Title: Temperature seasonality and nutrient enrichment drive intra-annual community turnover in global grasslands

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Abstract

In many grasslands, species with specific traits occupy unique temporal positions within communities. Such intra-annual segregation is predicted to be greatest in systems with high variability (i.e., seasonality) in precipitation and temperature because fluctuating environmental conditions select for species that capitalize on resources at different times. However, because most studies on intra-annual community dynamics have been conducted at individual sites, relationships between seasonality and intra-annual turnover at global scales have not yet been identified. Furthermore, the same characteristics that promote species-specific responses to seasonal fluctuations in environmental conditions may also drive species-specific responses to global change drivers such as eutrophication. Research provides evidence that eutrophication alters inter-annual plant community dynamics yet understanding of how it alters intra-annual dynamics remains limited.

We used early-season and late-season compositional data collected from 10 grassland sites around the world to ask how seasonality in precipitation and temperature as well as nutrient enrichment shape intra-annual turnover in plant communities. In addition, we assessed whether changes in the abundances of specific functional groups including annual forbs, perennial forbs, C3 and C4 graminoids, and legumes underpin compositional differences between early- and late-season communities and treatments. We found that temperature seasonality and intra-annual turnover were positively related but observed no relationship between precipitation seasonality and intra-annual turnover. These results conflict with theoretical predictions from earlier studies which suggest precipitation seasonality drives intra-annual turnover in plant communities. In addition, nutrient enrichment increased intra-annual turnover; this pattern was underpinned by increased replacement of species between early- and late-season communities in fertilized

conditions. This finding mirrors patterns observed at inter-annual scales and suggests fertilization can alter compositional dynamics via similar mechanisms at varied temporal scales. Finally, fertilization reduced the abundance of C4 graminoids and legumes and eliminated intra-annual differences in these groups. In contrast, fertilization resulted in intra-annual differences in C3 graminoids which were not observed in control conditions, and increased abundance of C3 graminoids and annual forbs overall. Our study provides novel insight into how seasonality and nutrient enrichment shape intra-annual grassland dynamics and highlights how discerning these patterns is essential to our understanding of biodiversity in these systems.

Keywords: community composition, grasslands, intra-annual climate variability, nutrient enrichment, Nutrient Network, precipitation seasonality, temporal beta-diversity, temporal niche segregation, temperature seasonality

Introduction

The importance of temporal separation of resource use by species, often termed "temporal niche segregation", has been recognized as an important component of species coexistence for decades (e.g., Wiens et al. 1977). 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. Similar dynamics occur in communities without C3 and C4 grasses present. For example, 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., Guimarães-Steinicke et al. 2019, Doležal et al. 2017). Theory suggests that predictable fluctuations in environmental conditions (i.e., seasonality) should promote unique temporal assemblages of species by allowing different species to capitalize on optimal conditions at different times (Tonkin et al. 2017). However, the same characteristics that promote species-specific responses to seasonal fluctuations in environmental conditions often drive species-specific responses to global change drivers such as eutrophication. For example, subordinate forbs and legumes that thrive at different time periods from dominant grasses are often reduced in fertilized conditions in European meadows (e.g., Doležal et al. 2017). Research from the last several years has elucidated how eutrophication alters inter-annual plant community dynamics (e.g., Hautier et al. 2014, Chen et al. 2021). Yet, interactions between global change drivers and intra-annual dynamics of plant communities remain largely unexplored (White and Hastings 2020).

Seasonality in temperature and precipitation may be particularly important drivers of temporal niche segregation, or intra-annual turnover, in plant communities as they influence plant physiology and phenology and modulate ecosystem processes related to water availability and nutrient cycling (Luo et al. 2020). Modeling studies have demonstrated how intra-annual variation in precipitation supports coexistence among plant species with slight ecological differences in germination requirements, growing season length, or seasonal growth activity (Mathias and Chesson 2013). Empirical evidence documenting the influence of seasonality on intra-annual turnover in plant communities mainly comes from studies of desert systems in which winter and summer annuals segregate temporally in response to seasonal fluctuations in precipitation (e.g., Mulroy and Rundel 1977, Guo and Brown 1997). In addition, studies in tropical forests (Sapijanskas et al. 2014) and grasslands (Fargione and Tilman 2005) have demonstrated how within-season niche partitioning enhances complementarity in resource use and coexistence among co-occurring species. However, because these studies have been conducted in individual plant communities, relationships between seasonality and intra-annual turnover at global scales have not yet been identified. In addition, plant communities adapted to seasonal segregation may be changing in composition and structure in response to global change drivers such as eutrophication.

