

Chronic fertilization and irrigation gradually and increasingly restructure grassland communities

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Abstract. Scientists have known for over a century that resource addition can lead to species loss from plant communities. Recent studies have also shown that resource addition can substantially restructure communities by altering their functional and taxonomic composition—even when species richness remains unchanged. Understanding which aspects of community structure are impacted by different resources and over which timescales will provide insight for management decisions and may also elucidate which measures can act as early warning indicators for subsequent changes in the community. Here, we take advantage of a long-term factorial experiment to understand how grassland plant communities respond to a decade of nitrogen fertilization ($14 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) and irrigation (25 mm water/week during the growing season). After 10 yr, fertilization and irrigation decreased species richness by 22% and 9%, while functional richness decreased by 31% and 41%. Abundance-weighted functional distance between treatments and controls increased by 55% and 24%, respectively. We expected that abundance-weighted measures would shift before presence-absence-based measures, but found limited evidence for this. Instead, our results suggest that species gains, which can occur quickly because they require the addition of only one individual, may serve as early indicators for subsequent community restructuring in the opposite direction. Overall, both chronic nitrogen fertilization and irrigation tended to have gradual and increasing impacts on community structure, but the magnitude of these effects varied greatly depending on the aspect of community structure investigated. Further study will be needed to determine the extent to which our results can be generalized to other resources or sites in order to develop management strategies to maintain both taxonomic and functional trait diversity in the face of chronic resource changes.

Key words: community structure; diversity; functional traits; nutrient addition; temporal trends; water addition.

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INTRODUCTION

Ecosystems are continually confronted with many long-term and directional changes in the supply of the major resources required by plants, including various nutrients (Galloway et al. 2004, IPCC 2014), water (Huntington 2006, Zhang et al. 2007), and CO₂ (IPCC 2014). Increased resource supply can restructure terrestrial plant communities (Lawes et al. 1882, Suding et al. 2005, Harpole et al. 2016) by altering functional and taxonomic richness, abundance, dominance, and composition. This community restructuring often occurs at the expense of species that would otherwise be dominant under low-resource conditions, where they are able to drive resources down to levels at which their competitors can no longer replace themselves (Tilman 1982, Dybzinski and Tilman 2007). When resources are added, these low resource levels will be exceeded and another resource will instead become limiting, leading to shifts in species dominance and composition over time (Dybzinski and Tilman 2007, Isbell et al. 2013b). This raises several so far unanswered questions: (1) Will changes in resource supply quickly restructure communities and have consistent and persistent effects, or instead restructure communities gradually and increasingly over time (Hillebrand et al. 2008, Smith et al. 2009, Mouillot et al. 2013b)? and (2) Do some resources, or combinations of resources, have a greater influence on community structure than others (DeMalach et al. 2017)?

Community restructuring by chronic resource addition could have several possible temporal trends. Building on the framework proposed by Smith et al. (2015), we outline several distinct hypotheses about these temporal trends and their implications for communities (Fig. 1). First, if the structure of a community is largely determined by factors that could interact with resource supply (e.g., herbivory, pathogens, temperature; Cleland et al. 2011), community responses to increases in resource supply could vary from one year to the next, appearing temporally variable (H1, temporally varying effect). On the other hand, if community structure is largely determined by resource limitation, community responses to increases in resource supply could grow, either linearly or non-linearly, over time as

favorable species increase in abundance and those disadvantaged decline (H2, gradual effect). This would lead to increasing differences between regions which either experience this pressure or not. Alternatively, a community could restructure rapidly once the resource addition exceeds a threshold (H3, abrupt change; Bestelmeyer et al. 2011, Isbell et al. 2013b). After reaching this threshold, the community may either continue to change or persist in its altered state. Finally, chronic resource addition may have a transient effect, where the community structure changes for a brief time before returning to its initial conditions (H4, transient effect). These transient effect dynamics may happen if species have time to acclimate to the increased resource supply so that even if new species can become dominant over short timescales, original composition will recover over longer timescales (Reich et al. 2018).

Different aspects of community structure may respond differently to a change in resource supply or follow different temporal trends (Smith et al. 2009, Mouillot et al. 2013b). For example, metrics weighted by species' abundances, including many trait-based metrics, may be more responsive than presence-absence metrics, such as species richness (Smith et al. 2009, Mouillot et al. 2013b). Further, rapid responses in first year of treatment may actually be opposite to the long-term trend while competitive dynamics are still in flux due to the initial increase resources. Changes in abundances or species number within the first year may impact many different taxonomic and functional metrics compared to ambient conditions while the community adjusts to the new resource regime. Additionally, many studies have only separately investigated either the effects of chronic nutrient addition on the species richness of grassland plant communities (Willems et al. 1993, Stevens et al. 2004, Clark and Tilman 2008, Harpole et al. 2016), or the divergence or convergence of species (Inouye and Tilman 1988, 1995, Houseman et al. 2008, Avolio et al. 2015) and functional (Weiher et al. 1998, Laliberte et al. 2013, Mason et al. 2013, La Pierre and Smith 2015) composition. Using both taxonomic and functional trait metrics may not only provide insight into the temporal trends of community structure response but also give a more comprehensive picture of the extent of long-term community restructuring.

