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Methods, Tools, and Technologies

Compositional variation in grassland plant communities

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Abstract

Human activities are altering ecological communities around the globe. Understanding the implications of these changes requires that we consider the composition of those communities. However, composition can be summarized by many metrics which in turn are influenced by different ecological processes. For example, incidence-based metrics strongly reflect species gains or losses, while abundance-based metrics are minimally affected by changes in the abundance of small or uncommon species. Furthermore, metrics might be correlated with different predictors. We used a globally distributed experiment to examine variation in species composition within 60 grasslands on six continents. Each site had an identical experimental and sampling design: 24 plots × 4 years. We

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expressed compositional variation within each site—not across sites—using abundance- and incidence-based metrics of the magnitude of dissimilarity (Bray–Curtis and Sorensen, respectively), abundance- and incidence-based measures of the relative importance of replacement (balanced variation and species turnover, respectively), and species richness at two scales (per plot-year [alpha] and per site [gamma]). Average compositional variation among all plot-years at a site was high and similar to spatial variation among plots in the pretreatment year, but lower among years in untreated plots. For both types of metrics, most variation was due to replacement rather than nestedness. Differences among sites in overall within-site compositional variation were related to several predictors. Environmental heterogeneity (expressed as the CV of total aboveground plant biomass in unfertilized plots of the site) was an important predictor for most metrics. Biomass production was a predictor of species turnover and of alpha diversity but not of other metrics. Continentality (measured as annual temperature range) was a strong predictor of Sorensen dissimilarity. Metrics of compositional variation are moderately correlated: knowing the magnitude of dissimilarity at a site provides little insight into whether the variation is driven by replacement processes. Overall, our understanding of compositional variation at a site is enhanced by considering multiple metrics simultaneously. Monitoring programs that explicitly incorporate these implications, both when designing sampling strategies and analyzing data, will have a stronger ability to understand the compositional variation of systems and to quantify the impacts of human activities.

KEYWORDS
Bray–Curtis dissimilarity, fertilization, grassland, NutNet, plant community, Sorensen dissimilarity, spatial variation, species composition, temporal variation, turnover, vegetation

INTRODUCTION

Predicting how global change or management actions affect the biodiversity of a site (Grab et al., 2019; Hautier et al., 2015; Komatsu et al., 2019) requires that we consider its compositional variation and how that variation is structured. There are many metrics to summarize community composition, and these metrics emphasize different elements of composition. For example, univariate measures such as species richness are easily understood but provide no information about species identity (Hillebrand et al., 2018). Numerous studies have emphasized the importance of moving beyond univariate metrics to better understand community response to environmental change (Avolio et al., 2015; Dornelas et al., 2014; Jones et al., 2017; Komatsu et al., 2019; Magurran et al., 2018; Yoccoz et al., 2018), though it is unclear which metrics of compositional variation to use in different contexts (Anderson et al., 2011; Legendre & De Cáceres, 2013). Since metrics emphasize different elements of compositional variation, they also provide different insights into the processes that structure biodiversity (Table 1). For example, metrics based on incidence only require the presence or absence of each species in each sample unit and thus emphasize colonization and extinction processes, while abundance-based metrics incorporate the abundances of those species present in each sample unit and therefore are more strongly affected by differences in abundance between sample units, particularly for large individuals or aggregations. Furthermore, overall variation can be partitioned into components such as nestedness and turnover that reflect different ecological processes. This partitioning can be done both for incidence- and abundance-based metrics (Baselga, 2010, 2013). These considerations suggest that an approach that simultaneously considers multiple metrics may be beneficial.

Considering multiple metrics is also beneficial if metrics covary with, and can be predicted by, different environmental factors. For example, precipitation gradients influence the turnover of rare bird species whereas temperature gradients influence the turnover of widespread bird species (Latombe et al., 2017), and whether drainages were glaciated or not during the Quaternary

TABLE 1 Metrics used in this study. The four metrics of compositional variation are combinations of theme (magnitude of dissimilarity or relative importance of replacement) and type (abundance-based or incidence-based). Metrics of richness (incidence-based) are calculated at two scales.

Theme	Type	Formula	Notes
Magnitude of dissimilarity			Overall magnitude of dissimilarity between two plot-years. Values range from 0 (identical composition) to 1 (completely different compositions).
Bray–Curtis	Abundance	$d_{BC} = (B + C)/(2A + B + C)$	Gives more weight to more abundant species.
Sorensen	Incidence	$\beta_{sor} = (b + c)/(2a + b + c)$	Gives equal weight to all species.
Relative importance of replacement			How much of the compositional variation between two plot-years is due to the replacement of one individual or species by another. Values range from 0% (none of the compositional variation is due to replacement or, equivalently, all is due to nestedness) to 100% (all of the compositional variation is due to replacement, none to nestedness).
Balanced variation (%)	Abundance	$100(\min(B,C)/(A + \min(B,C))/d_{BC})$	The abundance-based analogue of Simpson's index, reflecting changes in the relative cover of species, expressed as a percentage of Bray–Curtis dissimilarity. The balance of Bray–Curtis dissimilarity is due to unidirectional abundance gradients (i.e., the difference in total cover), which is the abundance-based analogue to nestedness. See Baselga (2013) for details.
Species turnover (%)	Incidence	$100(\min(b,c)/(a + \min(b,c))/\beta_{sor})$	Simpson's index (β_{sim}), expressed as a percentage of Sorensen dissimilarity. The balance of Sorensen dissimilarity is due to nestedness. See Baselga (2010) for details.
Richness			Univariate summary of species present in site.
Alpha diversity	Incidence		Mean richness per plot-year
Gamma diversity	Incidence		Total richness across all 96 plot-years. For a given alpha diversity, higher gamma diversity reflects more turnover among plot-years.

Note: Terminology follows Baselga (2010, 2013): $A = \sum_i \min(x_{ij}, x_{ik})$, $B = \sum_i x_{ij} - \min(x_{ij}, x_{ik})$, $C = \sum_i x_{ik} - \min(x_{ij}, x_{ik})$, x is the cover of species i in plots j and k, a is the number of species common to both plots, b is the number of species that occur in plot j but not in plot k, and c is the number of species that occur in plot k but not in plot j.

continues to determine the relative importance of nestedness among freshwater fish communities (Leprieur et al., 2011). With respect to plant communities, composition should be more consistent in productive sites, while turnover may be greater at sites with greater environmental heterogeneity or less predictable climates (Kraft et al., 2011). Aggregation can result from dispersal limitation and/or environmental filtering (Myers et al., 2013), suggesting that abundance-based metrics may be more strongly related to these types of factors than incidence-based metrics.

