

## RESEARCH ARTICLE

# Nutrient enrichment alters seasonal $\beta$ -diversity in global grasslands

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## Abstract

1. Intra-annual (i.e. seasonal) temporal niche partitioning is essential to the maintenance of biodiversity in many plant communities. However, understanding of how climate and global change drivers such as eutrophication influence seasonal niche partitioning in plant assemblages remains limited.
2. We used early-season and late-season compositional data collected from 10 grassland sites around the world to explore relationships between climate variability and intra-annual species segregation (i.e. seasonal  $\beta$ -diversity) and to assess how nutrient enrichment alters seasonal  $\beta$ -diversity in plant communities. We then assessed whether changes in seasonal  $\beta$ -diversity in response to nutrient enrichment are underpinned by species turnover or nestedness and determined how specific functional groups (i.e. annual forbs, perennial forbs, C3 and C4 graminoids and legumes) respond to eutrophication within and across early and late sampling dates.
3. We found a positive relationship between intra-annual temperature variability and seasonal  $\beta$ -diversity but observed no relationship between intra-annual precipitation variability and seasonal  $\beta$ -diversity. Nutrient enrichment increased seasonal  $\beta$ -diversity and increased turnover of species between early- and late-season communities. Nutrient enrichment reduced the abundance of C4

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graminoids and legumes within and across sampling timepoints and eliminated intra-annual differences in these groups. In contrast, nutrient enrichment resulted in seasonal differences in C3 graminoids, which were not observed in control conditions and increased abundance of C3 graminoids and annual forbs within and across early and late sampling dates.

4. *Synthesis*: Our understanding of how grasslands respond to various components of global change is primarily based on studies that document community changes at inter-annual scales. Using early-season and late-season compositional data from 10 grassland sites around the world, we show that nutrient enrichment increases seasonal  $\beta$ -diversity and alters intra-annual dynamics of specific functional groups in unique ways.

#### KEYWORDS

community composition, grasslands, intra-annual climate variability, nutrient enrichment, Nutrient Network, temporal beta-diversity, temporal niche segregation

## 1 | INTRODUCTION

Ecologists have investigated the mechanisms by which climate shapes plant diversity for decades (e.g. Harrison et al., 2020; Hawkins et al., 2003; Rosenzweig, 1995). While most research examines associations with mean climate conditions, numerous theoretical (e.g. Adler & Drake, 2008; Chesson, 2000; Lewontin & Cohen, 1969) and empirical (e.g. Knapp et al., 2002; Letten et al., 2013; Levine & Rees, 2004) studies have highlighted the importance of temporal climate variability in structuring populations and communities. Central to these studies is the notion that environmental fluctuations provide opportunities for temporal niche partitioning among species (e.g. Chesson, 2000; Chesson & Huntly, 1997). Within plant communities, intra-annual (i.e. seasonal) temporal niche partitioning is essential to the maintenance of biodiversity and regulation of ecosystem processes (Schofield et al., 2018). Seasonal niche partitioning has been shown to increase coexistence (e.g. Blackford et al., 2020), reduced competition (e.g. Monson et al., 1983), and shape trophic interactions (e.g. Souza et al., 2018). However, within-season community dynamics are studied less frequently than inter-annual dynamics and our understanding of how seasonal niche partitioning responds to global change drivers remains limited (White & Hastings, 2020).

Intra-annual fluctuations in temperature and precipitation may be particularly important drivers of intra-annual temporal niche partitioning in plant communities as they influence plant germination, physiology, and phenology, and modulate ecosystem processes related to water availability and nutrient cycling (Knapp et al., 2002; Luo et al., 2020). However, across global grasslands, temperature variability and precipitation variability are uncorrelated (Gilbert et al., 2020) and may affect seasonal community dynamics via unique mechanisms. Both modelling and empirical studies demonstrate that intra-annual variation in precipitation supports coexistence among plant species via its effects on germination, dormancy, and seasonal growth activity (e.g. Guo & Brown, 1997; Kimball et al., 2011; Levine

et al., 2011; Mathias & Chesson, 2013; Mulroy & Rundel, 1977). On the other hand, changes in seasonal composition related to intra-annual temperature variability are most often attributed to the influence of temperature on plant physiology and associated resource acquisition (e.g. Kemp & Williams, 1980; Monson et al., 1983). Although most evidence documenting the influence of intra-annual climate variability on temporal niche segregation comes from studies of desert systems, temporal segregation of coexisting species is evident in diverse ecosystems including tropical forests (Sapijanskas et al., 2014) and grasslands (Fargione & Tilman, 2005).

In many grasslands, species with specific strategies optimally utilize resources under different environmental conditions and thus coexist by occupying unique temporal positions within communities. For example, in grasslands co-dominated by C3 and C4 grasses, C3 grasses grow and set seed primarily in early to mid-season and C4 grasses grow and set seed primarily in late season (e.g. Kemp & Williams, 1980; Monson et al., 1983). Similar dynamics occur in communities without C3 and C4 grasses present. For instance, in temperate European grasslands early-season grasses and forbs contribute most to productivity at the beginning of the season, whereas late-season grasses contribute most to productivity late in the growing season (e.g. Doležal et al., 2019; Guimarães-Steinicke et al., 2019). However, the same characteristics that promote species-specific responses to fluctuations in environmental conditions often drive species-specific responses to global change drivers such as eutrophication. For example, working in European meadows, Doležal et al. (2019) found that subordinate species with distinct phenologies from dominant species are often reduced in fertilized conditions. Research from the last several years has elucidated how eutrophication alters inter-annual plant community dynamics (e.g. Chen et al., 2022; Hautier et al., 2014). Yet, interactions between eutrophication and intra-annual dynamics of plant communities remain largely unexplored.

Eutrophication in grasslands leads to reduced plant species richness and diversity (e.g. Harpole et al., 2016; Hautier et al., 2009).

Evidence for these patterns has primarily been gathered from studies that measure plant community composition once a year, usually at the peak of biomass production (e.g. Borer et al., 2014). However, research has demonstrated that diverse resource-use strategies allow distinct species assemblages to dominate at different points within a growing season (Doležal et al., 2019; Guimarães-Steinicke et al., 2019; Huang et al., 2019). Seasonal differences in plant communities can be assessed using measures of dissimilarity (i.e. seasonal  $\beta$ -diversity *hereafter*) and its components of “nestedness” (i.e. species in compared communities are subsets of one another) and “replacement” or “turnover” (i.e. species in compared communities are unique) (Baselga, 2009). In grassland systems, nutrient enrichment has been shown to promote the dominance of specific species for longer periods of time, reducing overall dissimilarity among early- and late-season communities (Doležal et al., 2019). Further, the addition of multiple limiting nutrients can reduce the importance of species-specific trade-offs associated with competition for particular nutrients (Harpole et al., 2016) that are most limiting at different points throughout the growing season (Klaus et al., 2016). Assessing how nutrient enrichment affects compositional dissimilarity between early and late-season assemblages would clarify whether patterns of reduced diversity in response to fertilization at inter-annual scales are underpinned by changes in dissimilarity at intra-annual scales.

Changes in overall diversity in responses to nutrient enrichment often result from changes in the abundance of species that are affected by nutrient enrichment in different ways. Nitrogen enrichment reduces the abundance of legumes and nutrient conservative C4 grasses but increases the abundance of nutrient acquisitive C3 grasses (e.g. Suding et al., 2005; Tognetti et al., 2021). Fertilization with multiple nutrients can further alter community composition by causing shifts in the relative abundance of species from specific functional groups (Wilcots et al., 2021). When nutrient enriched communities become dominated by specific species or functional groups, ecosystem stability may be reduced via a loss of asynchronous species responses to environmental fluctuations (Hautier et al., 2014; Hector et al., 2010). In addition, nutrient additions that result in the loss of forb and legume species can have cascading effects on organisms at other trophic levels, such as pollinators, that often depend on these groups for floral resources at specific times of the year (Burkle & Irwin, 2010; Dyer et al., 2021). Understanding how nutrient enrichment affects the abundances of specific functional groups at specific timepoints in the growing season (i.e. early vs. late) and between timepoints is essential to identifying when compositional changes take place and which species drive them.