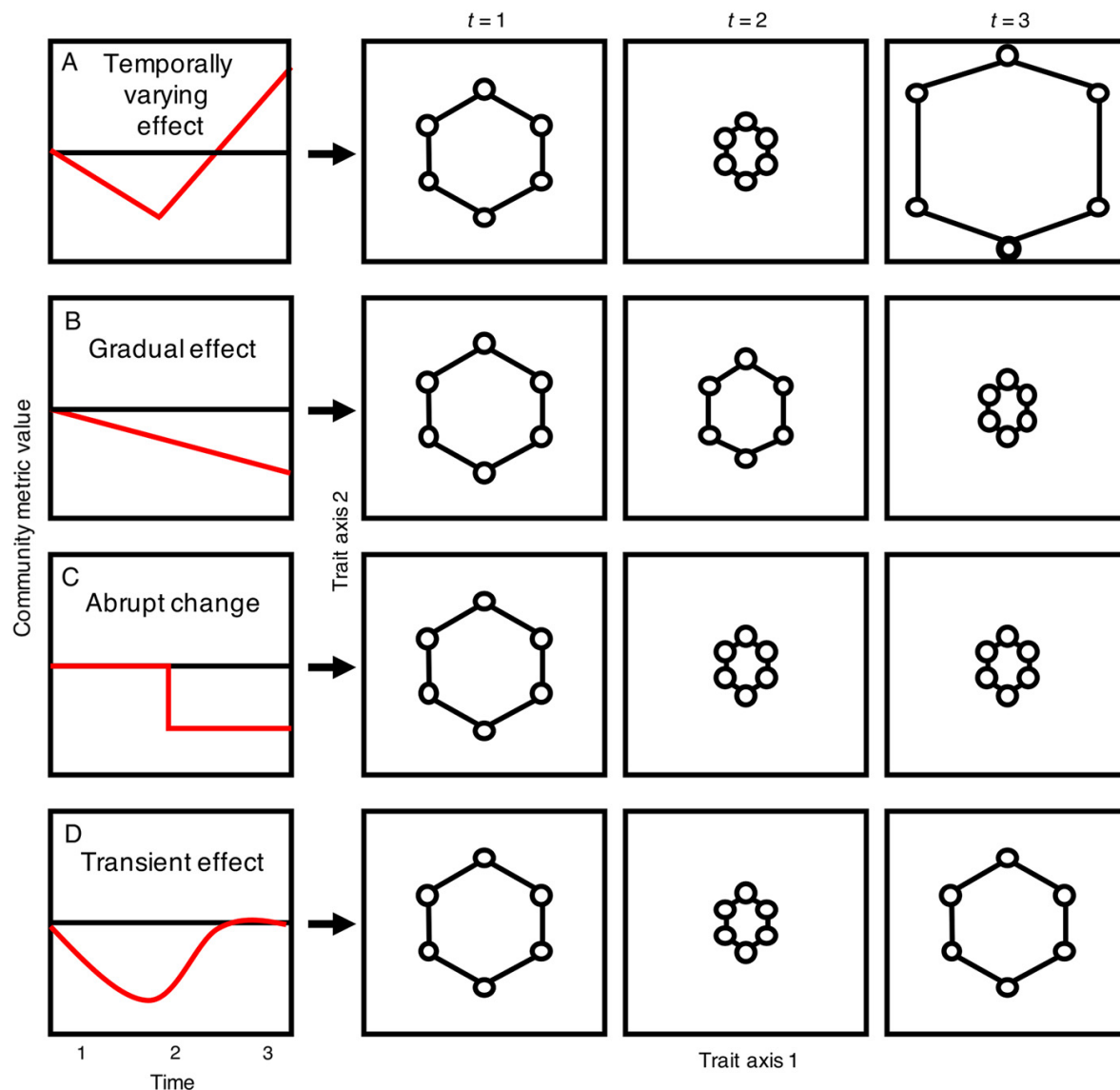


Fig. 1. Graphical representation of how chronic resource addition can alter measures of community composition through time. In the simplest case where the ambient plots (black line) stay static through time, the solid red line is the hypothetical response to a chronic resource addition. Communities can either (A;H1) have inconsistent responses year to year (temporally varying effect), (B;H2) increasingly deviate (gradual change), (C;H3) have a sudden, but persistent shift (abrupt change), or (D;H4) an initial effect that diminishes through time (transient effect). Functional richness responses are illustrated here, but we studied temporal trends in several metrics of community structure.

Considering how both functional and taxonomic metrics respond through time can give insight into exactly what is driving changes perhaps concurrent changes in other metrics. For example, differences in species richness indicate changes in the number of species, but do not

provide information regarding whether the species gained or lost are similar to or different from the original community. In contrast, functional richness decreases indicate that the community lost functionally unique species (i.e., had different traits than the original species) or were

replaced by species more functionally similar to the remaining community (or vice versa for functional richness increases; Cornwell et al. 2006, Villéger et al. 2008, Boersma et al. 2016). Yet, such patterns in functional richness could be generated both by concurrent changes in species richness and by species composition turnover (Fig. 2; Mayfield et al. 2010). Likewise, turnover in functional or taxonomic composition as well as shifts in relative abundances could occur without affecting functional or species richness indices (Fig. 2). Therefore, by using both functional trait metrics and traditional taxonomic community metrics we can more fully characterize how communities respond to different resource additions (Mason et al. 2005, Boersma et al. 2016) and the temporal trends of these responses (Smith et al. 2009, Mouillot et al. 2013b).

The objective of this study is to determine the extent to which temporal trends in community restructuring depend on the type of resource added and the metric of community structure investigated. Here, we examine temporal trends in the effects of chronic addition of water and nitrogen, two commonly limiting plant resources, on grassland plant community structure, including multiple aspects of taxonomic and functional composition. We use a 10-yr, full factorial water and nitrogen addition experiment at

Cedar Creek (East Bethel, Minnesota, USA; Yang et al. 2018). We consider changes in several aspects of community structure: species richness and evenness, functional trait means and variance (functional dispersion, functional richness, and functional distance), community-weighted means of traits, and species and functional group abundances.

METHODS

Study system

This study was conducted at Cedar Creek Ecosystem Science Reserve, East Bethel, Minnesota, USA. Soils at Cedar Creek are characterized as nutrient-poor entisols derived from a glacial outwash sand plain (Tilman 1987). Average wet N deposition rates are $\sim 0.6 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (58% NH_4 , 42% NO_3 ; Clark and Tilman 2008). According to Köppen and Geiger classification (2006), the climate is characterized as cold continental with hot summer, but without dry season (Peel et al. 2007). The mean growing season (May–August) precipitation is approximately 420 mm, mean minimum growing season temperature is 12°C , and mean maximum growing season temperature is 25°C (1982–2016 period; <http://www.cedarcreek.umn.edu/research/data>). Plots are burned every year and fenced to prevent deer herbivory.

