



















LETTER

Determinants of community compositional change are equally affected by global change

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Abstract

Global change is impacting plant community composition, but the mechanisms underlying these changes are unclear. Using a dataset of 58 global change experiments, we tested the five fundamental mechanisms of community change: changes in evenness and richness, reordering, species gains and losses. We found 71% of communities were impacted by global change treatments, and 88% of communities that were exposed to two or more global change drivers were impacted. Further, all mechanisms of change were equally likely to be affected by global change treatments—species losses and changes in richness were just as common as species gains and reordering. We also found no evidence of a progression of community changes, for example, reordering and changes in evenness did not precede species gains and losses. We demonstrate that all processes underlying plant community composition changes are equally affected by treatments and often occur simultaneously, necessitating a wholistic approach to quantifying community changes.

KEYWORDS

data synthesis, evenness, global change experiments, herbaceous plants, reordering, richness, species gains, species losses

INTRODUCTION

Global environmental change is altering environmental conditions and species interactions (Turner et al., 2020; Tylianakis et al., 2008; Vitousek, 1994), which collectively have broad effects on plant community composition (Clark et al., 2001; Ellis et al., 2012; Franklin et al., 2016). Using multivariate measures of community composition, global syntheses of observational and experimental studies have documented community composition changes over time (Blowes et al., 2019; Dornelas et al., 2014) and in response to experimental manipulations of global change drivers (GCDs) (Komatsu et al., 2019). However, using multivariate measures to document changes in community composition does not yield insights into the processes underlying these changes. In some cases, temporal changes in community composition reflect losses and gains of species (Blowes et al., 2019; Dornelas et al., 2014). In other cases, changes in community composition reflect internal community dynamics such as reordering—the change in species ranks based on their abundances (Jones et al., 2017)—or changes in evenness. Thus, to generate greater insights into the consequences of environmental change on communities, we need to understand how determinants of composition change respond to GCDs across a range of ecosystem types.

Community composition, the identities and abundances of species, can only change in five ways (reviewed in Avolio et al., 2015, 2019). Observed changes in community composition are based on physiological responses of species that alter species interactions (such as competition and herbivory), which in turn affects rates of

growth, births and deaths and ultimately the abundances of species in a community (Vellend, 2010). Changes in abundances can result in a change in (1) *evenness* and (2) *reordering* of species ranks in a community. Reordering results from changes in the relative abundances and the resultant rank of species in the community (Collins et al., 2008). If deaths outnumber births, eventually, a species will be (3) *lost* and become locally extinct. Species may be (4) *gained* through colonisation processes. Finally, the gains and losses of species (i.e., *species turnover*) may or may not affect (5) *richness* depending on whether these processes balance. These five determinants of community change are hypothesised to occur in a hierarchical progression in response to GCDs that chronically alter resource availability (Smith et al., 2009). First, through physiological responses, which result in changes in abundances and reordering and changes in evenness, followed by turnover of species. Although the processes determining community change in response to GCDs are hypothesised to be predictable, this has never been directly studied. Further, understanding how and when different processes of community change occur is important for gaining a predictive understanding of plant community changes over time.

Global changes that alter resource supply can affect all aspects of community change. For example, irrigation has been found to cause dominant species to become more abundant, reducing evenness (Collins et al., 2012; Kardol et al., 2010). Nutrient additions can result in species gains with nitrophilous species immigrating into communities (Robinson et al., 1998), and species can be lost because of reduced niche space imposed by light limitations (Borer et al., 2014; Harpole

et al., 2016; Hautier et al., 2009). Reordering has been reported with elevated CO₂ (Langley & Megonigal, 2010) and climatic extreme events of drought and heatwave (Hoover et al., 2014). However, GCDs rarely occur in isolation (Yue et al., 2017), and thus, comanipulation of multiple resources may accelerate or exacerbate community changes (Harpole et al., 2016; Kimmel et al., 2019; Koerner et al., 2016; Zavaleta et al., 2003). Komatsu et al., (2019) found community composition became more different from controls in treated plots that had a greater number of experimental manipulations. Moreover, nonresource manipulations, such as heatwaves or grazing, can interact with resource manipulations to either magnify or dampen their effects. For example, Koerner et al., (2014) found more variable precipitation patterns delayed recovery from a grazing event, while conversely, Kaarlejärvi et al., (2017) found that herbivory reversed the effects of warming in a tundra community.

Given the multiple GCDs and the numerous ways plant communities can respond, synthesis across community types and GCDs is needed to determine which processes of community change, if any, are generalisable. We use a collection of GCD experiments in the Community Responses to Resource Experiments (CoRRE) database that includes experiments where at least one plant resource that is experimentally manipulated, sometimes in combination with non-plant resource manipulations, to study patterns of community change. Plant resource manipulations include CO₂, water and nutrient (e.g., nitrogen and phosphorus) additions and altered precipitation patterns. Non-plant resource manipulations include elevated temperature, burning, herbivory and tilling regimes. Using the CoRRE database, Komatsu et al., (2019) found that GCD treatments caused the composition of treated communities to be more dissimilar from control communities. However, because this analysis was based on multivariate measures of community composition, the mechanisms underlying the differences between control and treated communities remains unknown. Here, we study the processes underlying community composition changes to investigate whether changes in richness and evenness, reordering and species gains and losses are affected by GCD treatments and if treatment effects differ by manipulation type (e.g., resources vs. nonresources) or treatment (e.g., elevated CO₂). We hypothesised that all processes of community change will be affected by GCD treatments but that a progression of community change will occur from evenness to reordering to species gains and losses, as predicted by the Hierarchical Response Framework (Smith et al., 2009). Finally, we hypothesised that multiple resource additions will result in greater changes than single resource treatments. We addressed these hypotheses by leveraging data from a range of sites and assessed whether ecosystem attributes contribute to responsiveness of community change processes, because the response of a community to GCD treatments can depend on local

abiotic conditions (Seabloom et al., 2021; Walker et al., 2006).