Eutrophication in grasslands leads to reduced plant species richness and diversity (e.g., Hautier et al. 2009, Harpole et al. 2016). 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 in different points within a growing season (Doležal et al. 2017, Guimarães-Steinicke et al. 2019, Huang et al. 2019). In

grassland systems, nutrient enrichment may promote the dominance of species with specific traits for longer periods of time and reduce overall turnover among early- and late-season communities (Doležal et al. 2017). Further, the addition of multiple limiting nutrients may reduce the importance of species-specific trade-offs associated with competition for particular nutrients (Harpole et al. 2016) which may be most limiting at different points throughout the growing season (Klaus et al. 2016). Assessing how nutrient enrichment affects compositional turnover between early and late-season assemblages would clarify whether patterns of reduced diversity in response to fertilization at inter-annual scales are underpinned by reduced turnover 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. For example, 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 (Hector et al. 2010, Hautier et al. 2014). 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 (Burkle and Irwin et al. 2010, Dyer et al. 2021). Understanding how nutrient enrichment affects the abundances of specific functional groups at specific timepoints in

137 the growing season (i.e., early vs late) and between timepoints would clarify when compositional
138 changes or shifts in dominance take place and which species drive them.

139 In this study, we used above-ground species composition data collected early and late in the
140 growing season from 10 grassland sites around the world to assess how seasonality in
141 temperature and precipitation as well as eutrophication influence intra-annual turnover of plant
142 assemblages. The 10 sites are part of the Nutrient Network – a globally replicated experiment in
143 which herbaceous plant communities are supplemented with fertilizer. Data from each site
144 spanned between 4 and 10 years. We used data from untreated plots to assess relationships
145 between precipitation and temperature seasonality (estimates obtained from WorldClim; Fick
146 and Hijmans 2017) and intra-annual compositional turnover across our study sites. We then
147 examined the effects of fertilization on intra-annual turnover and its components of nestedness
148 and replacement. Finally, to determine which species underpin changes in intra-annual turnover
149 in response to fertilization, we assessed overall changes in abundance of different functional
150 groups (i.e., C3 graminoids, C4 graminoids, annual forbs, perennial forbs, legumes) between
151 early and late timepoints and fertilization treatments. Our hypotheses are that:

152 H1. Sites with high intra-annual variability in temperature and precipitation (i.e., high
153 seasonality) have high intra-annual turnover.

154 H2. Fertilization decreases intra-annual turnover because a subset of species will dominate
155 across early and late sampling timepoints.

156 H3. Differences in early-season vs. late-season community composition in response to
157 fertilization are underpinned by increased abundances of resource acquisitive species
158 (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)

Methods

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 (μ) (Borer et al. 2014). While most Nutrient Network sites collect compositional data once a year, data from this subset of sites is collected twice each growing season (named "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 replicated control and NPKμ plots at these sites from 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^{-2} 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^{-2} 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. For additional details about experimental design, please see Borer et al. (2014).

Quantifying temperature and precipitation seasonality

Estimates of temperature and precipitation seasonality for each site were obtained from WorldClim (Fick and Hijmans 2017). Temperature and precipitation seasonality for each site are based on monthly totals of precipitation and temperature where "Temperature seasonality" is the standard deviation of monthly temperature * 100 and "Precipitation seasonality" is the coefficient of variation of monthly precipitation totals for a given year. In both cases, higher values indicate higher variance or greater fluctuations in temperature and precipitation within a year. We chose to use annual seasonality 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. Between 18 and 30 years of precipitation and temperature seasonality data were used to obtain average seasonality values for each site based on data availability in WorldClim.

Quantifying intra-annual turnover in communities

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., α-diversity) and overall richness of species at regional scales (i.e., γ-diversity) (e.g., Chase and 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 and Myers 2011). More specifically, larger z-scores indicate higher dissimilarity between communities, whereas lower deviations indicate lower dissimilarity.