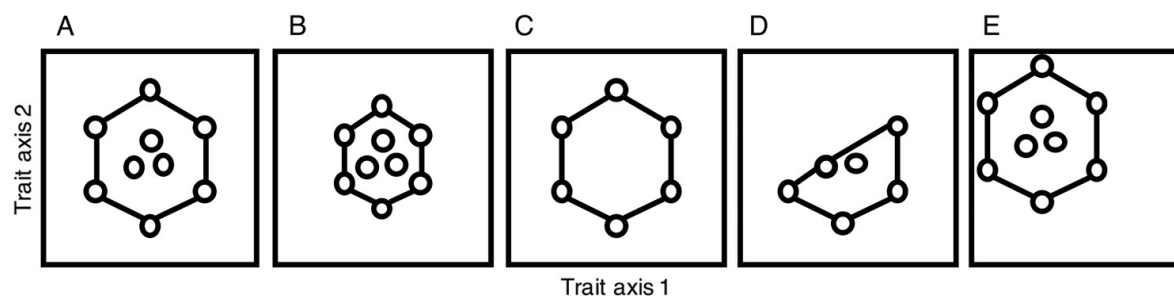


Fig. 2. Multiple trait-based and taxonomic measures provide complementary information when characterizing community restructuring. We show several hypothetical responses of community (A), which is comprised of nine species, to resource addition. Each circle is a species, plotted according to its trait values. Functional richness, the volume of the convex hull, is shown by the area inside of the connected species. For example, resource addition may have no effect on species richness, but decrease functional richness (B); or have no effect on functional richness, but decrease species richness (C); or decrease both species richness and functional richness (D); or decrease neither species richness nor functional richness, but shift the community to a different region of trait space, which can be captured by functional distance (E).

Experimental design

Thirty-six 9×9 m plots were planted with the same mixture of 32 grassland species in early spring of 1994 and again in 1995 (Tilman et al. 1997). Starting in 2007, plots were randomly assigned to one of the six treatments, which included all combinations of two water treatments (ambient and +25 mm/week during the growing season) and three nitrogen fertilization treatments (ambient, +7 g N·m⁻²·yr⁻¹, or +14 g N·m⁻²·yr⁻¹). This water addition increases the total amount of water by ~80% during the average growing season, while the N fertilization rates are at levels relevant for understanding the impact of global wet deposition (Clark and Tilman 2008) and agricultural fertilization rates, respectively. Water was added to plots weekly from May to September via a sprinkler system, and nitrogen was added once in the beginning of each growing season as NH₄NO₃ (Farrior et al. 2013, Yang et al. 2018). Here, we show results from four of these treatments to simplify presentation (ambient, +water, +14 g N, and +water +14 g N, $n = 24$), but similar results were obtained using both N addition treatments or grouping the N addition treatments together (Appendix S1: Table S1). During 2007, 2009, 2010, 2015, and 2016, biomass from four strips per plot, each 10×600 cm, was harvested, sorted to species, dried, and weighed. Non-planted species (weeds) were not removed from these plots, resulting in a total of 37 unplanted species observed across all plots and years. Overall, 96% of the biomass sampled across all plants and years was from the original 32 planted species.

Taxonomic metrics

We determined species richness (i.e., the number of species in a plot), inverse Simpson's evenness (Simpson 1949), and relative abundances of each species based on the harvested biomass from each plot. The biomass of the ten most abundant species over all plots and experiment years comprised ~82% of all biomass sampled. These ten species were *Andropogon gerardii* (29.4%), *Sorghastrum nutans* (9.8%), *Schizachyrium scoparium* (8.5%), *Poa pratensis* (8.4%), *Lupinus perennis* (6.8%), *Dalea purpurea* (5.6%), *Coreopsis palmata* (3.9%), *Bouteloua gracilis* (3.1%), *Liatris aspera* (3%), and *Solidago rigida* (2.9%). For analyses of individual species' biomass, the square

root of the biomass was used as the response variable in order to meet model assumptions of normality.

Functional traits

We characterized each species by four different functional traits, which can be indicative of success when resource supplies increase (Craine et al. 2002, Sandel et al. 2010, La Pierre and Smith 2015). We included plant height (m) because it is associated with the ability to compete for light resources (Gaudet and Keddy 1988, Westoby 1998) and two leaf economics traits (specific leaf area [SLA], mm²/mg, and leaf tissue nitrogen per dry mass [leaf N], mg/g) because they are associated with the trade-off between acquisitive, fast-growing, but short-lived leaves and conservative, slow-growing, but long-lived leaves (Wright et al. 2004, Reich 2014). We also included photosynthetic pathway (C3/C4) because it is related to seasonality and resource use efficiency. Trait data were obtained from Cedar Creek datasets (<http://www.cedarcreek.umn.edu/research/data>) and the global plant trait database, TRY (Kattge et al. 2011; www.try-db.org, see Appendix S1: Table S2 for a summary of data used and associated references). We averaged each trait over all records for each species when more than one observation existed in the databases. Over half of the species had more than 10 observations, and dominant species had from 50 to 650 observations. Species missing information for more than two traits were excluded from trait-based analyses, though we were able to characterize between 87% and 100% of species and 89% and 100% of biomass present in each treatment and year with available data (Appendix S1: Table S3). While species may shift their trait values in response to changing environmental conditions (Lepš et al. 2011), species reordering, gains, and losses are expected to dominate community responses over the longer timescales of our experiment (Smith et al. 2009). Thus, characterizing species by average values captures changes in the *types* of species but not intraspecific trait responses.