In this study, we used above-ground species composition data collected early and late in the growing season from 10 grassland sites around the world to explore relationships between intra-annual variability in temperature and precipitation and seasonal  $\beta$ -diversity, and to assess how eutrophication influences seasonal  $\beta$ -diversity of plant assemblages. The 10 sites are part of the Nutrient Network, a globally replicated experiment in which herbaceous plant communities are supplemented with fertilizer. Compositional data from each site spanned between 4 and 11 years. We used data from untreated plots

to explore relationships between intra-annual precipitation and temperature variability and seasonal  $\beta$ -diversity across our study sites. We then examined the effects of fertilization on seasonal  $\beta$ -diversity and its components of nestedness and turnover. Finally, to determine which species underpin changes in seasonal  $\beta$ -diversity in response to fertilization, we assessed overall changes in abundance of different functional groups (i.e. C3 graminoids, C4 graminoids, annual forbs, perennial forbs, legumes) between early and late timepoints and fertilization treatments. Our hypotheses were that:

**H1.** Sites with high intra-annual variability in temperature and precipitation would have high seasonal  $\beta$ -diversity.

**H2.** Fertilization would decrease seasonal  $\beta$ -diversity because a subset of species would dominate across early and late sampling timepoints and neither species nestedness nor turnover would be increased under fertilized conditions.

**H3.** Differences in early-season versus late-season community composition in response to fertilization would be underpinned by increased abundances of resource acquisitive species (e.g. C3 graminoids, annual forbs) and decreased abundances of species with more conservative strategies (e.g. C4 graminoids, perennial forbs, legumes) within and between specific timepoints (i.e. early vs. late).

## 2 | MATERIALS AND METHODS

### 2.1 | Study design and site locations

Data for this study were collected from 10 grassland sites from around the world that are part of the Nutrient Network, a globally distributed experiment in which plant communities are supplemented with factorial combinations of nitrogen (N), phosphorous (P), potassium (K) and micronutrients ( $\mu$ ) (Borer et al., 2014). While most Nutrient Network sites collect above-ground compositional data once a year, data from this subset of sites is collected twice each growing season (“early” and “late” *hereafter*). These sites are distributed across five continents, in Africa (ukul.za), Australia (burrawan.au), Europe (bayr.de, cereep.fr, frue.ch, jena.de), North America (arch.us, temple.us, sevi.us) and South America (chilcas.ar) (Table S1).

Compositional data used in this study were collected from 3 to 5 blocks per site with replicated control and fertilized (i.e. NPK $\mu$ ) plots. Compositional data were gathered for between 4 (bayr.de) and 11 years (ukul.za) (mean length of experiment is 6.5 years, details in Table S1). Fertilized plots at all sites besides cereep.fr received 10 g m<sup>-2</sup> of N, P and K annually with a one-time addition of micronutrients; fertilized plots at the cereep.fr site received 2.5 g m<sup>-2</sup> annually with a one-time addition of micronutrients. Despite this different

application rate, all results were qualitatively similar whether the cereep.fr site was or was not included in analyses, so we retain it in the results presented here. No permits were required to collect these data. For additional details about experimental design, please see Borer et al., 2014.

## 2.2 | Quantifying intra-annual temperature and precipitation variability

We used coefficients of variation (CV) as our measures of intra-annual temperature and precipitation variability. We obtained monthly mean temperature and precipitation values for each site from WorldClim (Fick & Hijmans, 2017) for as many years as data were available between 2006 and 2020 (Table S1). WorldClim provides monthly temperature values, which are calculated from daily values. Temperature CV was calculated as the ratio of the standard deviation of monthly mean temperatures (°K) from a given year to the mean monthly temperature in that year. Precipitation CV was calculated as the ratio of the standard deviation of total monthly precipitation (mm) from a given year to the mean monthly total precipitation in that year. Yearly CVs were then used to estimate average temperature and precipitation CV for each site. In both cases, higher CV values indicate higher variance or greater fluctuations in temperature and precipitation within a year. We chose to use annual variability values rather than growing season values because winter precipitation at some of our sites (e.g. sevi.us) is an important driver of plant community dynamics.

## 2.3 | Quantifying seasonal $\beta$ -diversity

Dissimilarity indices are useful tools for measuring differences between communities in space or time. However, dissimilarity indices can be influenced by local community size (i.e.  $\alpha$ -diversity) and overall richness of species at regional scales (i.e.  $\gamma$ -diversity) (e.g. Chase & Myers, 2011). Deviations from null expectations of dissimilarity (e.g. z-scores) can help determine whether compositional differences, independent of local community size and regional species pools, drive dissimilarity patterns (e.g. Chase & Myers, 2011). More specifically, larger z-scores indicate higher dissimilarity between communities, whereas lower deviations indicate lower dissimilarity.

To quantify dissimilarity between early and late communities in control and NPK $\mu$  treatments at each site, we used deviations from expected values of the Bray–Curtis dissimilarity index (Figure 1). We did this by first permuting species abundances (i.e. absolute values of species cover) from permanent m<sup>2</sup> survey plots 100 times while holding overall richness and total abundances of species constant within a plot at a given sampling timepoint (i.e. early or late season). We used 100 permutations for “early” communities and 100 permutations for “late” communities to obtain mean and standard deviation values for expected (i.e. null) dissimilarity in each plot. We then calculated z-scores for each early-to-late comparison for each plot, year, and treatment combination using the following formula:

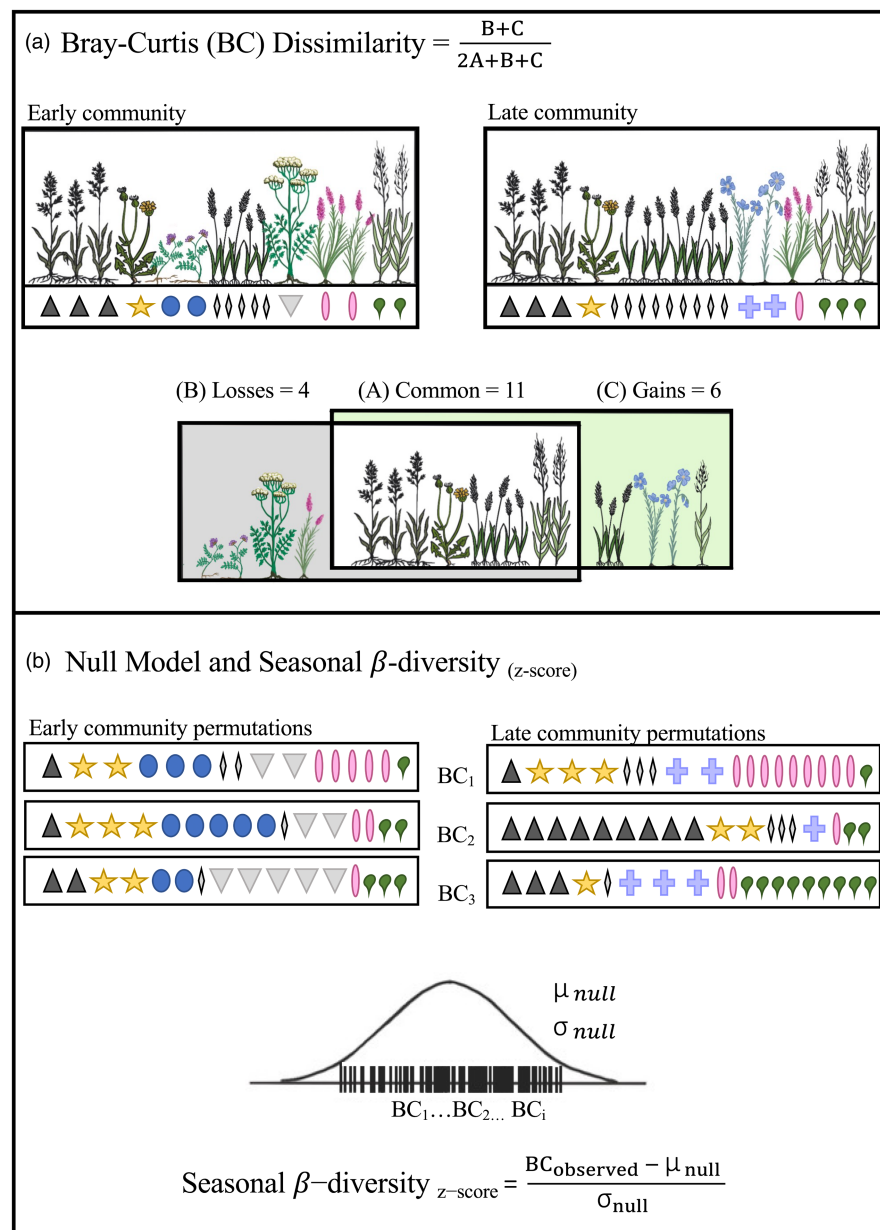
$$\text{Seasonal } \beta\text{-diversity}_{(z\text{-score})} = \frac{BC_{\text{observed}} - \mu_{\text{null}}}{\sigma_{\text{null}}}$$