Studies often examine large-scale compositional variation among sites (e.g., Baselga, 2010; Kraft et al., 2011; Mugnai et al., 2022; Myers et al., 2013) or small-scale variation within a site (e.g., Zhou et al., 2019). Few studies have compared small-scale, within-site variation among sites, yet such comparisons are critical to understanding whether the small-scale variation is predictable (Jiménez-Alfaro et al., 2018) and whether the underlying mechanisms are consistent among sites (e.g., De Cáceres et al., 2012; Myers et al., 2013). This knowledge is fundamental to improving vegetation classifications (Tierney et al., 2018) and informing site management. For example, it may be easier to establish new species at a site where compositional variation is primarily driven by colonization and extinction processes than at a site where compositional variation is primarily abundance-based. Conversely, biotic regulation of ecosystem services such as productivity may be stronger at sites where compositional variation is primarily abundance-based, as per the mass ratio hypothesis (Smith et al., 2020).

Here, we analyzed small-scale (i.e., within-site) compositional variation of grassland plant communities using multiyear data from 60 sites of a globally distributed experiment. Sites had identical experimental and sampling designs. We assessed species composition separately for each site and then compared patterns among sites. Although small-scale compositional variation can be attributed to specific sources (spatial patterning, temporal patterning, treatment effects, and interactions thereof), we focused primarily on overall variation, asking: (1) How does small-scale compositional variation differ among grasslands? (2) Can compositional variation within a site be predicted by its biotic and abiotic context? and (3) Does a combination of metrics enhance our understanding of the ecological processes at individual sites? We calculated compositional variation using four dissimilarity-based compositional metrics and two richness metrics. The compositional metrics are related to the magnitude of dissimilarity and to the relative importance of replacement. Within each of these themes, one metric reflected species incidence (i.e., presence/absence) while the other also incorporated information about the abundance of each species. The richness metrics, alpha (richness per plot-year) diversity and gamma (richness across all plot-years; site-level) diversity, provided univariate comparisons to the compositional metrics. Since the terminology surrounding composition can be confusing (Anderson et al., 2011), we use "variation" to refer to the compositional variation in a site, and "predictor" rather than "explanatory variable" to avoid confusion between the closely related words variable and variation.

METHODS

We used data from the NutNet multiple-nutrient addition experiment, as detailed in Borer, Harpole, et al. (2014). At each site, the experiment has a completely randomized block design. Plots are 5 × 5 m and separated by at least 1 m. Eight factorial combinations of nitrogen, phosphorus, and potassium were added annually; plots receiving potassium also received a one-time application of micronutrients at the start of the experiment. We measured plant community composition in one permanent 1 × 1 m quadrat per plot, visually estimating the aerial cover of each plant species. Additionally, we measured plant production as peak total aboveground biomass (live and dead) within two 0.1-m^2 strips (0.1 × 1 m) per plot. Biomass was clipped, dried at 60°C to constant mass, and weighed.

We used data from sites that met three criteria: (1) each nutrient combination was tested in one plot per block and in at least three blocks per site, (2) plots were measured during four consecutive growing seasons (pretreatment and 3 years of treatment), and (3) every plot was measured every year. Sites with more than three blocks were subsetted, usually by using the first three blocks. The resulting dataset had an identical structure for every site: 24 plots (8 nutrient combinations × 3 blocks) and 96 plot-year combinations (24 plots × 4 years). Sixty sites met these criteria, providing 5760 site-plot-year combinations for this analysis. These sites span 16 countries on six continents (Appendix S1: Table S1 and Figure S1). By standardizing sampling efforts across sites, we avoided methodological differences in spatial or temporal extent of sampling that could have skewed comparisons (Marion et al., 2017; White et al., 2006). We included all nutrient combinations to capture a wide range of compositional variation within sites but note that our objectives here do not include quantifying compositional differences among nutrient treatments.

Analyses of compositional change are sensitive to how taxa are identified. We reviewed the nomenclature within each site to ensure consistent naming over time. Taxonomic adjustments were made in 70% of sites (43 of 60), usually by aggregating taxa at the genus level when individuals were not identified as species in all years (Appendix S1: Table S2). For brevity, however, we refer to taxa as "species" throughout this study. The resulting dataset consists of ~70,000 records from 1737 vascular plant species.

We identified 10 site-level ecological and environmental predictors that we hypothesized might relate to compositional variation and that were available for all sites (Appendix S1: Table S3). Biomass was calculated as the mean total aboveground plant biomass (in grams per square meter) in unfertilized plots (both pretreatment data from all plots and untreated plots over time). This predictor serves as an index of net production, though it does not account for herbivory. Environmental heterogeneity was quantified as the CV of total aboveground plant biomass in unfertilized plots. We acknowledge that this is imperfect as biomass is also affected by biotic factors, but alternative predictors such as soil characteristics were not available for all sites. Climate was characterized by six relatively uncorrelated predictors extracted from WorldClim v2 (https://www.worldclim.org/data/worldclim21.html): mean annual precipitation (BIO12), precipitation seasonality (BIO15), mean annual temperature (BIO1), temperature seasonality (BIO4), temperature annual range (BIO7), and temperature of the wettest quarter (BIO8). Nitrogen deposition was estimated using the GEOS-Chem Chemical Transport Model (Ackerman et al., 2018). Management was coded as a binary predictor based on whether the site was subject to intentional actions such as burning, grazing, and other anthropogenic disturbances. The global distribution of our sites provided large gradients in these predictors—for example, biomass ranged from 33 to 1692 g m^{-2} y^{-1}, mean annual temperature from −3.3 to 24.1°C, and mean annual precipitation from 192 to 2114 mm among sites (Appendix S1: Table S1).

Statistical analyses

All analyses were done in R (version 4.2.1; R Core Team, 2022). Key functions and packages are highlighted where appropriate below; data and scripts are provided in https://doi.org/10.6073/pasta/8bc6b7f79701d2fc802ee5e46938fc96.