Functional trait metrics

We calculated three different functional trait metrics, each testing a specific aspect of functional composition response to increases in

resource supply. First, functional richness measures the amount of trait space occupied by a community based on the presence or absence of trait values, regardless of their relative abundance in the community (Mason et al. 2005, Cornwell et al. 2006). Significant decreases in functional richness indicate convergence toward a similar trait composition (Laliberté et al. 2013, Mason et al. 2013, Boersma et al. 2016). Functional richness is calculated as the convex hull of the multivariate trait space, the multidimensional space where each axis corresponds to a trait. Second, functional dispersion quantifies the spread of trait values in the community based on both presence and relative abundances (Laliberté and Legendre 2010). Significant changes in functional dispersion, without parallel changes in functional richness, can indicate shifts in trait value dominance and evenness (Boersma et al. 2016). Functional dispersion is calculated as the abundance-weighted average of the distance that each species (trait value combination) is away from an abundance-weighted centroid of the community (i.e., within a plot; Laliberté and Legendre 2010). Third, functional distance indicates whether treated plots are located in different areas of trait space compared to ambient plots (Boersma et al. 2016). Functional distance is calculated as the distance between the centroids of each pair of plots to determine whether distances between pairs of plots within the same treatments are less than those between treatments (Boersma et al. 2016). In our analyses, increases in functional distance through time indicate shifts in species abundance and species turnover, such that treatment plots are moving further away from ambient plots in trait space. For each trait, a community-weighted mean and a non-weighted mean were calculated for each plot at each year to investigate which types of species (e.g., Do we tend to move toward species with high tissue nutrient concentration?) were responding based on abundance and presence-absence. Lastly, we also grouped species into four functional groups based on broadly similar physiology and morphology: C4 grasses, C3 grasses, legumes, and all other non-legume forbs—to classify how these groups respond to our treatments. These functional groups have been previously shown to be responsive to long-term nutrient addition (Tilman et al. 1997, Reich et al. 2004).

We calculated functional richness and dispersion for each plot within each year using the FD package in R (Laliberté and Legendre 2010, Laliberté et al. 2015). We did the analyses with both z-transformed and untransformed trait values. There were no qualitative differences between the two methods, so we present data using untransformed trait values. We set $m = 4$ to compute functional richness since we characterized each species by four different traits. We calculated functional distance based on abundance-weighted and non-abundance-weighted distances between plots to assess the extent to which results depended on shifts in relative abundance, rather than changes in the presence or absence of species (Boersma et al. 2016); see *Statistical analyses* for a discussion on how this was modeled.

Statistical analyses

To determine how functional and taxonomic metrics responded to treatments, our estimated models considered (1) the three-way interaction of each treatment and experiment duration, (2) all pair-wise interactions, and (3) the main effect of each treatment and study duration. We included the average biomass production each year and the standardized precipitation-evapotranspiration index (SPEI; Vicente-Serrano et al. 2010) for the 5-month growing season (April–August) to control for their effects and get more precise estimates of the treatments effects on measures of community structure (Appendix S1: Fig. S1). We build off of previous frameworks for testing temporal trends (Smith et al. 2009, 2015), but determine temporal trends from statistical models which represent our hypothesized relationships and AIC model selection. Reflecting our hypotheses about temporal trends, we consider three candidate functional forms for the interaction between nutrient treatment, irrigation treatment, and experimental duration: linear (gradual response; H2), log-linear (gradual response; H2), and quadratic (transient response; H4), along with year as a factor (temporally varying response; H1). If there were only main effects for the treatments, we considered this a threshold response (H3). Model selection was based on the lowest AIC for the results shown, with $\Delta AIC > 2$ (Appendix S1: Table S1). If the three-way interaction between the two treatments and

year was not significant, it was removed for parsimony (Crawley 2013). We removed SPEI and biomass only if this improved AIC values by $\Delta AIC > 2$, which occurred only for SLA. Reflecting our hypotheses about temporal trends, if the quadratic form fit best, but had no treatment by year² interactions (e.g., no transient effect), the next best model was used.

To account for plot-by-plot variability, we considered models that included random slopes for each treatment and random intercepts for each plot. After model selection, we used random intercept-only models, which had the lowest AIC values ($\Delta AIC > 5$). To account for the repeated measures through time, we used compound symmetry covariance structures (Pinheiro and Bates 2000). All models selected had the compound symmetry structure. We were unable to consider other temporal covariance structures, such as a first-order autoregressive structure, because data were not collected every year. All analyses were completed in R v 3.3.3 (R Core Team 2017) using the lme function in the nlme package (Pinheiro et al. 2017).

We modeled both abundance-weighted and non-abundance-weighted functional distance as outlined in Boersma et al. (2016) using the MCMCglmm package in R (Hadfield 2010). We compared ambient plots to all treatment plots to determine whether increased resource supply causes communities to move to a different area of trait space. We constructed a trait matrix that included all species present for all years and an abundance matrix for all years to calculate centroids and distances between plots in multidimensional trait space (see Boersma et al. 2016). We then selected for only within-year distances. Comparisons were made between ambient plots and all treatment plots to determine how treatments impacted trait shifts. To account for the multiple comparisons between plots within each year, we modeled random effects as a multi-membership model where variance is equally distributed across all pairs of plots within each year. We also included average biomass for each year and the 5-month SPEI in our models to more accurately predict the impacts of the specific treatments on functional distance. The best model for the abundance-weighted distances included SPEI and biomass (Appendix S1: Fig. S1). The best model for the natural logarithm

of non-abundance-weighted distances included year as a factor (Appendix S1: Fig. S2).

RESULTS

Overall, we found that fertilization and irrigation caused most measures of community structure to gradually deviate from ambient plots, and these effects increased through time (Table 1, H2). Over the duration of the experiment, fertilization and irrigation impacted a similar number of community metrics. Under fertilization treatments, 11 measures of community structure responded with continuous gradual changes over time, four displayed temporally varying (but directional) changes, four changed abruptly, and one showed transient change. Under irrigation treatments, 12 measures of community structure exhibited continuous changes, five changed abruptly, three showed transient change, and one had a temporally varying response (Table 1). The trends in the community structure measures were often mirrored by species-specific and individual functional trait responses, although not always.

Taxonomic restructuring

Fertilization rapidly increased species richness in the first year, but had a continuous negative impact on species richness and Simpson's diversity over the duration of this experiment (Fig. 3A–B; Appendix S1: Fig. S1; H2). Overall, fertilization decreased species richness by 22% and Simpson's diversity by 45%. The effect of irrigation on species richness also increased over the duration of the experiment, amounting to a 9% decrease (Fig. 3B; Appendix S1: Fig. S1; H2). In contrast, irrigation did not have a significant effect on Simpson's diversity (Fig. 3A; Appendix S1: Fig. S1). Fertilization marginally decreased evenness within the first year, and this effect persisted at approximately the same magnitude during subsequent years (Fig. 3C; Appendix S1: Fig. S1; H3).