where  $BC_{\text{observed}}$  is the observed Bray–Curtis value from each plot in each year,  $\mu_{\text{null}}$  is the expected mean for each plot in each year obtained from the distribution of permuted dissimilarity estimates, and  $\sigma_{\text{null}}$  is the variance for each plot in each year obtained from the distribution of permuted dissimilarity estimates (Figure 1b). We used these z-scores as our estimates of seasonal  $\beta$ -diversity from each plot in each year. Comparisons from a given plot in a given year with less than four species at either the early or late sampling time point were removed prior to all analyses because communities with less than four species could not produce sufficient permutations to calculate reliable estimates of seasonal  $\beta$ -diversity. This resulted in the exclusion of 53 early-to-late comparisons from 888 comparisons total (i.e. 835 comparisons were included in analyses).

We also decomposed observed Bray–Curtis dissimilarity from each early-to-late comparison for each plot, year, and treatment into components of species “replacement” (i.e. turnover) and “nestedness” (Baselga, 2009). Nestedness captures the component of dissimilarity that results from one community being a subset of another community, whereas replacement captures the component of dissimilarity that results from certain species being lost and others gained between compared communities. We acknowledge that our assessment of seasonal  $\beta$ -diversity only accounts for patterns observed above-ground and that species may continue to be present, albeit not observed, below-ground. We used the beta.part package (Baselga & Orme, 2012) to obtain all dissimilarity estimates.

## 2.4 | Statistical models

We used two separate linear regression models to explore relationships between intra-annual temperature and precipitation variability and seasonal  $\beta$ -diversity of plant communities (Hypothesis 1, Table S3). In these models, average intra-annual temperature variability or precipitation variability for each site were included as a continuous predictor and average seasonal  $\beta$ -diversity estimates from control treatments from each site were included as a continuous response. We chose to assess these two climate variables independently in relation to  $\beta$ -diversity because precipitation CV and temperature CV are not correlated in our dataset, likely affect seasonal  $\beta$ -diversity via distinct mechanisms, and because our objective was to explore general patterns across sites. We examined how NPK $\mu$  treatment influenced seasonal  $\beta$ -diversity and its components of nestedness and turnover (Hypothesis 2, Table S3) using multilevel regression models with plot-level seasonal  $\beta$ -diversity, nestedness, and turnover values included as response variables, treatment as a predictor, and a random effect of block, nested within treatment year, nested within site. Because not all functional groups are present at all sites, functional group analyses were completed using data from sites that had specific functional groups present at >1% cover on average across years. We fit five separate multilevel regression models to quantify how abundance of specific functional groups (i.e. summed cover of



**FIGURE 1** Panel (a): Bray-Curtis dissimilarity is calculated using the formula  $\frac{B+C}{2A+B+C}$  where B denotes species lost from the early to late community, C denotes species gained from the early to late community, and A denotes shared species between the two communities. Panel (b): Null expectations of dissimilarity are obtained by permuting species abundances  $n$  number of times (3 times shown) while holding richness and total abundance within communities constant and calculating Bray-Curtis dissimilarity from these permuted communities. These values provide a distribution from which null mean ( $\mu_{\text{null}}$ ) and variance ( $\sigma_{\text{null}}$ ) values of dissimilarity are estimated. Deviation (i.e. Seasonal  $\beta$ -diversity (z-scores)) values are then obtained using the following formula: Seasonal  $\beta$ -diversity  $z\text{-score} = \frac{BC_{\text{observed}} - \mu_{\text{null}}}{\sigma_{\text{null}}}$  where  $BC_{\text{observed}}$  is the observed Bray-Curtis value from each early to late comparison,  $\mu_{\text{null}}$  is the expected mean from the distribution of permutation comparisons, and  $\sigma_{\text{null}}$  is the variance from the distribution of permutation comparisons. Symbols in both panels represent species.

all species belonging to annual forbs, perennial forbs, C3 grasses, C4 grasses and legumes from  $m^2$  plots) differed among early and late sampling timepoints and treatments (Hypothesis 3, Table S3). These models included treatment by season combinations as categorical predictors (i.e. control\_early, control\_late, NPK $\mu$ \_early, NPK $\mu$ \_late) and block nested within treatment year nested within site as a random effect. We chose to investigate only interactions because substantial research already documents how both main effects (i.e. season and eutrophication) affect functional groups.

For Bayesian inferences and estimates of uncertainty, all models described were fitted using the Hamiltonian Monte Carlo (HMC) sampler using Stan (Carpenter et al., 2017) and coded using the 'brms' package (Bürkner, 2017) in R (version V.2.1 R Core Development Team). All models were fit with 4 chains and 3500 iterations (Table S3). We used default priors for all models in which dissimilarity estimates (i.e. seasonal  $\beta$ -diversity, nestedness, turnover) were

included as response variables. In models assessing differences in functional group abundances between timepoints and treatments, default priors were used for C3 and C4 graminoid and perennial forb models, whereas weakly regularizing priors were used in models assessing differences in legume and annual forb due to low abundances of these functional groups (Table S3). We inspected the HMC chains to assess model convergence. For all models, we estimated the significance of effects by computing the difference between posterior distributions of interest and assessing whether the 90% credible interval of the difference contained zero.

### 3 | RESULTS

We found no significant correlations among climate variables within our dataset (Table S2). We found a positive relationship between

intra-annual temperature variability and seasonal  $\beta$ -diversity in unfertilized control plots (slope: 0.724, 90% credible interval (CI): 0.2306 to 0.1208; Figure 2a) and no relationship between intra-annual precipitation variability and seasonal  $\beta$ -diversity (slope: 0.0045, CI: -0.0117 to 0.0205; Figure 2b). Contrary to our hypothesis, we detected a significant positive effect of fertilization on seasonal  $\beta$ -diversity across sites (Figure 3). This result indicates greater dissimilarity between early and late season communities in fertilized conditions, even after accounting for differences in richness between the two treatments (average number of species per  $\text{m}^2$  in control: 12.8; average number of species per  $\text{m}^2$  in NPK $\mu$ : 11.5). However, seasonal  $\beta$ -diversity values were negative in most cases, indicating lower than expected dissimilarity between early-season and late-season communities. After decomposing observed seasonal  $\beta$ -diversity into components of nestedness and turnover, we found no differences between treatments in nestedness (Figure 4a) but higher turnover in fertilized conditions than in controls (Figure 4b).