To quantify intra-annual turnover between early and late communities in control and NPKμ 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^2 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 these 200 permuted communities (i.e., 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: $Turnover_{\ z} = \frac{BC_{observed} - \mu_{null}}{\sigma_{null}}$ where $BC_{observed}$ is the observed Bray-Curtis value from each plot in each year, μ_{null} is the expected mean for each plot in each year obtained from the distribution of permutation dissimilarly estimates, and σ_{null} is the variance for each plot in each year obtained from the distribution of permutation dissimilarly estimates (Figure 1b). We used these z-scores (indicated throughout as $turnover_z$) as our estimates of early to late dissimilarity from each plot in each year, hereafter referred to as "intra-annual turnover". 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 $turnover_z$. 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" 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

224 communities. We used the beta.part package (Baselga and Orme 2012) to obtain all dissimilarity
225 estimates.

226 *Statistical models*

227 We used two separate linear regression models to assess relationships between
228 temperature and precipitation seasonality and intra-annual turnover of plant communities. In
229 these models, average site temperature seasonality or precipitation seasonality values were
230 included as a continuous predictor and average $turnover_z$ estimates from control treatments from
231 each site were included as a continuous response. We examined how NPKμ treatment influenced
232 intra-annual turnover using a multilevel regression model with plot-level $turnover_z$ values
233 included as response variables, treatment as a predictor, and a random effect of block, nested
234 within treatment year, nested within site. Because not all functional groups are present at all
235 sites, functional group analyses were completed using data from sites that had specific functional
236 groups present at >1% cover overall. We fit five separate multilevel regression models to
237 quantify how abundance of specific functional groups (i.e., summed cover of all species
238 belonging to annual forbs, perennial forbs, C3 grasses, C4 grasses and legumes from m^2 plots)
239 differed among early and late sampling timepoints and treatments. These models included
240 treatment by season combinations as categorical predictors (i.e., control_early, control_late,
241 NPKμ_early, NPKμ_late) and block nested within treatment year nested within site as a random
242 effect (i.e., interactions were not assessed prior to investigating differences in means).

243 For Bayesian inferences and estimates of uncertainty, all models described were fitted
244 using the Hamiltonian Monte Carlo (HMC) sampler using Stan (Carpenter et al. 2017) and coded
245 using the 'brms' package (Bürkner et al. 2018) in R (version V.2.1 R Core Development Team).

All models were fit with 4 chains and 3000 iterations (Table S2). We used default priors for all models in which dissimilarly estimates (i.e., $turnover_z$, nestedness, replacement) 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 abundances (Table S2). 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.

Results

We found a positive relationship between temperature seasonality and seasonal turnover in unfertilized control plots (Slope: 0.0028, 90% Credible Interval (CI): 0.0004 to 0.0050) (Figure 2a) and no relationship between precipitation seasonality and seasonal turnover (Slope: -0.0052, CI: -0.0278 to 0.0166) (Figure 2b). Contrary to our hypothesis, we detected a significant positive effect of fertilization on seasonal $turnover_z$ across sites (Figure 3). This result indicates greater dissimilarity in fertilized conditions, even after accounting for differences in richness between the two treatments (average number of species per m^2 in control: 12.8; average number of species per m^2 in NPKμ: 11.5). However, $turnover_z$ values were negative in most cases, indicating lower than expected dissimilarity between early-season and late-season communities. After decomposing observed (i.e., Bray-Curtis) intra-annual turnover into components of nestedness and replacement, we found no differences between treatments in nestedness (Figure 4a) but higher replacement 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 (Fig. 5d) and legumes (Fig. 5e). Perennial forb cover was reduced with fertilization, but only at the late sampling timepoint (Fig. 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.

Discussion

Contrary to most empirical and theoretical studies to date (e.g., Mulroy and Rundel 1977, Mathias and Chesson 2013), we found temperature seasonality, not precipitation seasonality, to be positively related to intra-annual compositional turnover across our study sites. We suspect this relationship arises due to differences in annual systems, from which most evidence to date 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., Levine et al. 2011, Kimball 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). If precipitation is highly seasonal, distinct assemblages of annual species may be promoted early vs. late in the growing season. On the other hand, temperature and

temperature seasonality may be more important drivers of intra-annual dynamics in perennial systems because temperature is a key driver of species physiology which drives species temporal segregation in many perennial systems (e.g., Kemp and 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. But a positive, non-significant, relationship between annual species dissimilarity and precipitation seasonality (Supplementary Figure 1a) and a negative, non-significant, relationship between perennial species dissimilarity and precipitation seasonality (Supplementary Figure 1b) invite new questions about how precipitation seasonality influences intra-annual community dynamics across diverse ecosystems. Studies that explicitly manipulate precipitation seasonality across systems varying in temperature seasonality could help clarify how interactions between these two understudied components of climate change shape plant communities.