Functional restructuring

Fertilization caused a temporally variable decrease in functional richness over the duration of the experiment; there was an overall decline in functional richness resulting in a 31% decrease compared to ambient plots, but the magnitude of

Table 1. Most metrics of community composition had continuous gradual responses to chronic resource addition.

Metric	H1—temporally variable	H2—gradual	H3—abrupt	H4—transient	Rapid response
Community metrics					
Species richness		F, I			F
Simpson's diversity		F			
Evenness			F		
Functional richness	F				F
Functional dispersion					
Functional distance (AW)		F, I			
Functional distance (NW)	F				
Functional traits					
SLA					F, I
Leaf N			I		I
Height		F, F:I			F, I
Proportion C3		F	I		
SLA (NW)			F, I		F, I
Leaf N (NW)				I	
Height (NW)				I	
Proportion C3 (NW)		F, I, F:I			F
Functional groups					
C4 grasses		F	I		
C3 grasses		I	F		I
Legumes		I	F		I
Non-legume forbs		F, I, F:I			F, I
Dominant species					
<i>Andropogon gerardii</i>	F, I				
<i>Bouteloua gracilis</i>				F, I	
<i>Coreopsis palmata</i>		I			
<i>Dalea purpurea</i>		I			
<i>Liatris aspera</i>		F, I			
<i>Lupinus perennis</i>		F			
<i>Poa parentis</i>			I		
<i>Sorghastrum nutans</i>		I			
<i>Solidago rigida</i>		F, I, F:I			
<i>Schizachyrium scoparium</i>	F				
Total responses	F:4, I:1	F:11, I:12	F:4, I:5	F: 1, I:3	F: 7, I:7

Notes: Here, we show which hypothesis (Fig. 1) each metrics followed for nitrogen fertilization (F, +14 g N·m⁻²·yr⁻¹), irrigation (I, +25 mm H₂O/week May–September), or the interaction of the two (F:I). Functional trait shifts were quantified both by community-weighted means and by non-weighted (NW) means. Metrics were considered to have rapid responses, or responses in the first year which distinguished them from ambient plots, if the standard error for the treatment at year 1 did not overlap with ambient standard errors. Rapid responses were not characterized for species-specific responses. Detailed results and estimated effects can be found in Figs. 3, 4; Appendix S1: Fig. S1.

the effect was variable from year to year (Fig. 3D; Appendix S1: Fig. S1; H1). Fertilization also caused functional composition to become increasingly different from ambient plots over time when considering abundance-weighted distances resulting in fertilized plots to be about 55% more distant from ambient plots (Fig. 3F; Appendix S1: Fig. S1; H2). Fertilization also caused a temporally varying divergence when considering non-abundance-weighted distances (Appendix S1: Fig. S2; H1). Thus, fertilization

caused both a contraction of trait space and shifted the region of trait space occupied by each community (Fig. 2D). Irrigation also caused plots to diverge from ambient plots through time becoming 24% more distant from ambient plots, but only when considering abundance-weighted distances (Fig. 3F; Appendix S1: Fig. S1). While there was no temporal trend in the impact of irrigation on functional richness, it resulted in a 41% decrease compared to ambient plots by the end of the experiment. Functional dispersion did not

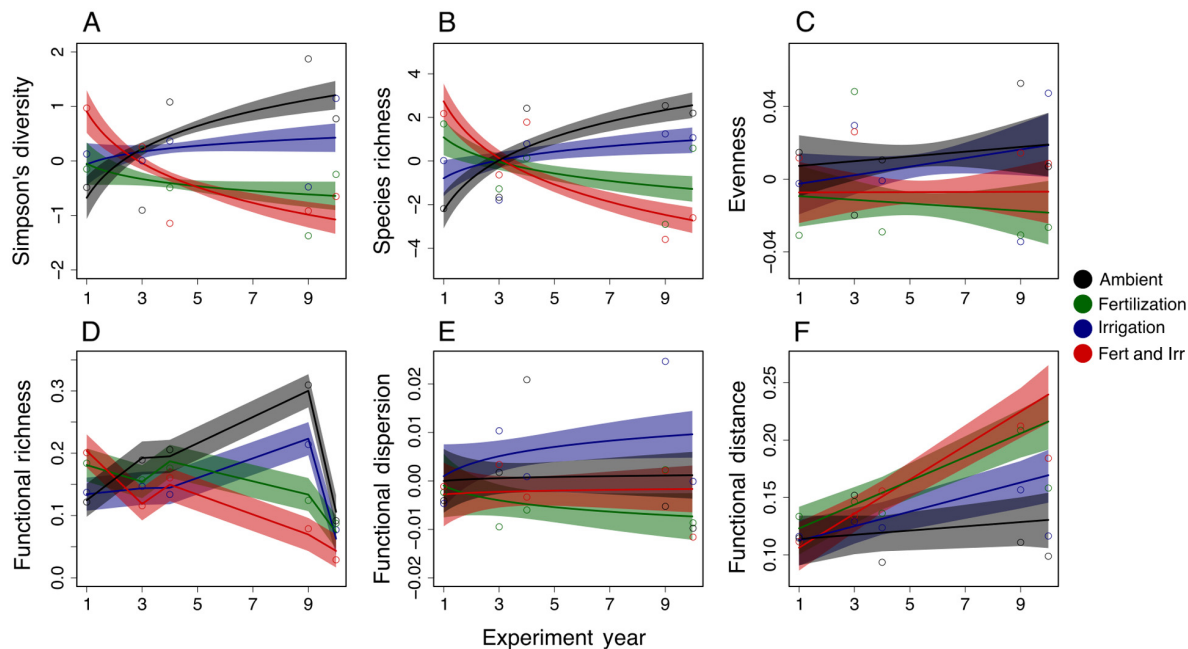


Fig. 3. Fertilization ($+14 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) and irrigation ($+25 \text{ mm H}_2\text{O}/\text{week}$ from May to September) tended to cause gradual and continuous effects on plant community structure compared to ambient plots. Fertilization had increasingly negative effects on both Simpson's diversity (A) and species richness (B), but had a significant abrupt effect on evenness (C). Irrigation only had an increasingly negative effect on species richness (B). Fertilization caused a temporally varying, but decreasing trend in functional richness (D). Irrigation and fertilization caused treated communities to become increasingly dissimilar from ambient communities (F) and did not impact functional dispersion (E). Y-axis values are residuals from partial regressions after accounting for SPEI and biomass, error bands show ± 1 standard error, and points represent observed average values.

respond to any of the treatments and remained relatively consistent through time (Fig. 3E; Appendix S1: Fig. S1).