We analyzed composition separately for each site. Composition was expressed as a plot-year × species matrix, with the abundance (i.e., cover) of each species as the elements in the matrix. This matrix was used to calculate four compositional metrics (Table 1). The Bray–Curtis and Sorensen dissimilarity indices account for the magnitude of compositional dissimilarity. Both indices express the dissimilarity between two plot-years in the range from 0 (identical) to 1 (completely different), but Bray–Curtis is abundance-based while Sorensen is incidence-based. The two replacement metrics express how much of the dissimilarity between two plot-years is due to replacement (Table 1; Baselga, 2010, 2013). Replacement and nestedness are additive and together account for the total dissimilarity between two sample units, so tests of each would not be independent. To avoid this, we focused on the relative importance of replacement by calculating the percentage of Bray–Curtis dissimilarity that is attributable to balanced variation (i.e., changes in abundance of dominant species), and the percentage of Sorensen dissimilarity that is attributable to species turnover. Bray–Curtis and Sorensen dissimilarities were decomposed into their additive aspects using the "bray.part" and "beta.pair" functions, respectively (betapart package, v.1.5.6; Baselga et al., 2022). An example of these calculations is provided in Appendix S2. For each compositional metric, the above calculations result in a dissimilarity matrix (96 × 96; 8 nutrient combinations × 3 blocks × 4 years) summarizing the compositional differences within a site. Matrices of the magnitude of dissimilarity contain as elements the dissimilarity between plot-years, while matrices of the relative importance of replacement contain as elements the percentage of compositional change between plot-years associated with balanced variation when abundance-based and with species turnover when incidence-based.

Species richness was quantified from the plot-year × species matrix at two scales for each site. Alpha diversity was calculated as the mean number of species per plot-year. Gamma diversity was calculated as the total number of species recorded in the 96 plot-years at the site. Richness values were log-transformed to better meet distributional assumptions.

Question 1: How does small-scale compositional variation differ among grasslands?

We expressed the overall compositional variation at each site as the mean of the site's dissimilarity matrix (i.e., across all 96 plot-years; Marion et al., 2017). For context, these values were compared to simple measures of spatial and temporal variation in composition, where spatial variation was calculated as the mean dissimilarity among the 24 plots in the pretreatment year and temporal variation as the mean dissimilarity among years for the three plots in which no nutrients were added (calculated separately for each plot and then averaged). We used a linear mixed model ("lmer" function in lme4 package, v.1.1-30; Bates et al., 2015) to test for differences between these three measures of variation (overall, spatial, and temporal) with site name included as a random effect. Pairwise comparisons among measures of variation were made with Tukey's honestly significant difference test.

Overall alpha and gamma diversity levels were compared among sites but were not calculated for spatial or temporal subsets (i.e., in the pretreatment year and within untreated plots over time, respectively) as richness is scale-dependent and thus is not directly comparable among subsets (Marion et al., 2017).

Question 2: Can compositional variation within a site be predicted by its biotic and abiotic context?

We tested how overall compositional variation, as expressed by each metric, related to the 10 potential site-level predictors. For each metric, we used the dredge function in the MuMIn package (version 1.46.0; Bartoń, 2022) to evaluate all subsets of the global model by ranking them based on Bayesian information criterion (BIC). To focus on models with similar explanatory ability, we restricted our attention to models within two units of the top model (Burnham & Anderson, 2002). Model-averaged coefficients were calculated across this set of models. Goodness of fit was assessed by calculating the model R^2, defined as the square of the correlation between the original dataset and the values predicted using the model-averaged raw coefficients. Model-averaged standardized coefficients were used to compare predictors, focusing on those identified as significant using $\alpha = 0.05$. To check the sensitivity of results to the modeling approach, we also tested predictors individually (Appendix S1: Table S3 and Figure S2) and through stepwise model selection (Appendix S3).

Question 3: Does a combination of metrics enhance our understanding of the ecological processes at individual sites?

We compared responses to questions 1 and 2 based on the different compositional metrics to assess the correspondence based on data type (i.e., abundance- or incidence-based) or focused on the same theme (i.e., magnitude of dissimilarity or relative importance of replacement). We also used scatterplots and Pearson correlation coefficients to compare the average values for each metric at each site. Finally, we considered the extent to which combinations of metrics provide unique information about the processes at each site. For each type of data, we plotted the themes against one another and assessed whether each site was above or below the median value for each metric. This produced four quadrants (low magnitude of dissimilarity and low relative importance of replacement [Low/Low], Low/High, High/Low, and High/High) and enabled us to identify sites in which the incorporation of abundance data strongly affected the calculated variation, sites in which variation primarily reflected differences in the magnitude of dissimilarity, and sites in which variation primarily reflected changes in the relative importance of replacement.

RESULTS

Question 1: How does small-scale compositional variation differ among grasslands?

Sites exhibited considerable variation in magnitude of dissimilarity but similar patterns for abundance- and incidence-based metrics. Overall mean abundance-based (Bray–Curtis) dissimilarity ranged from 0.23 to 0.89 among sites, with a mean of 0.56 (Figure 1A). Overall dissimilarity was significantly greater than spatial dissimilarity (i.e., pretreatment data from all 24 plots; mean = 0.49) and even greater than temporal dissimilarity (i.e., untreated plots over time; mean = 0.41; $F_{2,120} = 52.2$, $p < 0.001$). Incidence-based dissimilarities were lower than abundance-based dissimilarities: overall mean Sorensen dissimilarity ranged from 0.22 to 0.56 among sites, with an average of 0.38. Overall incidence-based dissimilarity was significantly greater than spatial dissimilarity (mean = 0.33), which was also significantly greater than temporal dissimilarity (mean = 0.26; Figure 1B; $F_{2,120} = 52.0$, $p < 0.001$).

Replacement accounted for most of the compositional variation and had similar patterns for both abundance- and incidence-based data. Balanced variation (e.g., when a decline in one species is offset by an increase in another species) accounted for 51%–96% of the overall abundance-based dissimilarity at different sites (mean = 82%; Figure 1C). Balanced variation accounted for less of the compositional variation when considering only temporal dissimilarities in untreated plots (71%; $F_{2,120} = 47.6$, $p < 0.001$). Species turnover (e.g., when the loss of one species is offset by the gain of another species) accounted for 27%–88% of the incidence-based compositional variation at different sites (mean = 70%; Figure 1D). Species turnover accounted for less of the compositional variation when considering only temporal dissimilarities in untreated plots (57%; $F_{2,120} = 39.1$, $p < 0.001$).

Alpha diversity ranged from 2.3 to 31.5 species per plot-year among sites (mean = 10.6). Gamma diversity, the total number of species identified in the 96 plot-years, ranged from 17 to 113 among sites (mean = 41.6).

Question 2: Can compositional variation within a site be predicted by its biotic and abiotic context?