The negative impacts of nutrient enrichment on grassland diversity have been extensively documented (e.g., Borer et al. 2017) and recent studies have identified higher turnover of species at inter-annual scales with nutrient addition (Koerner et al. 2016, Hodapp et al. 2018, Chen et al. 2021). Mirroring these results at intra-annual scales, we found that fertilization resulted in higher intra-annual turnover in community composition, despite lower richness in fertilized communities. Because we used deviations from null expectations as our response, 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 (Chen et al. 2021), we found that higher turnover with fertilization was driven by higher replacement of species, and not nestedness of species, between early and late-season communities. This suggests that fertilization increases temporal turnover among and within years by similar mechanisms, namely by unique

species occupying space within the community at different times (i.e., replacement) rather than species being lost from one timepoint to another (i.e., nestedness). At inter-annual scales, increased turnover and species replacement through time can result in reduced stability of ecosystem productivity (e.g., Koerner et al. 2016, Chen et al. 2021). 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., Suding et al. 2005, Isabell et al. 2013, Wilcots et al. 2021, Tognetti et al. 2021) and results are primarily attributed to physiological differences between these groups and concomitant shifts from below-ground competition for nutrients to aboveground 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 and Tilman 1990), lower water and photosynthetic nitrogen use efficiencies (Black 1971, Taylor et al. 2011, Ripley et al. 2010), and earlier phenologies due to lower optimal temperatures for photosynthesis (Kemp and 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. 2014). 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 intra-annual turnover of species across 10 global grasslands is related to temperature seasonality, not precipitation seasonality as predicted by previous studies. Given that both temperature and precipitation seasonality are expected to change in coming decades (Xu et al. 2013, Hajek and Knapp 2021) additional research that explicitly manipulates seasonality is needed to clarify how these understudied components of global change alter plant communities. In addition, we show that nutrient enrichment increases intra-annual turnover in grasslands via increased replacement of species between seasons. The resulting community shifts are underpinned by changes in abundance of specific functional groups. Namely, fertilization increases abundances of resource-acquisitive species (i.e., annual forbs, C3 graminoids) and decreases abundances of resource-conservative species (i.e., C4 graminoids, legumes) within and between early and late sampling timepoints. In addition, 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 cascading effects on ecosystem stability, multifunctionality, and the ability of these systems to recover from future perturbations. Our study provides novel insight into how seasonality 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.

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Figures:

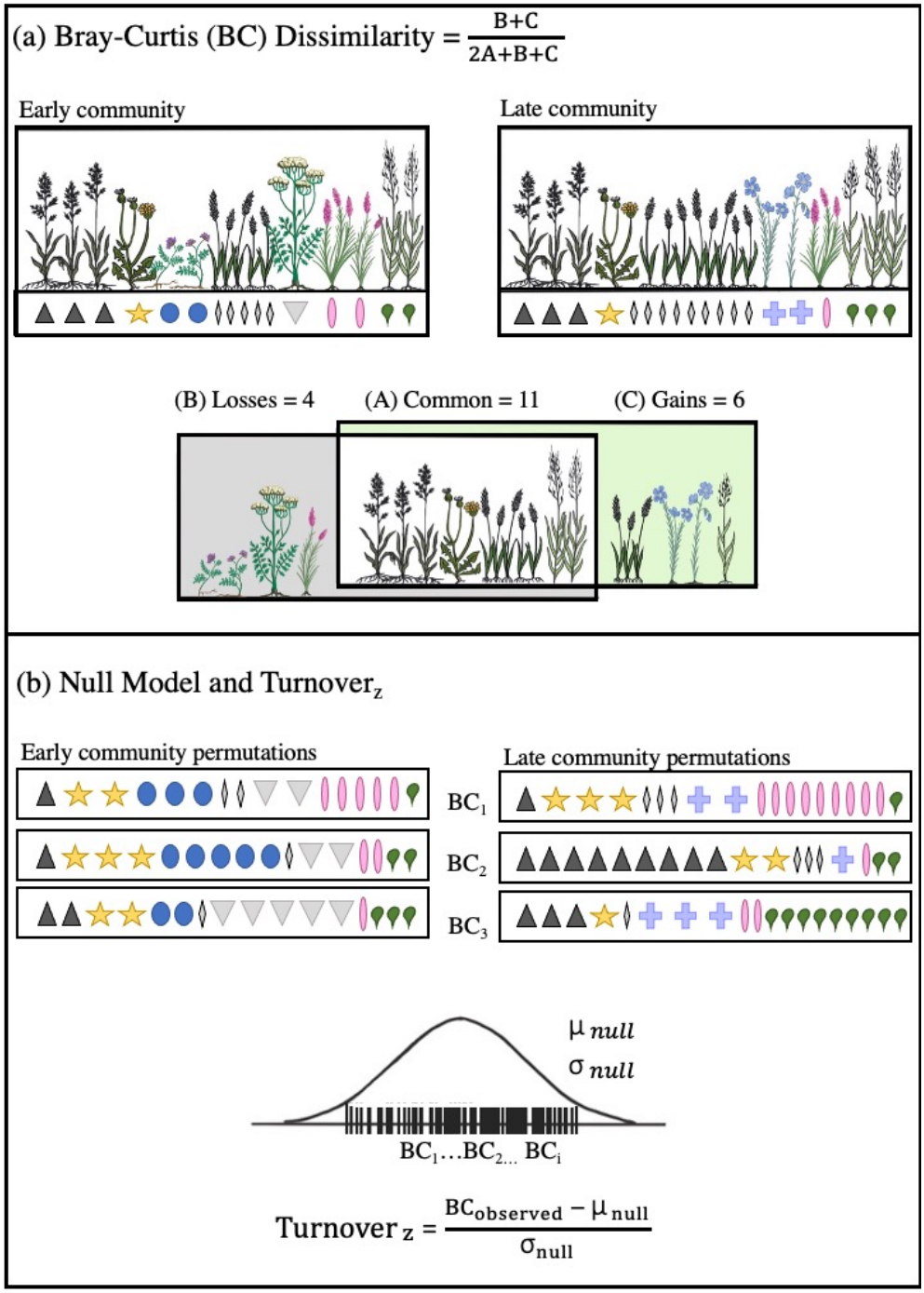
(a) Bray-Curtis (BC) Dissimilarity = $\frac{B+C}{2A+B+C}$
Early community
Late community
(B) Losses = 4
(A) Common = 11
(C) Gains = 6
(b) Null Model and Turnover$_z$
Early community permutations
Late community permutations
BC_1
BC_2
BC_3
μ_{null}
σ_{null}
$BC_1 \ldots BC_2 \ldots BC_i$
$\text{Turnover}_z = \frac{BC_{observed} - \mu_{null}}{\sigma_{null}}$

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 (μ_{null}) and variance (σ_{null}) values of dissimilarity are estimated. Deviation (i.e., z-scores, Turnover_z) values are then obtained using the following formula: $Turnover_z \frac{BC_{observed} - \mu_{null}}{\sigma_{null}}$ where $BC_{observed}$ is the observed Bray-Curtis value from each early to late comparison, μ_{null} is the expected mean from the distribution of permutation comparisons, and σ_{null} is the variance from the distribution of permutation comparisons. Symbols in both panels represent species.