Community-level functional responses

Functional group composition was influenced by both nitrogen addition and irrigation (Figs. 4, 5; Appendix S1: Table S4). Fertilization had a rapid and persistent effect on the proportion of the community represented by legumes (negative) and C3 grasses (positive; H3), and had gradual continuous effects on the proportion of non-legume forbs (negative) and C4 grasses (positive; Fig. 4A–D; H1). The decrease in non-legume forbs was mirrored by a continuous decrease in the proportion of the community-weighted mean proportion of C3 species and height (Fig. 4G–H; Appendix S1: Table S6). Irrigation had positive, rapid, and persistent impacts on the proportion of C4 grasses in the

community (H3), decreased the proportion non-legume forbs and C3 grasses through time (H1), and increased the proportion of legumes through time (Fig. 4A–D, H1). Plots that were both fertilized and irrigated decreased in non-legume forbs less than expected from the additive effects of each treatment separately (Fig. 4C). Changes in functional groups were mirrored by rapid decreases in community-weighted means of leaf N and proportion of C3 species (Fig. 4F and H; Appendix S1: Table S6). Most of the functional groups and community-weighted traits had rapid responses to at least one of the treatments in the first year of the experiment (Fig. 4, Table 1).

Species-specific responses

Irrigation caused changes in the biomass of eight of the ten most dominant species, whereas nitrogen caused changes in biomass of seven of

these ten species (Fig. 5; Appendix S1: Fig. S3). The most common response was a linear change through time (six of ten, H2). Species-specific responses reflected the trait and functional group responses. For example, fertilization had an increasingly positive effect on *Andropogon*

gerardii biomass, a C4 species with low tissue N and moderately high SLA. In contrast, fertilization had an increasingly negative effect on *Lupinus perennis* biomass, a C3 legume with high tissue nitrogen (Fig. 5; see Appendix S1: Fig. S3 for more details).