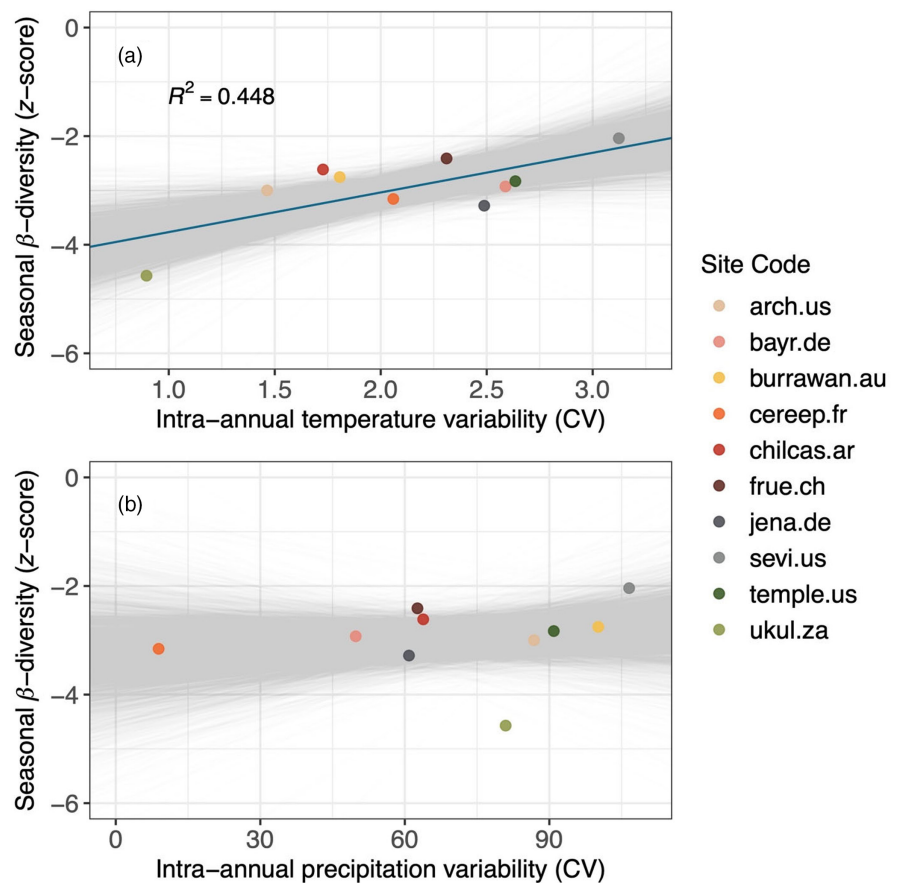
The effects of fertilization varied by functional group and between early and late sampling timepoints (Figure 5). At both sampling timepoints, fertilization resulted in higher cover of annual forbs (Figure 5A) and C3 graminoids (Figure 5C) and lower cover of C4 graminoids (Figure 5D) and legumes (Figure 5E). Perennial forb cover was reduced with fertilization, but only at the late sampling timepoint (Figure 5B). Patterns of functional group abundances between early and late sampling points also varied between control and fertilized treatments. In control but not fertilized treatments,

C4 graminoid abundance was higher at the later sampling point compared to early in the season and legume abundance was higher early in the season compared to late in the season. In contrast, abundance of C3 graminoids was higher early in the season compared to late in the season but only in fertilized treatments.

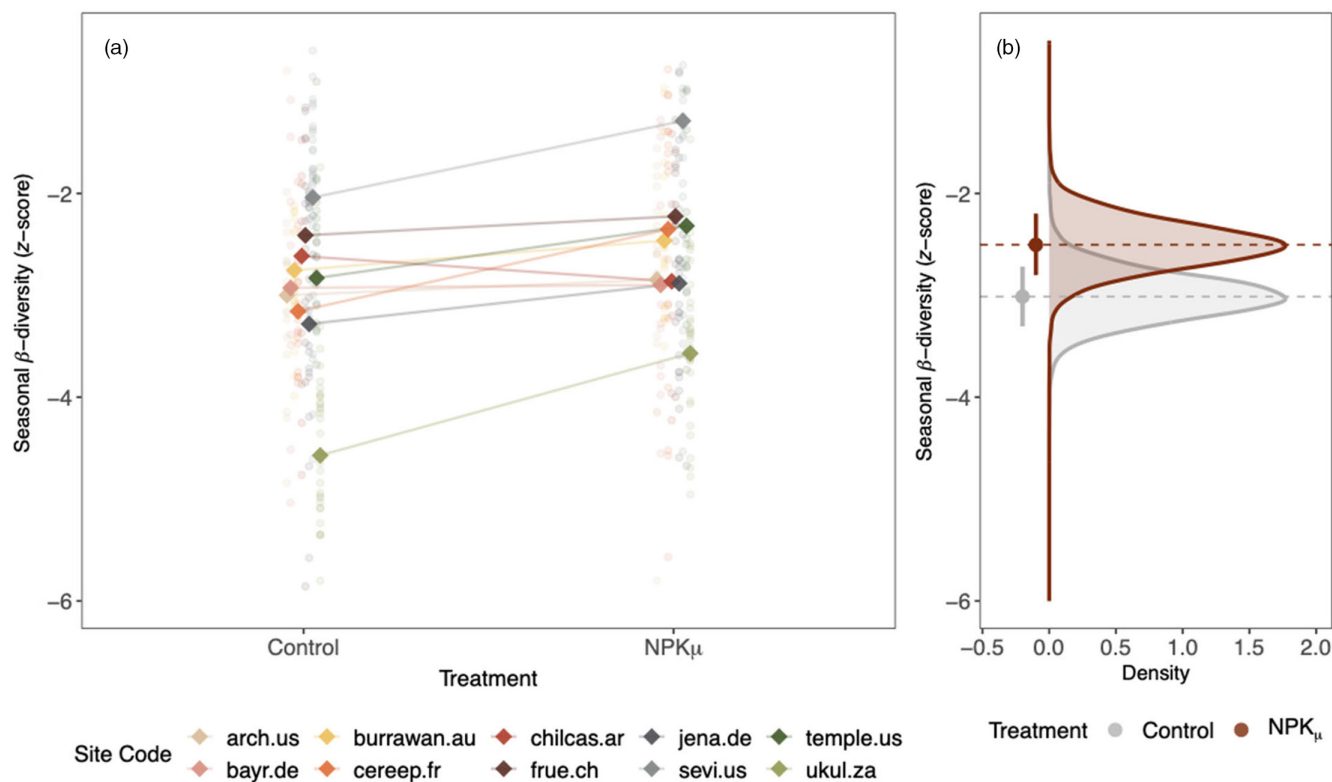
## 4 | DISCUSSION

Seasonal shifts in community composition have been documented in diverse grasslands, and have been shown to influence coexistence, competition and trophic interactions. Seasonal changes in plant communities can also result in distinct peaks in diversity and biomass (Fischer et al., 2023). Yet, most studies assessing how plant communities are responding to various global changes use data gathered once a year, usually at the peak of biomass production. We used early-season and late-season compositional data gathered from 10 grasslands sites around the world to identify relationships between intra-annual climate variability and seasonal  $\beta$ -diversity and to assess how nutrient enrichment alters seasonal community dynamics in herbaceous systems.

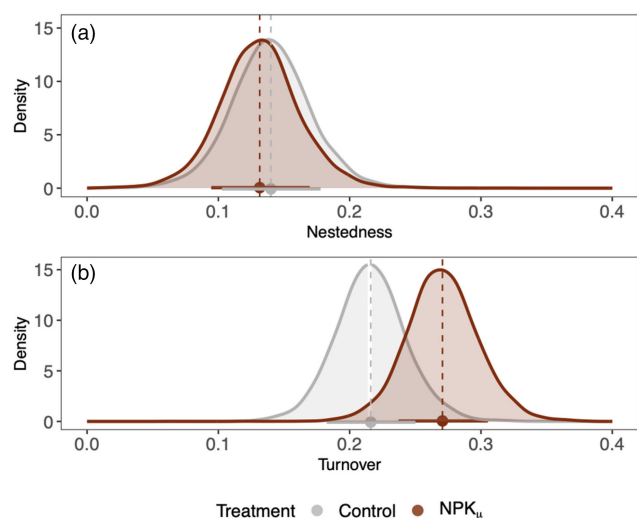
We found higher seasonal  $\beta$ -diversity in grasslands with high intra-annual temperature variability but observed no relationship between intra-annual precipitation variability and seasonal  $\beta$ -diversity. This finding suggests that positive relationships between  $\alpha$ -diversity and intra-annual temperature variability identified in



**FIGURE 2** Relationships between intra-annual temperature (panel a) and precipitation (panel b) variability and mean site-level seasonal  $\beta$ -diversity in control treatments. Grey lines show 500 predicated relationships from posterior model estimates and dark blue lines show averages of model predictions when the distribution of the slope estimate differed from zero at the  $\alpha=0.1$  probability level.