Figure 2

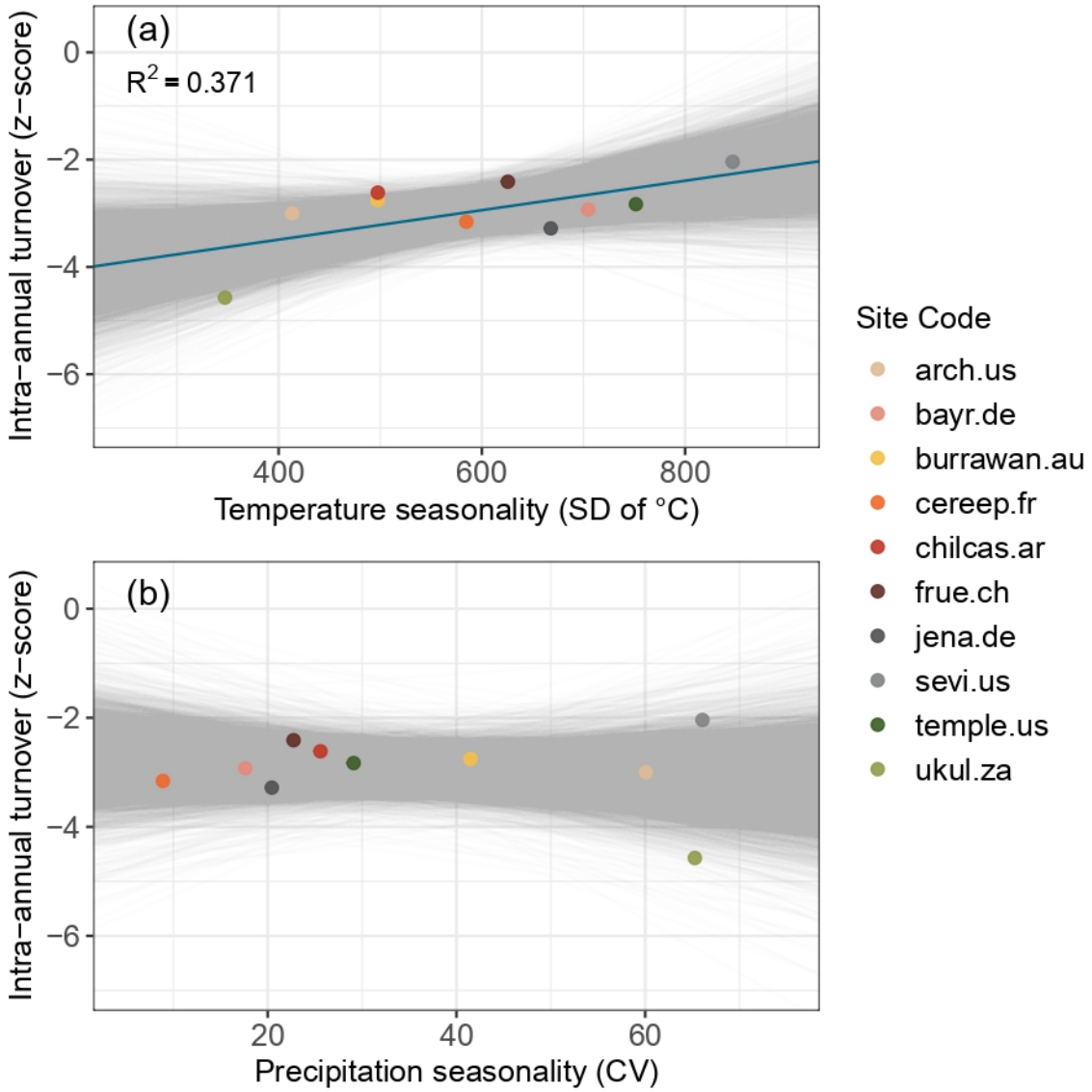

Figure 2: Relationships between temperature (panel a) and precipitation (panel b) seasonality and mean intra-annual turnover in control treatments. Gray lines show 500 predicated relationships from posterior model estimates and dark blue lines show averages of these expectations when the distribution of the slope estimate differed from zero at the $\alpha = 0.1$ probability level.