Overall compositional variation was related to multiple site-level predictors (Figure 2; Appendix S1: Table S4). Depending on the metric, two to five models had similar explanatory abilities as determined by BIC. Most predictors were retained in some of the final models, but only three were statistically significant for one or more composition metrics (Appendix S1: Table S5). Environmental heterogeneity (i.e., CV of aboveground biomass in unfertilized plots) had the most consistent effects across metrics: it was retained in at least one model for all metrics and was a statistically significant predictor for five of the six metrics. Results from model selection were largely consistent with results of simple linear regression (Appendix S1: Table S3 and Figure S2) and from stepwise model selection (Appendix S3).

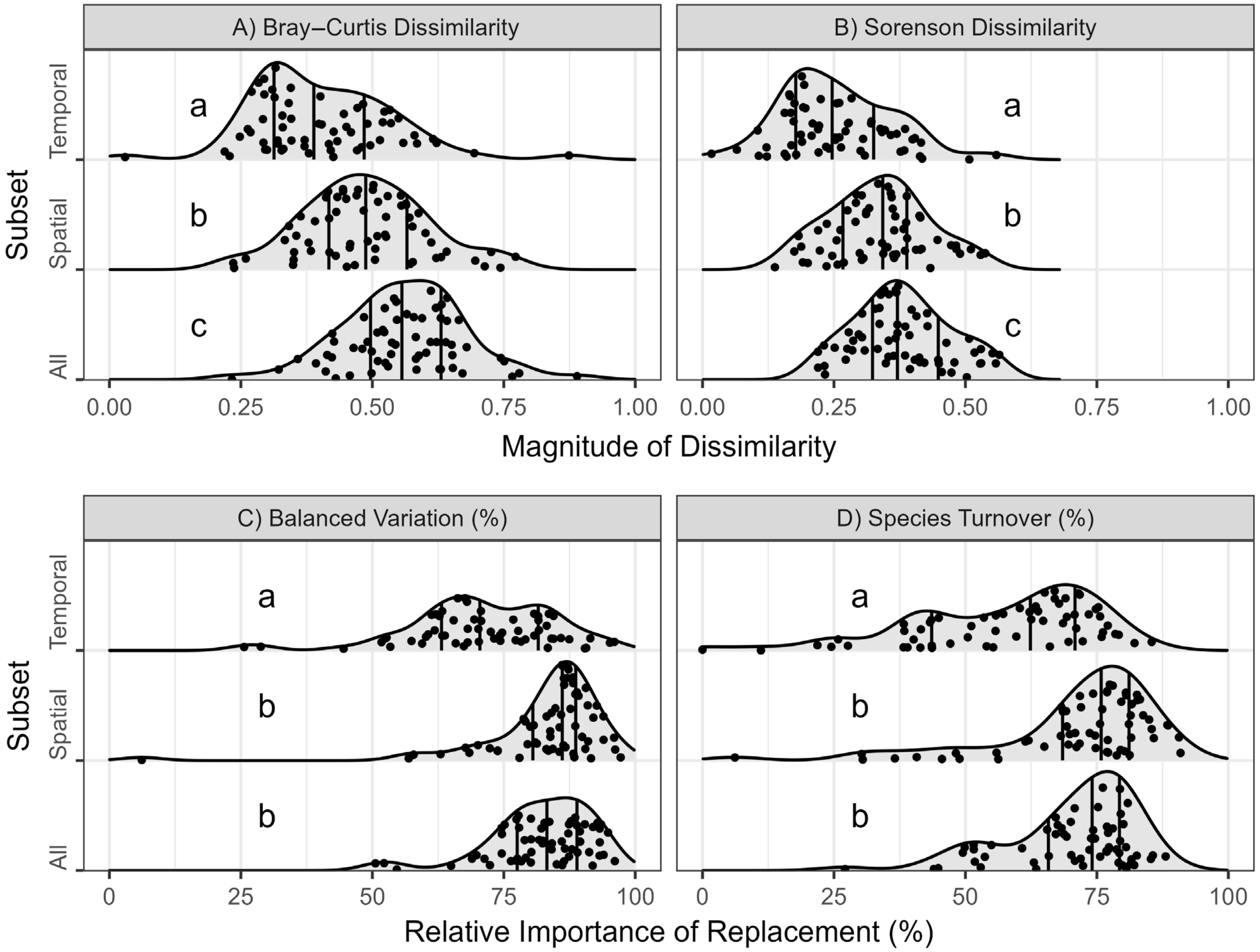

FIGURE 1 Four compositional metrics for three subsets: among all plot-year combinations (All), among plots in the pretreatment year only (Spatial), and among years in untreated plots (Temporal). The top row focuses on the magnitude of dissimilarity: (A) abundance-based (Bray–Curtis) dissimilarity and (B) incidence-based (Sorensen) dissimilarity. The bottom row focuses on the relative importance of replacement: (C) the percentage of Bray–Curtis dissimilarity due to balanced variation in abundance among species and (D) the percentage of Sorensen dissimilarity due to species turnover. Each site ($n = 60$) is a point within each subset. Vertical lines denote quartiles within the density plots. Within each graph, different lowercase letters indicate statistically significant differences among subsets ($\alpha = 0.05$).

The two metrics of magnitude of dissimilarity had different relationships with predictors (Figure 2). Abundance-based (Bray–Curtis) dissimilarity increased with environmental heterogeneity; biomass was also retained in one of the final models for this metric ($R^2 = 0.25$). Incidence-based (Sorensen) dissimilarity increased strongly with the annual temperature range; four other predictors were retained in a subset of the final models ($R^2 = 0.36$).

Regardless of whether abundance- or incidence-based data were used, the relative importance of replacement decreased with environmental heterogeneity (Figure 2). Biomass and mean annual precipitation were retained in a subset of the final models for balanced variation (abundance-based; $R^2 = 0.33$). Species turnover (incidence-based) decreased with biomass; the annual temperature range was retained in a subset of the final models for this metric ($R^2 = 0.22$).

Alpha diversity was strongly related to the predictors, but gamma diversity was not (Figure 2). Alpha diversity decreased with environmental heterogeneity and with biomass; four other predictors were retained in a subset of the final models for this metric ($R^2 = 0.50$). Gamma diversity also decreased with environmental heterogeneity, but biomass was the only other predictor retained in a subset of the final models for this metric ($R^2 = 0.10$).

Question 3: Does a combination of metrics enhance our understanding of the ecological processes at individual sites?