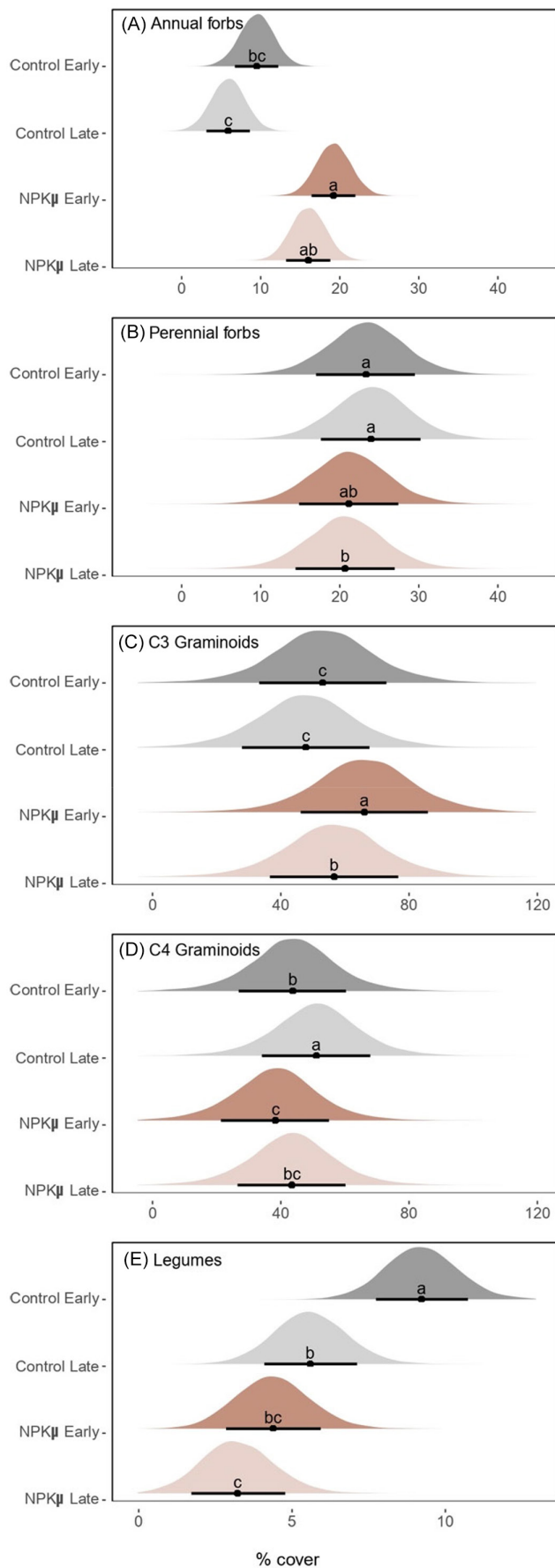
**FIGURE 3** Panel (a): Seasonal  $\beta$ -diversity in control and fertilized (i.e. NPK $\mu$ ) treatments. Circle points are seasonal  $\beta$ -diversity values (i.e. z-scores) from each plot in each year for a given site (different colours) and diamond points are average site-level seasonal  $\beta$ -diversity estimates for each site in each treatment. Panel (b): Posterior distributions of seasonal  $\beta$ -diversity in control and NPK $\mu$  treatments across all sites and years included in analyses. Horizontal lines and points denote estimated means and error bars denote 90% credible intervals of the distributions.



**FIGURE 4** Posterior distributions of nestedness (panel a) and turnover (panel b) components of observed Bray-Curtis dissimilarity in control and fertilized (i.e. NPK $\mu$ ) treatments across all sites and years included in analyses. Points and vertical lines denote estimated means and horizontal line segments denote 90% credible intervals of the distributions.

earlier studies (e.g. Boonman et al., 2021; Scheiner & Rey-Benayas, 1994) may be underpinned by the positive influence of intra-annual temperature variability on temporal segregation of species within

seasons. However, because our analyses were exploratory and because temperature variability is related to latitude, seasonal variation in day length, and growing season length, causal relationships between temperature variability and  $\beta$ -diversity ought to be confirmed with experimental research. Our findings also contradict several studies that implicate intra-annual precipitation variability as a key driver of seasonal  $\beta$ -diversity (e.g. Mathias & Chesson, 2013; Mulroy & Rundel, 1977). We suspect these contradictions arise due to differences in annual systems from which most evidence relating intra-annual precipitation variation to seasonal community dynamics has been gathered, and the predominantly perennial systems in our study. In annual systems, population, community, and ecosystem dynamics are often governed by interactions between intra-annual precipitation patterns and demographic traits related to dormancy and germination (e.g. Kimball et al., 2011; Levine et al., 2011; Shaw et al., 2022). In addition, in systems co-dominated by annuals and perennials, intra-annual variability in precipitation is often necessary for the persistence of annuals that occupy unique temporal niches in communities (e.g. Pérez-Camacho et al., 2012). On the other hand, intra-annual temperature variability may be a more important driver of intra-annual dynamics in perennial systems because temperature regulates plant physiology and shapes temporal segregation among many perennial plant species (e.g. Kemp & Williams, 1980; Monson et al., 1983). Given the low abundance of annual cover across our study sites (c. 11%), we are not able to test these patterns robustly.



**FIGURE 5** Posterior distributions of annual forbs (panel A, 6 sites included in analyses), perennial forbs (panel B, 10 sites included in analyses), C3 graminoids (panel C, 6 sites included in analyses), C4 graminoids (panel D; 6 sites included in analyses), and legumes (panel E; 8 sites included in analyses) early (dark colours) and late (light colours) in the growing season in control (grey) and fertilized (red) treatments. Different letters denote differences between groups at the  $\alpha = 0.1$  probability level, points denote mean estimates, and horizontal line segments denote 90% credible intervals of the distributions. Please note the different scales on the x-axes.

But our results invite new questions about how intra-annual climate variability influences seasonal community dynamics across herbaceous systems dominated by annuals, perennials, or both.

The negative impacts of nutrient enrichment on grassland diversity have been extensively documented (e.g. Borer et al., 2017) and recent studies have identified a positive effect of fertilization on temporal  $\beta$ -diversity at inter-annual scales (Chen et al., 2022; Hodapp et al., 2018; Koerner et al., 2016). Mirroring these results at intra-annual scales, we found that fertilization resulted in higher seasonal  $\beta$ -diversity. Because we used deviations from null expectations as our measure of seasonal  $\beta$ -diversity, we can be confident that these shifts arise from true changes in composition rather than random processes influenced by richness. Similar to results found at inter-annual scales by Chen et al., 2022, we found that higher temporal  $\beta$ -diversity with fertilization was driven by higher turnover of species, and not nestedness of species, between early and late-season communities. This suggests that fertilization increases temporal  $\beta$ -diversity among and within years by similar mechanisms, namely by unique species occupying space within the community at different times (i.e. turnover) rather than species being lost from one timepoint to another (i.e. nestedness). At inter-annual scales, increased temporal  $\beta$ -diversity and species turnover through time can result in reduced stability of ecosystem productivity (e.g. Chen et al., 2022; Koerner et al., 2016). Additional research focused on how nutrient enrichment alters composition and associated ecosystem functions within growing seasons would clarify whether similar patterns manifest at intra-annual scales.