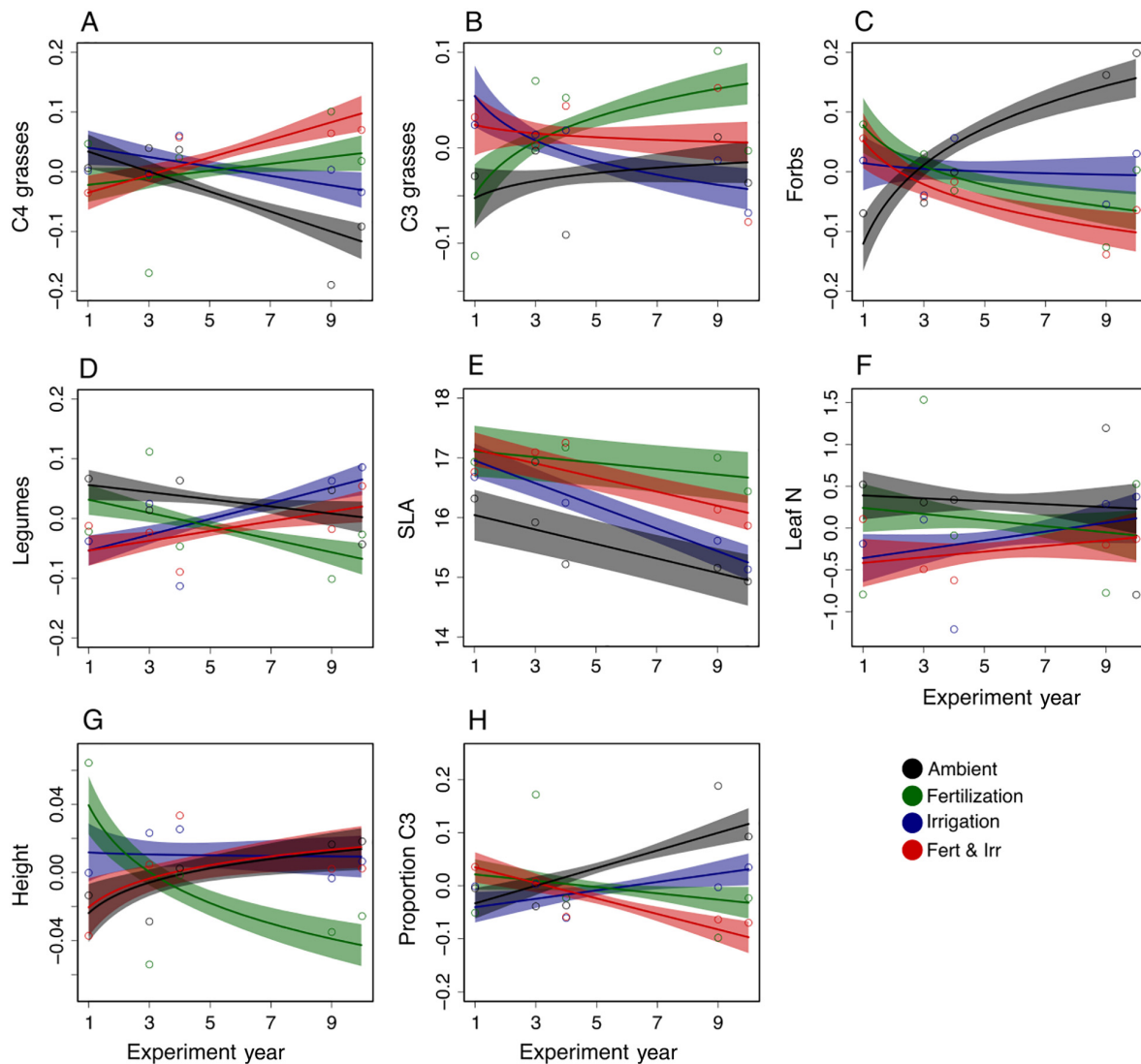


Fig. 4. Both functional group composition (A–D) and functional traits (E–H) were influenced by fertilization ($+14 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) and irrigation ($+25 \text{ mm H}_2\text{O}/\text{week}$ from May to September). Fertilization and irrigation both had rapid impacts on functional groups (A–D), which then tended to diverge from ambient plot temporal trends. Fertilization tended to have gradual continuous effects on traits (E–H), and irrigation tended to have immediate and smaller persistent impacts. Y-axis values are residuals from partial regressions after accounting for SPEI and biomass, except for SLA, where these variables were not included in the model (Appendix S1: Tables S4, S5). Error bands show ± 1 standard error, and points are observed average values.

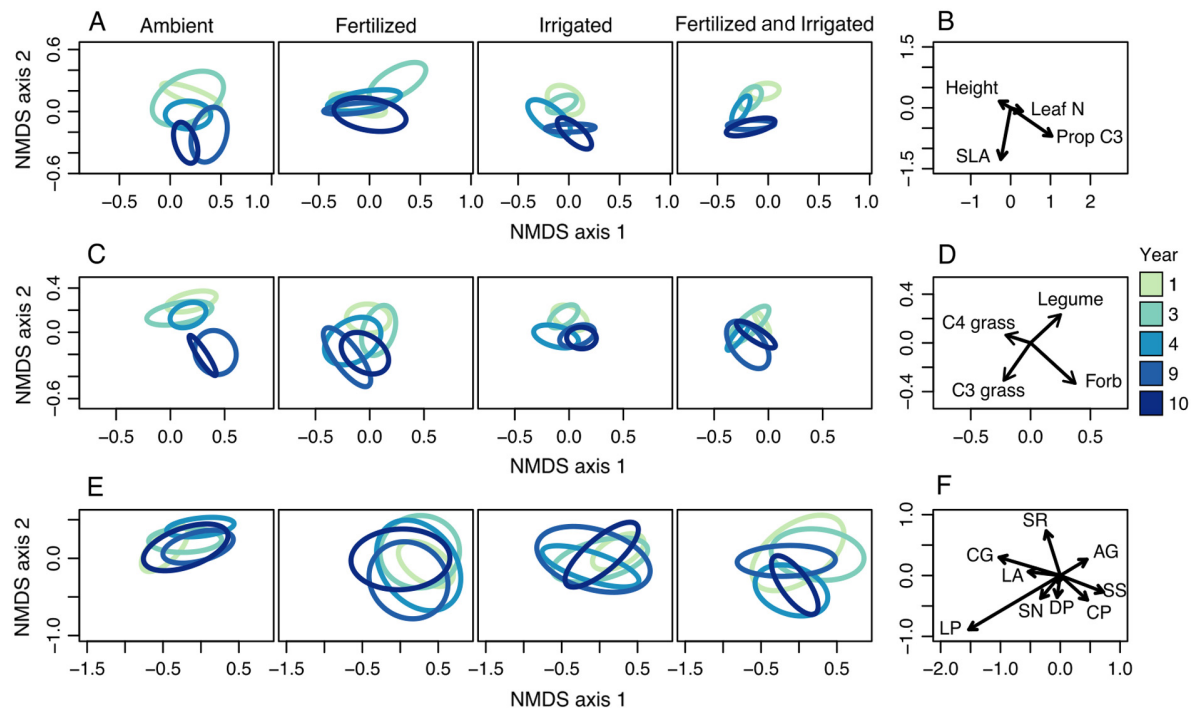


Fig. 5. Abundance-weighted trait values show a clearer response to resource addition through time in multidimensional space. Upper panels show shifts in trait space (A,B), middle panels show shifts in functional group space (C,D), and lower panels show shifts in species community space (E,F). Loadings for traits (B), functional groups (D), and species (E, 10 most abundant shown) show the direction for increasing values. Axes are the top two non-metric multidimensional scaling (NMDS) axes, which represent most of the variation in trait, functional group, or taxonomic space. Traits used include specific leaf area (SLA), maximum vegetative height (Height), leaf nitrogen content per dry mass (Leaf N), and photosynthetic pathway (C3). Species abbreviations are AG, *Andropogon gerardii*; BG, *Bouteloua gracilis*; CP, *Coreopsis palmata*; DP, *Dalea purpurea*; LA, *Liatris aspera*; LP, *Lupinus perennis*; SN, *Sorghastrum nutans*; SR, *Solidago rigida*; and SS, *Schizachyrium scoparium*. *Poa parentis* is not shown in (F) because its arrow is in same direction as DP but much smaller in magnitude.

DISCUSSION

Here, we show that temporal trends in the plant community response to chronic resource addition depend on both the resource and the specific aspect of community structure under consideration. In this experiment, we find that nitrogen fertilization and irrigation gradually and increasingly impacted many aspects of community structure. Few metrics had temporally varying or transient responses, while some had abrupt responses. Increasing species loss over time with nutrient addition is consistent with other previous studies both at our study site (Clark and Tilman 2008, Isbell et al. 2013a) and globally (Stevens et al. 2004,

Maskell et al. 2010, Harpole et al. 2016). We further show that several aspects of community structure had gradual and increasing responses to fertilization over time. Globally, the short-term effects of water addition on species richness are known to vary considerably across study sites but have a positive effect on average on species richness (DeMalach et al. 2017). Our results suggest that the long-term effects of increased water availability on community structure may be discernable from short-term studies because gradual, continuous responses were common. While many metrics had this gradual and continuous response to chronic resource addition, not all had the same temporal trends.