Figure 3

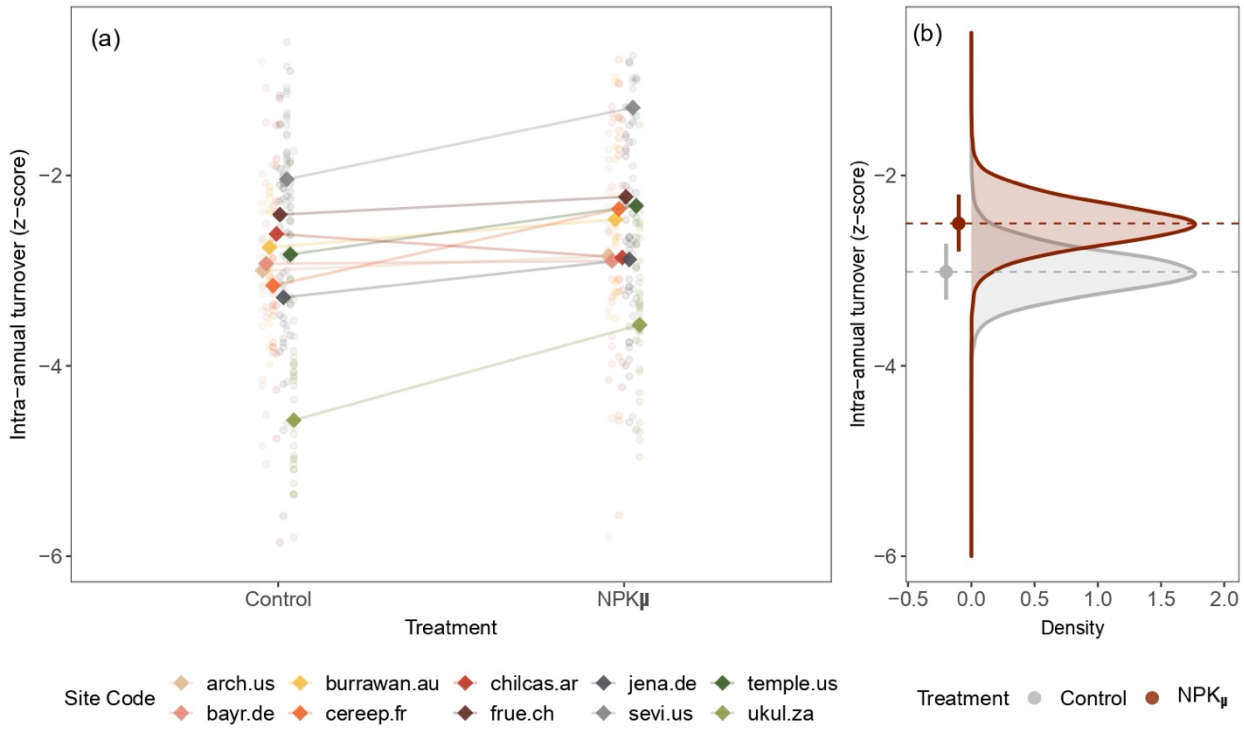

Figure 3: Panel a) Intra-annual turnover in control and fertilized (i.e., NPKμ) treatments. Circle points are turnover z-scores (i.e., deviations from null expectations) from each plot in each year for a given site (different colors) and diamond points are average site-level turnover estimates for each site in each treatment. Panel b) Posterior distributions of intra-annual turnover in control and NPKμ 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