As expected, fertilization resulted in higher abundance of resource acquisitive species (i.e. C3 graminoids, annual forbs) and lower abundance of resource conservative species (i.e. C4 graminoids, legumes, perennial forbs) within and across sampling timepoints. Numerous other studies have documented similar patterns at single timepoints (e.g. Isabell et al., 2013; Suding et al., 2005; Tognetti et al., 2021; Wilcots et al., 2021) and results are primarily attributed to physiological differences between these groups and concomitant shifts from below-ground competition for nutrients to above-ground competition for light (e.g. Borer et al., 2014; Harpole et al., 2017). Among other anatomical and physiological differences, compared to C4 species, C3 species (i.e. most of the annuals in our study and C3 graminoids) generally have lower C:N ratios (e.g. Wedin & Tilman, 1990), lower water and photosynthetic nitrogen use efficiencies (Ripley et al., 2010; Taylor et al., 2014), and earlier phenologies due to lower



optimal temperatures for photosynthesis (Kemp & Williams, 1980). These characteristics can lead to higher sensitivities of resource acquisitive species to nutrient limitation which allow them to increase in fertilized conditions (e.g. Zhong et al., 2019).

Fertilization made apparent seasonal differences in C3 graminoid abundance that were not present under control, while eliminating seasonal differences in abundance of C4 graminoids and legumes that were present in control treatments. Higher C3 graminoid abundance early in the season in fertilized treatments could reflect a higher capacity for growth of these species early in the season when resources are abundant, followed by more pronounced declines later in the season when resources are scarce (e.g. Yuan et al., 2007). In contrast, both C4 graminoids and legumes are adapted to resource-limited conditions, which can vary throughout growing seasons (Klaus et al., 2016). By altering resource conditions, fertilization likely modulates the low-resource periods during which these species thrive resulting in lower abundances of these species overall and homogenization of these groups across the growing season.

Our understanding of how grasslands respond to various components of global change is primarily based on studies that document community shifts at inter-annual scales. However, global changes may also disrupt within-season community dynamics. Here, we show that seasonal  $\beta$ -diversity across 10 global grasslands is related to intra-annual temperature variability and altered by eutrophication. Given that both intra-annual temperature variability (e.g. Xu et al., 2013) and precipitation variability (e.g. Hajek & Knapp, 2022) are expected to increase in coming decades with cascading effects on biodiversity and ecosystem functioning (Knapp et al., 2002), clarifying the effects of these understudied components of global change is essential to understanding how plant communities and ecosystems will change into the future. Investigations focused on specific components of climatic variability such as seasonality (i.e. the occurrence of certain events within a definite limited period, sensu Lieth, 1974) or predictability (i.e. the regularity of recurrence of the within cycle distribution of events, sensu Tonkin et al., 2017) would further illuminate how fluctuations in climate shape seasonal dynamics of plant communities. We also show that nutrient enrichment increases seasonal  $\beta$ -diversity and species turnover, enhances the abundance of resource-acquisitive species (i.e. annual forbs, C3 graminoids) within and between early and late-season communities, and decreases abundances of resource-conservative species (i.e. C4 graminoids, legumes) within and between early and late-season communities. In addition, our results suggest that fertilization results in homogenization of abundances of resource conservative species early to late in the growing season. If the effects of intra-annual community change mirror those at inter-annual scales, the community shifts we observed in our study could have subsequent impacts on ecosystem stability, multifunctionality, and the ability of these systems to recover from future perturbations. Our study provides new insight into the mechanisms by which climate variability and nutrient enrichment shape within-season community

dynamics in global grasslands and highlights how discerning these patterns is essential to our understanding of biodiversity in these valuable ecosystems.

## AUTHOR CONTRIBUTIONS

Magda Garbowski and Stan Harpole conceptualized this project. Magda Garbowski completed analyses with assistance from Hanna Holz, Stephanie Jurburg, and Emma Ladouceur. Magda Garbowski wrote the manuscript. Elizabeth Boughton, Anne Ebeling, Philip Fay, Yann Hautier, Anke Jentsch, Jason Martina, Timothy Ohlert, Xavier Raynaud, Christiane Roscher, Grégory Sonnier, Pedro Maximiliano Tognetti, Laura Yahdjian and Peter Wilfahrt collected data and edited the manuscript.

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## CONFLICT OF INTEREST STATEMENT

None of the authors have conflicts of interest. Yann Hautier is an Associate Editor of Journal of Ecology but took no part in the peer review and decision-making processes for this paper.

## PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14182>.

## DATA AVAILABILITY STATEMENT

Data associated with analyses can be found at: <https://doi.org/10.6084/m9.figshare.23624415.v1> (Garbowski et al., 2023b). Associated code can be accessed at: <https://doi.org/10.5281/zenodo.8215798> (Garbowski et al., 2023a).