Using multiple metrics of plant community composition allowed for a more comprehensive understanding of community restructuring and allowed us to tease apart changes in certain aggregate metrics. We found that both species richness and functional richness were declining in fertilized treatments, providing evidence that fertilization causes not only species loss, but also loss of functionally unique species. This effect is consistent with results from other sites (Suding et al. 2005) and provides evidence that the species lost as a result of resource addition were those with distinctive trait value combinations. The loss of distinctive trait value combinations can reduce ecosystem stability and affect functioning, potentially reducing the range of conditions in which the community can maintain high levels of productivity (Isbell et al. 2011, Mouillot et al. 2013a, Violle et al. 2017). Alternatively, their disappearance could increase ecosystem stability if highly stable species persist (Polley et al. 2007). Further, fertilized and irrigated plots occupy a different region of trait space compared to ambient plots. Specifically, we found that both fertilization and irrigation increased the abundance of species with higher SLA and decreased the abundance of C3 species, whereas irrigation shifted communities toward species with lower leaf nitrogen, which were consistent with some other studies (Sandel et al. 2010, La Pierre and Smith 2015, but see Isbell et al. 2013b). This contraction of trait space may indirectly impact certain ecosystem functions like productivity through time (Isbell et al. 2013a), if, for example, it reduces complementarity between species (Loreau and Hector 2001, Fargione et al. 2007). It could also potentially increase productivity by selecting for more productive species in the new environmental context (Roscher et al. 2012, Cadotte 2017). More studies are needed to understand the consequences of these trait shifts on ecosystem functioning.

We expected that abundance-weighted or functional trait metrics would shift before presence-absence-based measures (Hillebrand et al. 2008, Mouillot et al. 2013b), but found limited evidence for this. Instead, our results also suggest that species gains, which can occur quickly because they require the addition of only one individual, may serve as early indicators for subsequent species losses, which often take more

time because they require the loss of the last individual. Many of the metrics we tested showed a similar pattern where the response in year one was opposite that of the long-term trend. This suggests that the initial burst of resources may encourage the growth of species initially which are at a competitive disadvantage in the long term. While we found that many abundance-weighted metrics, including Simpson's diversity, evenness, and community-weighted means, can have rapid responses to chronic resource addition, these metrics did not necessarily deviate much from ambient temporal trends through time, indicating limits to their sensitivity. Conversely, we saw a rapid increase in both species richness and functional richness within the first year that indicates functionally unique species were added to the community. Rather than turnover, these species were lost over the duration of experiment because many of the dominant species and functional groups tended to increase over time. Further, many of the functional groups responded rapidly to irrigation, and community-weighted means of traits responded rapidly to both fertilization and irrigation. This suggests that the early-indicator metrics may differ from resource to resource. Nevertheless, it does not seem that abundance-weighted or functional trait metrics captured changes in community composition sooner than taxonomic measures.

Nitrogen and water are expected to restructure the community in different ways because of how these treatments were applied and how these resources interact within the system. In this experiment, nitrogen fertilization levels are more comparable to agricultural levels of nitrogen fertilization than rates of atmospheric N deposition. Irrigation treatment levels increased water by 80% compared to average ambient precipitation levels over the past 30 yr. Further, nitrogen was applied once at the beginning of the growing season, whereas irrigation occurred weekly throughout the growing season, so differences in resource addition frequency may cause differences in how plants compete for these resources. Irrigation likely reduced water stress throughout the season, whereas nitrogen addition may have had a disproportionate impact on species establishment early in the growing season. Furthermore, nitrogen can accumulate in the system

over multiple years (Isbell et al. 2013*b*), whereas although irrigation can alleviate water stress throughout the period of application, it is not retained by the sandy soils at our site, limiting the cumulative effect of chronic application. The resulting difference in effective resource availability over time may help to explain why the effects of nitrogen were greater in magnitude at our site. Cedar Creek is strongly nitrogen-limited, and adding nitrogen consistently increases aboveground plant biomass, reduces species richness, and shifts dominance (Tilman 1982, Clark and Tilman 2008, Isbell et al. 2013*a*). Nitrogen is therefore expected to have a greater effect on community structure than water availability, which is not a limitation at our site, except perhaps during droughts, rainfall being higher compared to many other grassland sites (Cleland et al. 2013). It follows that more xeric grasslands may have greater responses to water addition (Cleland et al. 2013, Wilcox et al. 2017). These experimental treatments could impact sites with different climates differently than what we found here, but we expect that gradual, continuous responses should dominate response to chronic pressures.

Environmental changes cause shifts in the functional structure of a community as the result of species replacement and within-species variation of trait values (Lepš et al. 2011). In this paper, we focused on the trait variability between species, that is, using one average trait value for each species for all plots, because variation between species is thought to be greater than variation within a single species (but see Albert et al. 2010, Moran et al. 2016). Further, we were interested in long-term trends, which are primarily related to species replacement (i.e., changes in species composition or abundance). However, the use of average trait values can mask within-species variation, that is, the variation between individuals exposed to different environmental conditions (Smith et al. 2009). Therefore, using average trait values may conceal some changes in community structure that could otherwise be detected by measuring traits for every species in every treatment during every year (Jung et al. 2010, Violle et al. 2012). However, these intraspecific differences are expected to be more important in the case of short-term assessment (Smith et al. 2009, Auger and Shipley 2013) when

the taxonomic structure of the community is more similar to previous states. There is still clearly a need to sort out how important intraspecific trait variation is in determining community structure and over what timescales it is relevant.

Overall, we found that chronic resource additions resulted in continuous, gradual changes in communities, consistent with H2, and that nitrogen and irrigation impacted a similar number of metrics. For metrics that responded to both fertilization and irrigation, fertilization had much a larger effect size. While gradual and increasing changes were the most common, we found evidence for each of our hypothesized trends under both treatment regimes. Because of this array of responses, further research is needed to determine the extent to which our results can be generalized to other resources or sites. Understanding these temporal trends at different sites and for different resources will help inform our expectations for when and how much chronic resource addition will modify communities. We will also be able to show what metrics are early indicators of future change. Thus, discerning exactly when and where we expect these temporal trends to occur will help us develop management strategies to maintain both taxonomic and functional trait diversity in the face of these chronic resource changes.

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figures, analyses, and writing; DT designed experiment and contributed to writing; IA, GB, JC, and JK contributed to plant trait data and writing; and FI contributed to analyses and writing.

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