Some, but not all, compositional metrics were correlated (Figure 3). The strongest correlations were between metrics of the same theme: between Bray–Curtis and Sorensen

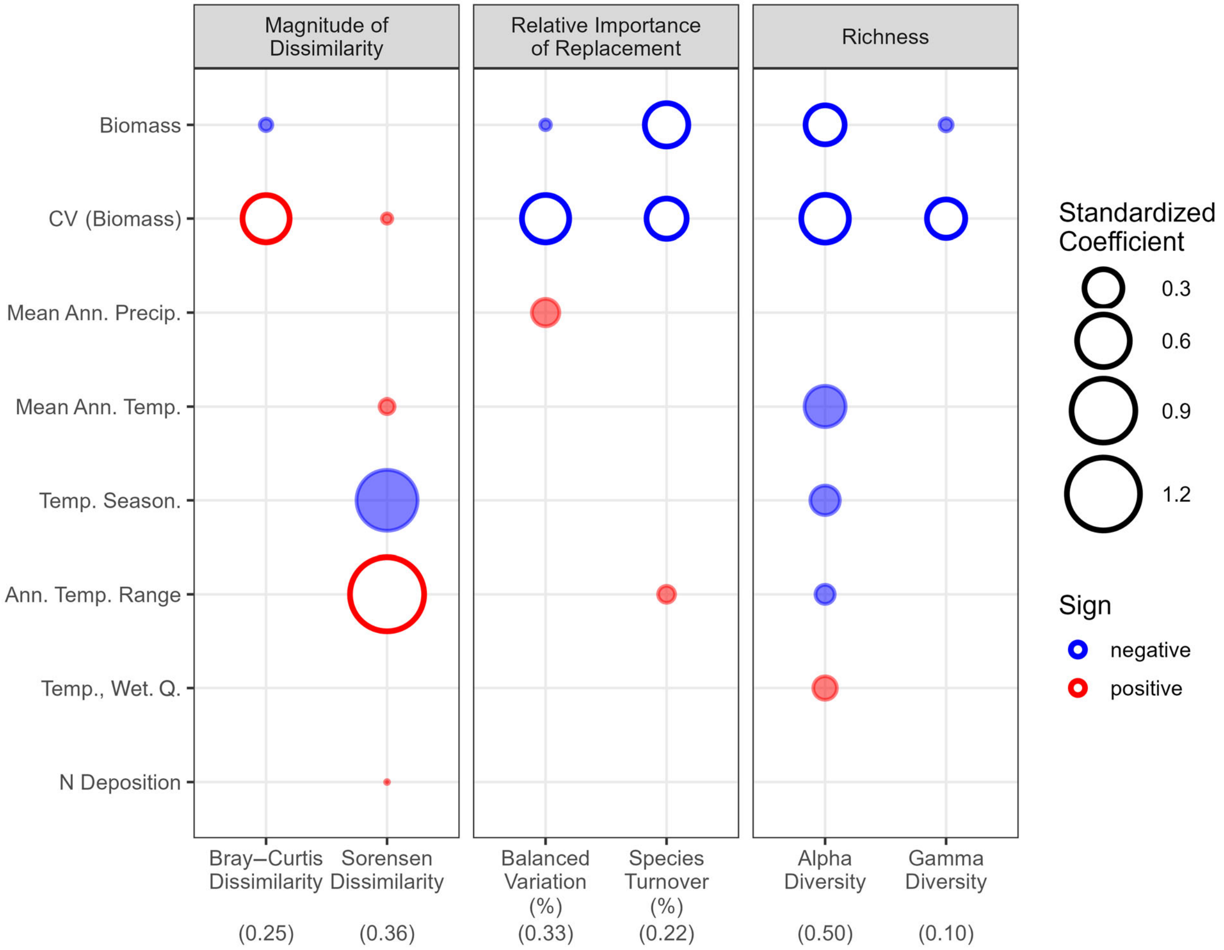

FIGURE 2 Dot plot of standardized regression coefficients for predictors retained following multimodel inference based on a global model with 10 potential predictors. Metrics are arrayed along the *x*-axis with their overall R^2 in parentheses; predictors are on the *y*-axis. Symbols are colored by sign (positive or negative), scaled according to effect size (magnitude of standardized coefficient), and open or filled based on whether or not they were statistically significant in the final subset of models for a metric. Numerical summaries for all predictors are provided in Appendix S1: Tables S4 and S5. Simple linear models for each combination of predictor and metric are shown in Appendix S1: Figure S2. Ann., annual; Precip., precipitation; Season., seasonality; Temp., temperature; Wet. Q., wettest quarter.

dissimilarities ($R^2 = 0.620$) and between balanced variation and species turnover ($R^2 = 0.571$). The two incidence-based metrics (Sorensen dissimilarity and species turnover) were moderately correlated ($R^2 = 0.401$), but the two abundance-based metrics (Bray–Curtis dissimilarity and balanced variation) were uncorrelated ($R^2 = 0.090$).

Compositional and richness metrics had different relationships. Bray–Curtis dissimilarity was uncorrelated with either richness metric while Sorensen dissimilarity was correlated with gamma diversity ($R^2 = 0.372$) but not with alpha diversity ($R^2 = -0.166$). Metrics of the relative importance of replacement were strongly correlated with both richness metrics ($R^2 \geq 0.433$).

Many patterns were broadly similar between metrics of the same theme. For example, patterns of spatial and temporal variation were similar for the two metrics quantifying the magnitude of dissimilarity (Figure 1A,B) and for the two metrics examining the relative importance of replacement (Figure 1C,D). Similarly, metrics of the same type tended to respond in the same direction to environmental heterogeneity and biomass but not to climate-based predictors (Figure 2).

Other patterns varied strongly between abundance- and incidence-based metrics. Abundance-based metrics were larger than incidence-based metrics: the mean difference between Bray–Curtis and Sorensen dissimilarity values was 0.18 (range = −0.15 to 0.38) and the mean difference between balanced variation and species turnover was 12% (range = −4% to 38%). Sites were distributed across the space defined by the magnitude of dissimilarity and relative importance of replacement (Figure 4). However, the location of sites within this space depended on the type of metric: more than half of the sites (32 of 60) were assigned to different quadrants for