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## REFERENCES

- Adler, P. B., & Drake, J. M. (2008). Environmental variation, stochastic extinction, and competitive coexistence. *The American Naturalist*, 172(5), 186–195.
- Baselga, A. (2009). Partitioning the turnover and nestedness components of beta-diversity. *Global Ecology and Biogeography*, 19(1), 134–143.
- Baselga, A., & Orme, D. L. (2012). betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3, 808–812.
- Blackford, C., Germain, R. M., & Gilbert, B. (2020). Species differences in phenology shape coexistence. *The American Naturalist*, 195, E168–E180.
- Boonman, C. C. F., Santini, L., Robroek, B. J. M., Hoeks, S., Kelderman, S., Dengler, J., Bergamini, A., Biurrun, I., Carranza, M. L., Cerabolini, B. E. L., Chytrý, M., Jandt, U., Lysenko, T., Stanisci, A., Tatarenko, I., Růsina, S., & Huijbregts, M. A. J. (2021). Plant functional and taxonomic diversity in European grasslands along climatic gradients. *Journal of Vegetation Science*, 32(3). <https://doi.org/10.1111/jvs.13027>
- Borer, E. T., Grace, J. B., Harpole, W. S., MacDougall, A. S., & Seabloom, E. W. (2017). A decade of insights into grassland ecosystem responses to global environmental change. *Nature Ecology and Evolution*, 1, 0118.
- Borer, E. T., Seabloom, E. W., Gruner, D. S., Harpole, W. S., Hillebrand, H., Lind, E. M., Adler, P. B., Alberti, J., Anderson, T. M., Bakker, J. D., Biederman, L., Blumenthal, D., Brown, C. S., Brudvig, L. A., Buckley, Y. M., Cadotte, M., Chu, C., Cleland, E. E., Crawley, M. J., ... Yang, L. H. (2014). Herbivores and nutrients control grassland plant diversity via light limitation. *Nature*, 508, 517–520.
- Burke, L. A., & Irwin, R. E. (2010). Beyond biomass: Measuring the effects of community-level nitrogen enrichment on floral traits, pollinator visitation and plant reproduction. *Journal of Ecology*, 98(3), 705–717.
- Bürkner, P. C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, 80(1), 1–28.
- Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., & Riddell, A. (2017). Stan: A probabilistic programming language. *Journal of Statistical Software*, 76(1), 1–32.
- Chase, J. M., & Myers, J. A. (2011). Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 366, 2351–2363.
- Chen, Q., Wang, S., Seabloom, E. W., MacDougall, A. S., Borer, E. T., Bakker, J. D., Donohue, I., Knops, J. M. H., Morgan, J. W., Carroll, O., Crawley, M., Bugalho, M. N., Power, S. A., Eskelinen, A., Virtanen, R., Risch, A. C., Schütz, M., Stevens, C., Caldeira, M. C., ... Hautier, Y. (2022). Nutrients and herbivores impact grassland stability across spatial scales through different pathways. *Global Change Biology*, 28, 2678–2688.
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31, 343–366.
- Chesson, P., & Huntly, N. (1997). The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *The American Naturalist*, 150, 519–553.
- Doležal, J., Lanta, V., Mudrák, O., & Lepš, J. (2019). Seasonality promotes grassland diversity: Interactions with mowing, fertilization and removal of dominant species. *Journal of Ecology*, 107, 203–215.
- Dyer, A. G., Jentsch, A., Burd, M., Garcia, J. E., Giejsztowt, J., Camargo, M. G. G., Tjørve, E., Tjørve, K. M. C., White, P. S., & Shrestha, M. (2021). Fragmentary blue: Resolving the rarity paradox in flower colours. *Frontiers in Plant Science*, 11, Article 618203.
- Fargione, J., & Tilman, D. (2005). Niche differences in phenology and rooting depth promote coexistence with a dominant C4 bunchgrass. *Oecologia*, 143, 598–606.
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315.
- Fischer, F. M., Chytrý, K., Chytrá, H., Chytrý, M., & Těšitel, J. (2023). Seasonal beta-diversity of dry grassland vegetation: Divergent peaks of above-ground biomass and species richness. *Journal of Vegetation Science*, 34, e13182.
- Garbowski, M., Boughton, E., Ebeling, A., Fay, P., Hautier, Y., Holz, H., Jentsch, A., Jurburg, S., Ladouceur, E., Martina, J., Ohlert, T., Raynaud, X., Roscher, C., Sonnier, G., Tognetti, P. M., Yahdjian, L., Wilfahrt, P., & Harpole, S. (2023a). Data from: Nutrient enrichment alters seasonal beta-diversity in global grasslands. <https://doi.org/10.5281/zenodo.8215798>
- Garbowski, M., Boughton, E., Ebeling, A., Fay, P., Hautier, Y., Holz, H., Jentsch, A., Jurburg, S., Ladouceur, E., Martina, J., Ohlert, T., Raynaud, X., Roscher, C., Sonnier, G., Tognetti, P. M., Yahdjian, L., Wilfahrt, P., & Harpole, S. (2023b). Data from: Nutrient enrichment alters seasonal beta-diversity in global grasslands. <https://doi.org/10.6084/m9.figshare.23624415.v1>
- Gilbert, B., MacDougall, A. S., Kadoya, T., Akasaka, M., Bennett, J. R., Lind, E. M., Flores-Moreno, H., Firn, J., Hautier, Y., Borer, E. T., Seabloom, E. W., Adler, P. B., Cleland, E. E., Grace, J. B., Harpole, W. S., Esch, E. H., Moore, J. L., Knops, J., McCulley, R., ... Fay, P. A. (2020). Climate and local environment structure asynchrony and the stability of primary production in grasslands. *Global Ecology and Biogeography*, 29, 1177–1188.
- Guimarães-Steinicke, C., Weigelt, A., Ebling, A., Eisenhauer, N., Duque-Lazo, L., Reu, B., Roscher, C., Schumacher, J., Wagg, C., & Wirth, C. (2019). Terrestrial laser scanning reveals temporal changes in biodiversity mechanisms driving grassland productivity. *Advances in Ecological Research*, 61, 133–161.
- Guo, Q., & Brown, J. H. (1997). Interactions between winter and summer annuals in the Chihuahuan desert. *Oecologia*, 111, 123–128.
- Hajek, O. L., & Knapp, A. K. (2022). Shifting seasonal patterns of water availability: Ecosystem responses to an unappreciated dimension of climate change. *New Phytologist*, 233, 119–125.
- Harpole, W. S., Sullivan, L. L., Lind, E. M., Firn, J., Adler, P. B., Borer, E. T., Chase, J., Fay, P. A., Hautier, Y., Hillebrand, H., MacDougall, A. S., Seabloom, E. W., Bakker, J. D., Cadotte, M. W., Chaneton, E. J., Chu, C., Hagenah, N., Kirkman, K., la Pierre, K. J., ... Stevens, C. J. (2017). Out of the shadows: Multiple nutrient limitations drive relationships among biomass, light and plant diversity. *Functional Ecology*, 31, 1839–1846.
- Harpole, W. S., Sullivan, L. L., Lind, E. M., Firn, J., Adler, P. B., Borer, E. T., Chase, J., Fay, P. A., Hautier, Y., Hillebrand, H., MacDougall, A. S., Seabloom, E. W., Williams, R., Bakker, J. D., Cadotte, M. W., Chaneton, E. J., Chu, C., Cleland, E. E., D'Antonio, C., ... Wrapp, P. D. (2016). Addition of multiple limiting resources reduces grassland diversity. *Nature*, 537, 1–9.
- Harrison, S., Spasojevic, M. J., & Li, D. (2020). Climate and plant community diversity in space and time. *Proceedings of the National Academy of Sciences of the United States of America*, 117(9), 4464–4470.
- Hautier, Y., Niklaus, P. A., & Hector, A. (2009). Competition for light causes plant biodiversity loss after eutrophication. *Science*, 324, 636–638.
- Hautier, Y., Seabloom, E., Borer, E., Adler, P. B., Harpole, W. S., Hillebrand, H., Lind, E. M., MacDougall, A. S., Stevens, C. J., Bakker, J. D., Buckley, Y. M., Chu, C., Collins, S. L., Daleo, P., Damschen, E. I., Davies, K. F., Fay, P. A., Firn, J., Gruner, D. S., ... Hector, A. (2014). Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature*, 508, 521–525.
- Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guégan, J.-F., Kaufman, D. M., Kerr, J. T., Mittelbach, G. G., Oberdorff, T., O'Brien,

