; power analysis shows that when the desired power to detect a treatment effect is 80%, our study design can detect an effect corresponding to $R^2 = 0.35$. This coefficient is higher than most multiple correlation coefficients we observed (Cohen 1988). A recent study also demonstrated that both N interaction and asymmetric competition for soil resources affect plant productivity and plant species composition in prairie and tundra plant communities, but that these two drivers do not interactively effect either productivity or composition (Farrer and Suding 2016). In addition, additional data collected in our study plots in 2013 show that both living *Festuca* individuals and belowground legacy effects (Kostenko *et al.* 2012) from dead *Festuca* individuals affect mycorrhizal communities on neighbouring *Helianthella* individuals similarly (Jeremiah Henning, unpublished data). Because the mycorrhizal community associated with a plant's roots can determine of the rate at which that plant can take up soil resources such as N (Read and Pérez-Moreno 2003), the persistence of *Festuca*-associated mycorrhizae may explain the lack of interaction between removal and fertilization. As we plan to continue maintaining the experimental treatments and collecting data over the next several years, we hypothesize that such interactions may manifest once the legacy effects of *Festuca* become more attenuated.

Interannual variation and shifting dominance in time

The study system is dominated by long-lived species that are adapted to deal with fluctuations in temperature, precipitation, herbivory, physical damage and resource availability both within and among growing seasons. As a result of these fluctuations, grasses including *Festuca* are more dominant in drier years, while asters such as *Helianthella* have much greater cover and live aboveground biomass in wetter years. This may have large impacts on year-to-year C storage in the system, because *Festuca* litter is much more recalcitrant and ties up C and N in undecomposed tissue for many years, as confirmed by a decomposition experiment at an adjacent site (Shaw and Harte 2001). However, in the wetter years, light becomes limiting, and forbs such as *Helianthella* that are superior competitors for light are able to suppress *Festuca* and prevent it from accumulating biomass. This plant community may maintain stability in the face of among-year changes because the bulk of the biomass shifts between two or more dominant species that achieve relative abundance peaks at different moisture levels (Allan *et al.* 2011). This storage effect arises from functional tradeoffs and may explain the coexistence of multiple dominant plant species within a community (Angert *et al.* 2009). Furthermore, the effects of yearly climate fluctuations are dampened by the large storehouse of biomass and nutrients belowground, especially in tap-rooted forbs such as *Helianthella*. Due to the resilience conferred by this storage effect, it is possible that only repeated extreme events would cause a regime shift (Biggs *et al.* 2009) that would significantly change properties such as C cycling.

Alternatively, the general lack of community response, and the very modest ecosystem-level responses, to N addition that we observed in this study may reflect that N is not the primary limiting factor in this system, as we had at first assumed (LeBauer and Treseder 2008). Based on both theoretical (Harpole and Suding 2011) and empirical (van der Werf *et al.* 1993) evidence, we predicted that N addition would favor species with fast-growing, competitive traits including low LMA and high tissue N:P ratios. We further predicted that competitive species would increase even more with added N when released from suppression by the dominant species (Gundale *et al.* 2012). In contrast to our predictions, community composition and soil C efflux was unaffected by N addition both with and without *Festuca*, while both aboveground biomass and soil C efflux were qualitatively higher in years with higher precipitation. This pattern suggests that N may only be limiting in this ecosystem when water limitation is alleviated. Any release from precipitation limitation may not have lasted long enough, or reached a sufficient threshold, to cause any significant differences in response to elevated N among species.

In addition to temporal scale, spatial scale may obscure the effect of dominant species removal: it is not clear across what distance plant individuals interact with one another in this community. While 2 to 5 tussocks of *Festuca* were removed from each removal plot, it is possible that only a subset of plants within the 1 m^2 plot were affected by these removals. Aggregating response variables at the plot scale may have obscured any effects.

CONCLUSION

We experimentally manipulated multiple global change drivers, tested ecological niche theory, and took a trait-based approach to predict how plants respond to biotic and

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abiotic changes in their environment. The results we generated with this innovative approach indicate (i) that the presence of a dominant grass species is more important than the level of N addition for community structure, although both may select for particular trait combinations among the remaining species, (ii) that the level of N addition affects C dynamics more than the dominant grass species and (iii) that the dominant species and N addition did not affect the plant community or ecosystem C cycling interactively. Shifts over time in relative abundance of plant species partly compensated for the loss of a dominant grass species. In addition, we found that chronic addition of soil N only had moderate effects on C cycling processes and that plant community structure was largely unchanged in response to N addition. These results may indicate that the insurance and storage effects confer resilience and maintains diversity in montane meadow communities. Approaches such as this one, replicated across sites, would greatly improve global vegetation models (Dukes *et al.* 2014) by enabling them to incorporate the storage effect that confers resilience to plant communities by the rapidly shifting dominance of different plant species from year to year.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Journal of Plant Ecology* online.

ACKNOWLEDGMENTS

We thank L. Moorhead and M. Rúa for helpful suggestions on drafts of this manuscript, the staff of the Rocky Mountain Biological Laboratory (RMBL) for their support, and the organizations that funded this research: the Department of Ecology and Evolutionary Biology, University of Tennessee (Q.D.R., J.A.H.), the RMBL Dr Jean Langenheim Fellowship (Q.D.R.), the RMBL Dr Lee R. G. Snyder Memorial Fellowship (J.A.H.), and the Fran Hunter Fellowship (J.A.H.). N.J.S. and A.T.C. thank the Danish National Research Foundation for its support of the Center for Macroecology, Evolution and Climate.

Data accessibility. Data associated with this manuscript are freely available and are archived at https://doi.org/10.6084/m9.figshare.4719199.v1.

Conflict of interest statement. None declared.

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