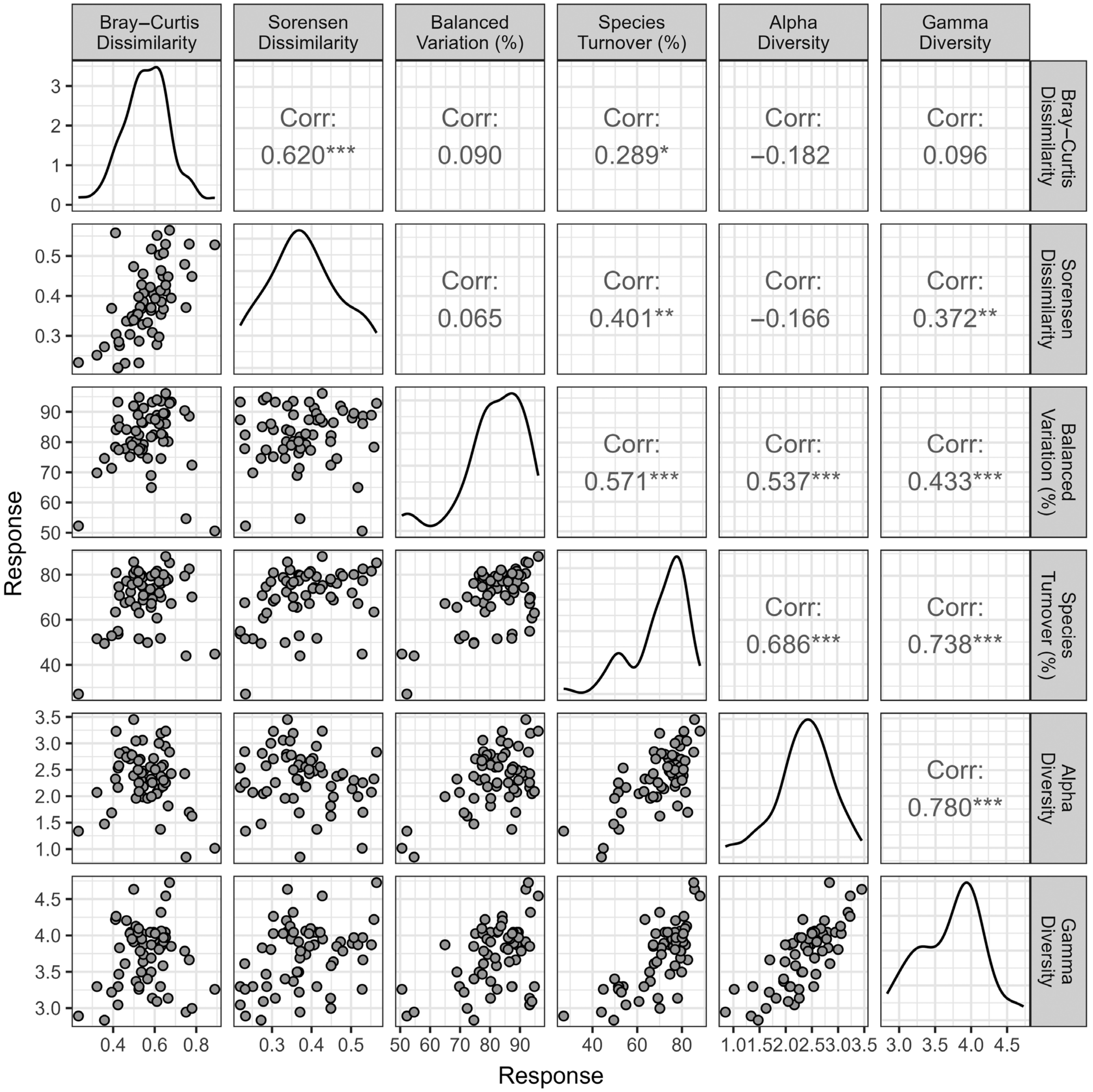

FIGURE 3 Scatterplot matrix showing patterns among six metrics (four compositional metrics and two richness metrics). Compositional metrics are averaged across all plot-year combinations (also summarized in the "All" subset in Figure 1). The diagonal values show the distribution of each metric across sites ($n = 60$). Metrics are graphed against one another below the diagonal, and Pearson correlations (Corr) are shown above the diagonal.

abundance- and incidence-based metrics (Appendix S1: Table S6). The incorporation of abundance information caused changes primarily in the relative importance of replacement at some sites (lines trending toward vertical in Figure 4), primarily in the magnitude of dissimilarity at other sites (lines trending toward horizontal), and in both aspects at the remaining sites.

DISCUSSION

By leveraging a standard experimental protocol, we systematically quantified compositional variation within multiple grassland plant communities. Our work contributes to a general understanding of compositional variation in four ways that are essential to consider as we