- E. M., Porter, E. E., & Turner, J. R. G. (2003). Energy, water, and broad-scale geographic patterns in species richness. *Ecology*, 84(12), 3105–3117.
- Hector, A., Hautier, Y., Saner, P., Wacker, L., Bagchi, R., Joshi, J., Scherer-Lorenzen, M., Spehn, E. M., Bazeley-White, E., Weilenmann, M., Caldeira, M. C., Dimitrakopoulos, P. G., Finn, J. A., Huss-Danell, K., Jumpponen, A., Mulder, C. P., Palmberg, C., Pereira, J. S., Siamantziouras, A. S., ... Loreau, M. (2010). General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. *Ecology*, 91(8), 2213–2220.
- Hodapp, D., Borer, E. T., Harpole, W. S., Lind, E. M., Seabloom, E. W., Adler, P. B., Alberti, J., Arnillas, C. A., Bakker, J. D., Biederman, L., Cadotte, M., Cleland, E. E., Collins, S., Fay, P. A., Firn, J., Hagenah, N., Hautier, Y., Iribarne, O., Knops, J. M. H., ... Hillebrand, H. (2018). Spatial heterogeneity in species composition constrains plant community responses to herbivory and fertilization. *Ecology Letters*, 21, 1364–1371.
- Huang, L., Xue, W., & Herben, T. (2019). Temporal niche differentiation among species changes with habitat productivity and light conditions. *Journal of Vegetation Science*, 30, 438–447.
- Isabell, F., Reich, P. B., Tilman, D., Hobbie, S. E., Polasky, S., & Binder, S. (2013). Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 11911–11916.
- Kemp, P. R., & Williams, G. J. A. (1980). Physiological basis for niche separation between *Agropyron Smithii* (C3) and *Bouteloua Gracilis* (C4). *Ecology*, 61, 846–858.
- Kimball, S., Gremer, J. R., Angert, A. L., Huxman, T. E., & Venable, D. L. (2011). Fitness and physiology in a variable environment. *Oecologia*, 169(2), 319–329. <https://doi.org/10.1007/s00442-011-2199-2>
- Klaus, V. H., Boch, S., Boeddinghaus, R. S., Hölzel, N., Kandeler, E., Marhan, S., Oelmann, Y., Prati, D., Regan, K. M., Schmitt, B., Sorkau, E., & Kleinebecker, T. (2016). Temporal and small-scale spatial variation in grassland productivity, biomass quality, and nutrient limitation. *Plant Ecology*, 217, 843–856.
- Knapp, A. K., Fay, P. A., Blair, J. M., Collins, S. L., Smith, M. D., Carlisle, J. D., Harper, C. W., Danner, B. T., Lett, M. S., & McCarron, J. K. (2002). Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science*, 298, 2202–2205.
- Koerner, S. E., Avolio, M. L., la Pierre, K. J., Wilcox, K. R., Smith, M. D., & Collins, S. L. (2016). Nutrient additions cause divergence of tallgrass prairie plant communities resulting in loss of ecosystem stability. *Journal of Ecology*, 104, 1478–1487.
- Letten, A. D., Ashcroft, M. B., Keith, D. A., Gollan, J. R., & Ramp, D. (2013). The importance of temporal climate variability for spatial patterns in plant diversity. *Ecography*, 36(12), 1341–1349.
- Levine, J. M., McEachern, A. K., & Cowan, C. (2011). Seasonal timing of first rain storms affects rare plant population dynamics. *Ecology*, 92(12), 2236–2247. <https://doi.org/10.1890/11-0471.1>
- Levine, J. M., & Rees, M. (2004). Effects of temporal variability on rare plant persistence in annual systems. *The American Naturalist*, 164, 350–363.
- Lewontin, R. C., & Cohen, D. (1969). On population growth in a randomly varying environment. *Proceedings of the National Academy of Sciences of the United States of America*, 62(4), 1056–1060.
- Lieth, H. (1974). *Phenology and seasonality modeling*. Springer-Verlag.
- Luo, Y., el-Madany, T., Ma, X., Nair, R., Jung, M., Weber, U., Filippa, G., Bucher, S. F., Moreno, G., Cremonese, E., Carrara, A., Gonzalez-Cascon, R., Cáceres Escudero, Y., Galvagno, M., Pacheco-Labrador, J., Martín, M. P., Perez-Priego, O., Reichstein, M., Richardson, A. D., ... Migliavacca, M. (2020). Nutrients and water availability constrain the seasonality of vegetation activity in a Mediterranean ecosystem. *Global Change Biology*, 26, 4379–4400.
- Mathias, A., & Chesson, P. (2013). Coexistence and evolutionary dynamics mediated by seasonal environmental variation in annual plant communities. *Theoretical Population Biology*, 84, 56–71.
- Monson, R. K., Littlejohn, R. O., & Williams, G. J. (1983). Photosynthetic adaptation to temperature in four species from the Colorado short-grass steppe: A physiological model for coexistence. *Oecologia*, 58, 43–51.
- Mulroy, T. W., & Rundel, P. W. (1977). Annual plants: Adaptations to desert environments. *Bioscience*, 27, 109–114.
- Pérez-Camacho, L., Rebello, S., Hernández-Santana, V., García-Salgado, J., Pavón-García, J., & Gómez-Sal, A. (2012). Plant functional trait responses to interannual rainfall variability, summer drought and seasonal grazing in Mediterranean herbaceous communities. *Functional Ecology*, 26, 740–749.
- Ripley, B., Frole, K., & Gilbert, M. (2010). Differences in drought sensitivities and photosynthetic limitations between co-occurring C3 and C4 (NADP-ME) panicoid grasses. *Annals of Botany*, 105, 493–503.
- Rosenzweig, M. L. (1995). *Species diversity In space and time*. Cambridge University Press. 436 pp.
- Sapjanskas, J., Paquette, A., Potvin, C., Kunert, N., & Loreau, M. (2014). Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences. *Ecology*, 95, 2479–2492.
- Scheiner, S. M., & Rey-Benayas, J. M. (1994). Global patterns of plant diversity. *Evolutionary Ecology*, 8, 331–347.
- Schofield, E. J., Rowntree, J. K., Paterson, E., & Brooker, R. W. (2018). Temporal dynamism of resource capture: A missing factor in ecology? *Trends in Ecology & Evolution*, 33, 277–286.
- Shaw, E. A., White, C. T., Silver, W. L., Suding, K. N., & Hallett, L. M. (2022). Intra-annual precipitation effects on annual grassland productivity and phenology are moderated by community responses. *Journal of Ecology*, 110(1), 162–172. <https://doi.org/10.1111/1365-2745.13792>
- Souza, C. S., Maruyama, P. K., Aoki, C., Sigrist, M. R., Raizer, J., Gross, C. L., & de Araujo, A. C. (2018). Temporal variation in plant-pollinator networks from seasonal tropical environments: Higher specialization when resources are scarce. *Journal of Ecology*, 106, 2409–2420.
- Suding, K. N., Collins, S. L., Gough, L., Clark, C., Cleland, E. E., Gross, K. L., Milchunas, D. G., & Pennings, S. (2005). Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 4387–4392.
- Taylor, S. H., Ripley, B. S., Martin, T., de-Wet, L. A., Woodward, F. I., & Osborne, C. P. (2014). Physiological advantages of C4 grasses in the field: A comparative experiment demonstrating the importance of drought. *Global Change Biology*, 20, 1992–2003.
- Tognetti, P. M., Prober, S. M., Báez, S., Chaneton, E. J., Firn, J., Risch, A. C., Schuetz, M., Simonsen, A. K., Yahdjian, L., Borer, E. T., Seabloom, E. W., Arnillas, C. A., Bakker, J. D., Brown, C. S., Cadotte, M. W., Caldeira, M. C., Daleo, P., Dwyer, J. M., Fay, P. A., ... Sankaran, M. (2021). Negative effects of nitrogen override positive effects of phosphorus on grassland legumes worldwide. *Proceedings of the National Academy of Sciences of the United States of America*, 118, e2023718118.
- Tonkin, J. D., Bogan, M. T., Bonada, N., Rios-Touma, B., & Lytle, D. A. (2017). Seasonality and predictability shape temporal species diversity. *Ecology*, 98, 1201–1216.
- Wedin, D. A., & Tilman, D. (1990). Species effects on nitrogen cycling: A test with perennial grasses. *Oecologia*, 84, 433–441.
- White, E. R., & Hastings, A. (2020). Seasonality in ecology: Progress and prospects in theory. *Ecological Complexity*, 44, 100867.
- Wilcots, M. E., Harpole, W. S., Seabloom, E. W., & Borer, E. T. (2021). Community change can buffer chronic nitrogen impacts, but multiple nutrients tip the scale. *Ecology*, 102, e03355.
- Xu, L., Myneni, R. B., Chapin, F. S., Callaghan, T. V., Pinzon, J. E., Tucker, C. J., Zhu, Z., Bi, J., Clais, P., Tømmervik, H., Euskirchen, E. S., Forbes, B. C., Piao, S. L., Anderson, B. T., Ganguly, S., Nemani, R. R., Goetz, S. J., Beck, P. S. A., Bunn, A. G., ... Stroeve, J. C. (2013). Temperature and vegetation seasonality diminish over northern lands. *Nature*, 3, 581–586.

- Yuan, Z., Liu, W., Niu, S., & Wan, S. (2007). Plant nitrogen dynamics and nitrogen-use strategies under altered nitrogen seasonality and competition. *Annals of Botany*, *100*, 821–830.
- Zhong, S., Xu, Y., Meng, B., Loik, M. E., Ma, J. Y., & Sun, W. (2019). Nitrogen addition increases the sensitivity of photosynthesis to drought and re-watering differentially in C3 versus C4 grass species. *Frontiers in Plant Science*, *10*, 815.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Table S1.** Nutrient Network sites used in this study with associated latitude (i.e. Lat), longitude (i.e. Long), mean annual temperature (i.e. MAT), mean annual precipitation (i.e. MAP), temperature coefficient of variation (i.e. Temp CV) and precipitation coefficient of variation (i.e. Precip CV). Number of years and range of years used to obtain seasonal  $\beta$ -diversity and climate CV values used in analyses are shown in two right-most columns.

**Table S2.** Pearson correlations for climate variables across our study sites (left side of table). Abbreviations are as follow: MAT: mean annual temperature; MAP: mean annual precipitation; Temp CV: temperature coefficient of variation; Precip CV: precipitation coefficient of variation. None of the correlations are significant at the  $p=0.05$  level.

Range of values for climate variables in our study ( $n=10$ ) and the larger Nutrient Network dataset (NutNet) dataset (right side of table).

**Table S3.** All models were fit using the brms package in R (Bürkner, 2022) with 1600 iterations for warmup. We visually inspected predicted versus observed values and distributions of residuals to assess model performance. For functional group abundance models, we included block nested within treatment year nested within site as a random effect. “trt\_sampling” refers to categorical variables created for treatment and sampling timepoint combinations (i.e. control\_early, control\_late, NPK $\mu$ \_early, NPK $\mu$ \_late).

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