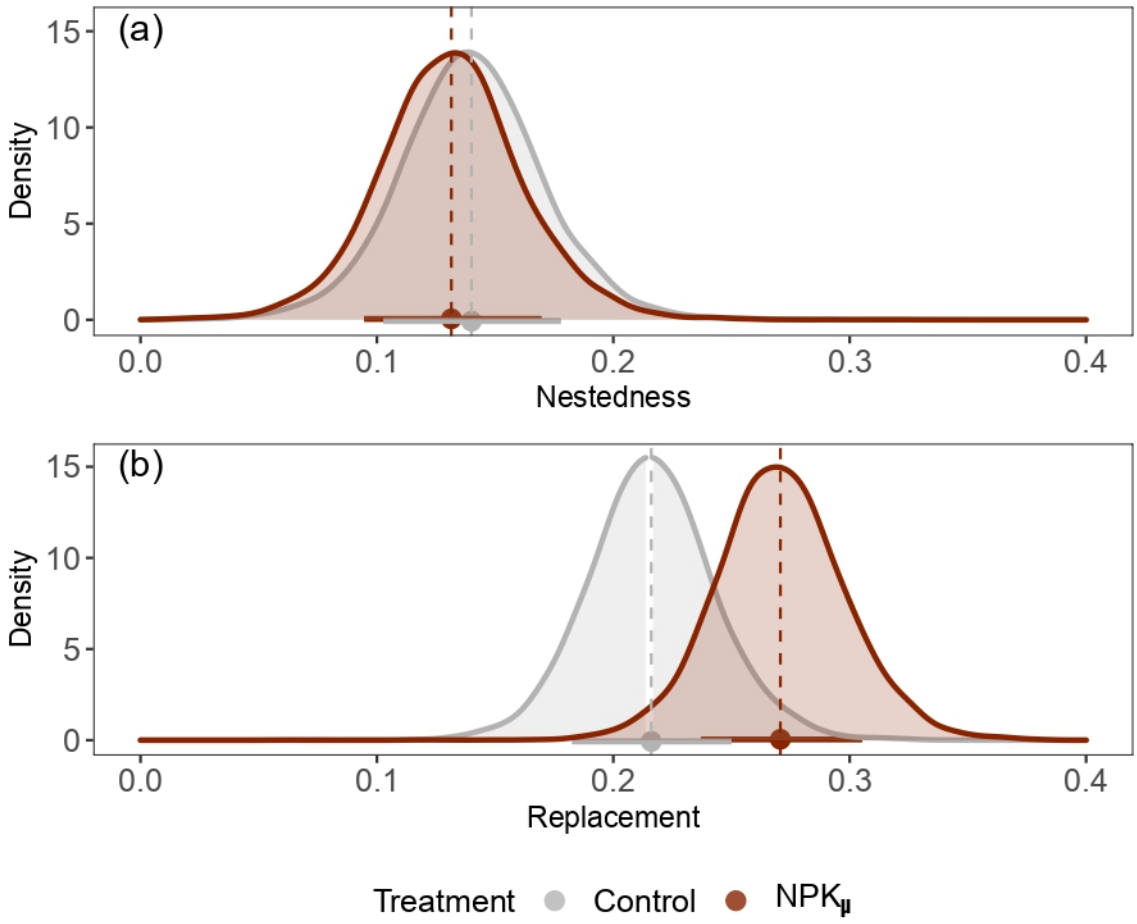

Figure 4: Posterior distributions of nestedness (panel a) and replacement (panel b) components of Bray-Curtis dissimilarity in control and fertilized (i.e., NPK) treatments across all sites and years included in analyses. Points and vertical lines denote estimated means and horizonal line segments denote 90% credible intervals of the distributions.

Figure 5

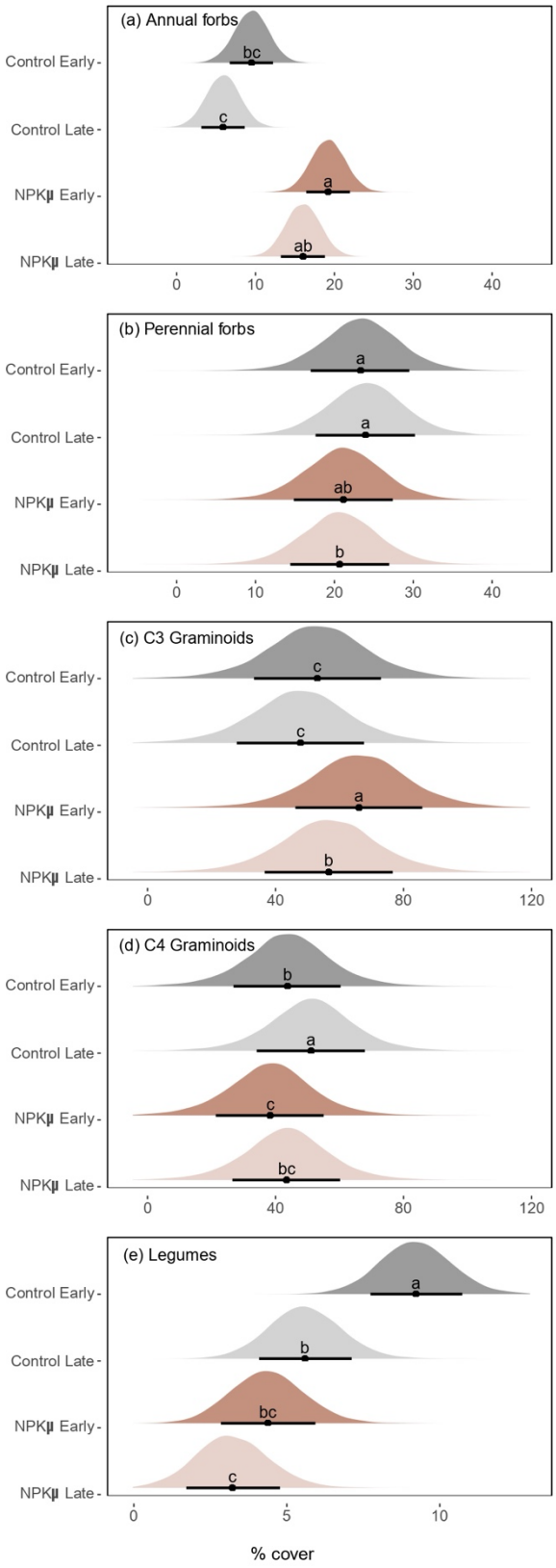

Figure 5: Posterior distributions of annual forbs (panel a, 6 sites included in analyses), perennial forbs (panel b, 10 sites included in analyses), C3 graminoids (panel c, 6 sites included in analyses), C4 graminoids (panel d; 6 sites included in analyses), and legumes (panel e; 8 sites included in analyses) early (dark colors) and late (light colors) 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 horizonal line segments denote 90% credible intervals of the distributions. Please note the different scales on the x-axes.