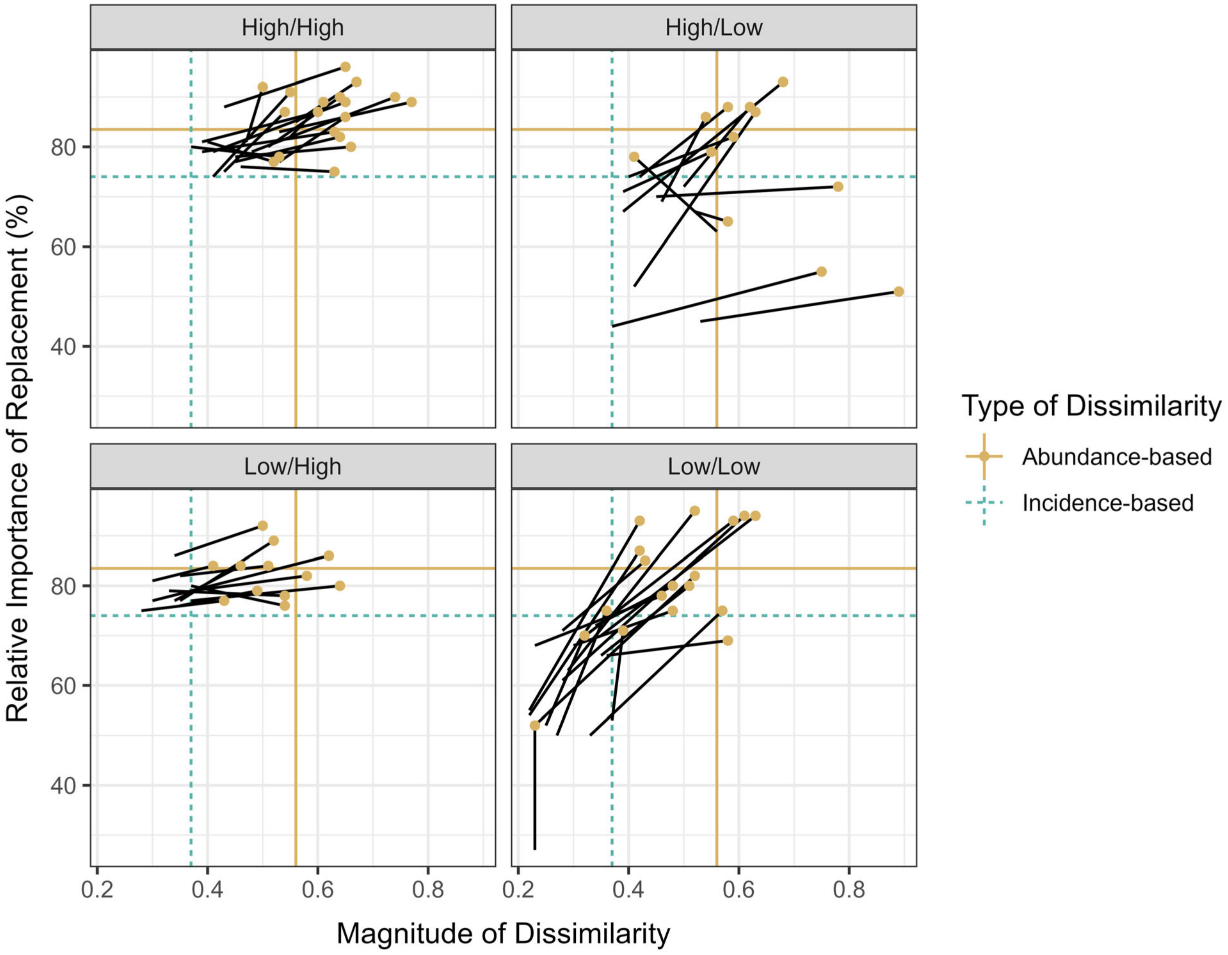

FIGURE 4 Scatterplot showing the range of differences among sites when characterized by multiple compositional metrics. The horizontal axis is the magnitude of dissimilarity (Bray–Curtis dissimilarity and Sorensen dissimilarity) and the vertical axis is the relative importance of replacement (balanced variation and species turnover). Color, symbol shape, and line type distinguish abundance-based metrics (Bray–Curtis dissimilarity and balanced variation) from incidence-based metrics (Sorensen dissimilarity and species turnover). The horizontal and vertical lines show the median for each compositional metric, defining four quadrants for each type of dissimilarity. Panels delineate quadrants based on incidence-based metrics. Each black line connects the incidence-based metrics (no symbol) and abundance-based metrics (brown symbol) for a site ($n = 60$; also reported in Appendix S1: Table S6). Line length reflects the difference between abundance- and incidence-based metrics at a site. Line angle reflects the importance of changes in magnitude of dissimilarity compared to relative importance of replacement at a site: a line is horizontal if the incorporation of abundance information greatly alters the amount of dissimilarity at the site but not the relative importance of replacement, vertical if this information strongly alters the relative importance of replacement but not the magnitude of dissimilarity, and at a 45° angle if it equally alters both aspects.

seek to understand anthropogenic impacts on ecological communities. First, we show that substantial compositional variation is the norm within grassland plant communities around the globe. Second, we demonstrate that differences in the magnitude and type of variation are predictable based on the characteristics of a site's plant community and climate. Third, we advocate for analyses using multiple compositional metrics to improve our ecological understanding of ecosystems. Finally, we highlight some implications for ecological monitoring, centered on the need to account for spatiotemporal variability in community structure.

Compositional variation is the norm

Overall, our results highlight the need to recognize the dynamic nature of grasslands (Gibson, 2009). Within-site compositional variation was high, for example, mean Bray–Curtis dissimilarity was above 0.5 in three-quarters of sites (Figure 1A). These consistent, large amounts of small-scale variation are surprising given the range of contexts in which sites were located and that the experimental design specified that plots be established in homogeneous vegetation. Although ecologists know conceptually that communities change over time, our language does not always reflect this. For example, the word "control" has connotations of stability, yet we found considerable compositional variation spatially in the pretreatment year and temporally in untreated plots. This effect is not a result of our inclusion of nutrient addition treatments in the analysis: compositional variation spanned similar ranges when considering posttreatment years or individual nutrient addition treatments (Appendix S1: Figure S3). Instead, this variation is a natural part of grassland dynamics.

Although lower than spatial variation, temporal variation in composition remained strikingly large and would have been even larger if we had not adjusted the taxonomic nomenclature within sites to avoid "spurious" compositional changes associated with differences in naming conventions among years. Furthermore, most of the compositional variation in untreated plots was due to replacement (Figure 1C,D), as appears to be the norm in many systems (Soininen et al., 2018). Clearly, it is inappropriate to assume that composition is static, even when communities are not being intentionally managed.

Predicting compositional variation

To our knowledge, this is the first global-scale study to demonstrate that compositional variation within grasslands is related to site-level predictors (see van Breugel et al. (2019) for an example in tropical secondary forests and Leprieur et al. (2011) for an example in freshwater fish communities). Differences among sites are not a function of geography (Appendix S1: Figure S1) but instead likely reflect other site-specific factors such as historical contingencies and landscape position (MacDougall et al., 2014; Price et al., 2022).

Environmental heterogeneity, quantified as the CV in aboveground biomass in unfertilized plots, was the key predictor of most metrics. This effect was largely driven by approximately seven highly heterogeneous sites (Appendix S1: Figure S2), many of which were semiarid grasslands with low biomass and patchy vegetation cover. This measure of environmental heterogeneity was intended as a surrogate for differences among plots in soil chemistry, resource availability, disturbance history, initial species composition, and other edaphic characteristics. Future work should seek to distinguish these factors and explore other measures of intra-site heterogeneity. For example, light interception is important for plant diversity in grassland communities (Borer, Seabloom, et al., 2014) but was not available for all sites in this study. Similarly, soil characteristics can relate to richness and composition (Gilbert et al., 2020; Pennington et al., 2017) but were not available for all sites. In addition, our measure of environmental heterogeneity did not account for spatial distance among plots, which can be an important driver of replacement.

Changes in dominant species disproportionately affect abundance-based metrics so we expected biomass to relate more strongly to these than to incidence-based metrics, but this was not the case. Biomass was negatively related to Bray–Curtis dissimilarity when tested individually (Appendix S1: Figure S2); the fact that it was not identified as a significant predictor through model averaging suggests that its effects are correlated with those of other predictors. Instead, biomass was only significantly related to an incidence-based metric, species turnover, after model averaging. The negative relationship here may reflect the dominance of productive sites by fewer species (Wedin & Tilman, 1990) and thus the increasing importance of nestedness in determining which species can establish or persist in these communities.

While concordant with previous biogeographic work in global drylands (Ulrich et al., 2014), this study extends our understanding of climatic controls on composition and suggests additional areas for future research. The strongest climate-related predictor in our study, annual temperature range, is a measure of continentality: larger values reflect greater seasonal differences and thus stronger temperature limits on the length of the growing season. The strong positive relationship of annual temperature range with Sorensen dissimilarity but not with Bray–Curtis dissimilarity (Figure 2; Appendix S1: Figure S2) suggests that the heterogeneity of grassland communities under continental climates arises more from controls on the establishment of rare species than on the dynamics of common species. However, this is in contrast to Ulrich et al. (2014), who found that climate variables were more strongly related to abundance-based than incidence-based metrics. Four other climate-related predictors were related to compositional metrics when tested individually (Appendix S1: Table S3)—interestingly, each was associated with a different response—but were not statistically significant after model averaging. Some studies have related grassland compositional change to precipitation (Anderson, 2008; Cleland et al., 2013), but no precipitation-related predictors were significant in our final set of models. Further research would be required to determine whether climate predictors interact with other predictors or are more strongly associated with compositional variation over time than with spatial variation among plots. In addition, it is important to note that our climate predictors characterized heterogeneity within rather than among years, and are based on long-term climate normals rather than the actual weather during the years of this study.

Using multiple metrics

Compositional data have complex multivariate structures, yet ecologists often summarize them with a single metric—perhaps the one currently in fashion or most familiar (Ricotta & Podani, 2017). Our results demonstrate that novel ecological insights can be generated by examining compositional variation using multiple metrics (Chao et al., 2014). Together, abundance- and incidence-based metrics provide insight into whether dominant or rare species are driving changes (see also Wilfahrt et al., 2021). Most sites exhibited larger Bray–Curtis than Sorensen dissimilarities and larger balanced variation than species turnover, suggesting that compositional variation was more strongly related to changes in the relative abundance of extant species than to species extinctions or to colonization by new species. This conclusion is consistent with Avolio et al. (2019), who found that species reordering explained most of the change in community composition over time. However, these patterns were not universal: two sites exhibited smaller Bray–Curtis than Sorensen dissimilarities and six sites exhibited smaller balanced variation than species turnover, suggesting stronger roles for species extinction and colonization at these sites. The mechanisms that drive community dynamics can be organized in a temporal hierarchy (Smith et al., 2009), so changes in abundance or evenness could be an early indicator of future species losses (Hillebrand et al., 2008). We expect patterns would differ if longer time frames were considered, if composition was quantified at different spatial scales (Seabloom et al., 2021), or if these mechanisms operate at different rates among sites.

There are also potentially important differences among sites in how the compositional metrics relate. Sites are dispersed widely throughout the space defined by magnitude of dissimilarity and relative importance of replacement (Figure 4, and insets in Appendix S1: Figure S1). In other words, knowing the magnitude of dissimilarity at a site gives little insight into the relative importance of replacement at that site. Further research is required to understand the ecological significance of these patterns. For example, are these patterns stable over time? Would knowledge of both the magnitude of dissimilarity and relative importance of replacement at a site improve our ability to predict its sensitivity to experimental manipulations or to climate change?

The four metrics used here are not the only ways to quantify compositional variation. Species abundance curves differ among grasslands (Ulrich et al., 2022) and can provide insight into temporal dynamics (Avolio et al., 2019). In addition, we expressed abundance in terms of cover, but other measures (e.g., Zhang et al., 2019) could lead to complementary insights. Finally, abundance can be partitioned to distinguish common and rare species and can be related to phylogenetic and functional diversity (Mugnai et al., 2022; Riva & Mammola, 2021).

Implications for monitoring and analysis

The results of this study have implications for monitoring programs and our ability to detect experimental treatment effects. There is a growing global collective of ecosystem observatories (e.g., NEON [https://www.neonscience.org/], TERN [https://www.tern.org.au/], and SAEON [http://www.saeon.ac.za/]) that seek to detect ecological changes across broad gradients. Monitoring programs are often designed to collect data efficiently given their scale and extent, and therefore may simplify the types of data that are collected—measuring frequency rather than abundance, for example, or estimating cover by a functional group rather than by species. However, our results demonstrate the value of comprehensive data: species-specific abundance data provide the ability to understand multiple facets of composition. For example, abundance data can be converted to presence/absence data during analysis, but not vice versa. Abundance data also provide a necessary basis for weighting the traits of individual species (de Bello et al., 2007). The most consistent data will be collected by the same individuals using the same methods (Nguyen et al., 2015). Morrison et al. (2020) compared presence/absence records from multiple observers in the same year and reported that pseudo-turnover—apparent changes in composition that are instead a result of observer error—was 24% at the 1-m^2 scale. However, the importance of observer error is also temporally scale dependent: observer errors were smaller than other sources of change for observation periods of a decade or longer (Futschik et al., 2020).

During analysis, we encourage researchers to consider multiple metrics and thereby assess different aspects of compositional variation (Anderson et al., 2011; Avolio et al., 2021). Our results also suggest that studies in which spatial or temporal aspects of the design differ among sites should evaluate whether these differences affect the conclusions. A consistent and robust sampling design is always an asset. The classic before–after control–impact (BACI) design provides a robust way to measure biodiversity responses (Christie et al., 2019), particularly when paired with analytical techniques—whether univariate or multivariate—that account for multiple sources of variation. The high amounts of compositional variation that we observed spatially in the pretreatment year and temporally in untreated plots (Figure 1) also highlight the importance of incorporating both types of controls as in a BACI design.

CONCLUSIONS

We focused on grasslands, one of the most threatened ecosystems on Earth (Strömberg & Staver, 2022), but our results are applicable to all ecosystems. Quantifying and predicting compositional variation are fundamental to understanding the dynamics of a system and can inform models predicting the impacts of global change on biodiversity. We show that grassland plant communities are highly variable but that the overall level of within-site compositional variation can be linked to site-level predictors. Using multiple metrics to explore multivariate data provides insights beyond those produced by any single metric. Ultimately, detecting the effects of treatments or other perturbations on ecological communities will require a deep understanding of the compositional variation of those communities.

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Author contributions and site-specific acknowledgments are provided in Appendix S1: Table S7.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and scripts (Bakker et al., 2023) are available from the Environmental Data Initiative Data Portal: https://doi.org/10.6073/pasta/8bc6b7f79701d2fc802ee5e46938fc96.

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SUPPORTING INFORMATION

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

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