METHODS

Data

We subset out datasets with five or more years of community data from the CoRRE database (corredata.weebly.com). The CoRRE database consists of 100+ experiments that manipulate at least one plant resource in an herbaceous ecosystem. Although an experiment had to include a resource manipulation treatment to be included in the CoRRE database, not all treatments in an experiment had to be resource manipulations; thus, we have nonresource treatments such as warming and herbivory. Each experiment in the database has species abundance data for every species recorded in each plot. Plots are assigned as either control or a treatment. This resulted in 58 experimental datasets and 219 control-to-treatment comparisons. Fifty-one of the experiments took place in intact communities, four were in communities that were planted or seeded at the start of the experiment and an additional three experiments added seeds/plants to intact communities. Fifty-one of the studies started collecting community data in the first 2 years of the experiment. See Table S1 for details. Across all experiments, we had 23 common GCD treatments (e.g., N addition; Table 1). We grouped all treatments into four manipulation type categories: single resource treatment, multiple resource treatment, nonresource treatment and resource and non-resource combination treatment (Table 1). Of the single manipulation treatments, seven were replicated five or more times across four or more sites, and thus, we focus on these treatments specifically. These treatments included increases in CO₂, water (irrigation), temperature, N, P and multiple nutrients (typically N and P together, but see Table 1 for more details) and altered precipitation variability (a change in the frequency or amount of rainfall events but not rainfall totals).

Calculating temporal community changes between sampling periods

Avolio et al., (2019a) developed methods to directly quantify all five processes underlying community composition change using rank abundance curves that incorporate species identity. For each plot in each experiment, we studied year-to-year changes in evenness, rank, gains, losses and richness (Table S2), described in detail in Avolio et al., (2019). Briefly, no two measures are strongly correlated (all $r < 0.51$), and all are independent of the richness and evenness of the sampled community (Avolio et al., 2019). Changes in evenness measure temporal variation in abundances among species within

TABLE 1 Global change driver treatments used across the 58 experiments

Treatment	Control–treatment comparisons	Number of locations	Notes
Single resource treatments—71 total control treatment comparisons			
CO ₂ ^a	7	4	
Drought	3	2	
Irrigation ^a	12	9	
N ^a	32	15	
P ^a	9	4	
Precipitation variability ^a	8	4	
Multiple resource treatments—60 total control treatment comparisons			
3 resources	1	1	CO ₂ , irrigation and N
Irrigation + CO ₂	1	1	
Multiple nutrients ^a	51	10	Includes some combination of N, P, K and other micronutrients
N + CO ₂	3	3	
N + irrigation	4	4	
Nonresource treatments—31 total control treatment comparisons			
Other nonresources	24	8	Nonresources include burning, mowing, herbivory, removal of herbivory, fungicide, plant diversity, plant community composition, soil depth, tilling and their combinations.
Temperature ^a	7	7	
Resource and nonresource treatments—57 total control treatment comparisons			
CO ₂ + temperature	2	2	
Drought + temperature	1	1	
Irrigation + other nonresource	6	1	Nonresources include varying plant community composition and removing herbivory.
Irrigation + temperature	5	5	
Multiple nutrients + other nonresource	12	4	Nonresources include burning, herbivory, removing herbivory, fungicide and their combinations.
Multiple resources + temperature	6	3	Resources include some combination of CO ₂ , irrigation and N
N + other nonresource	15	6	Nonresources include burning, mowing, herbivory, plant community composition, stone, tilling and their combinations.
N + temperature	3	3	
P + other nonresource	6	2	Nonresources include burning, mowing, herbivory and their combinations.
Precipitation variability + temperature	1	1	

Note: See Table S1 for more details. Control–treatment comparisons are how many times a particular treatment occurred across all 58 experiments; we count each treatment in an experiment as a replicate (there were 219 total control–treatment comparisons). To be included in the CoRRE database, an experiment had to include a resource manipulation treatment; however, several also had nonresource manipulation such as herbivory. In the notes column we include details about what the nonresource manipulations were in these experiments.

^aSingle treatments that have five or more replicates and were performed at four or more locations (not including nonresources), enabling us to examine global change driver (GCD) treatment-specific responses to that treatment.

a community, while changes in ranks reflect reordering of species abundances within the community. For the latter, an extreme example would be the rarest species becoming the most abundant or vice versa. Species gains result in greater richness and species losses result in lower richness; however, gains and losses can cancel

each other out and result in no change in richness. We calculated how the five rank abundance curve (RAC)-based measures changed between consecutive time points (e.g., t1 to t2) using the `codyn::RAC_change()` function based on relative abundance data (Hallett et al., 2020). From `RAC_change()` output, we used the

absolute value of richness and evenness change (Table S2), whereas all other community change measures are always positive. All code is available at github.com/mavolio/CoRRE-Community-Change-Paper.

Statistical analyses

We performed all statistical analyses in R (R Foundation for Statistical Computing, Vienna, Austria) using a significance level of $\alpha = 0.05$. We corrected all tests for multiple hypothesis testing using the Benjamini–Hochberg method (Benjamini & Hochberg, 1996) and gave details below.

To test whether the five processes of community change differed between control and treated plots, we fit nested generalised additive models (GAMs) on the cumulative measure of change over time for all replicates in a treatment (Figure S1). We used cumulative change to make the net effect of interannual changes more apparent. For example, many gains in only 1 year of an experiment would result in a peak in gains in that year only, making it difficult to compare curve shapes across all years. However, these same data plotted as cumulative change would show a sharp increase in that year, and the curve would then level off (diagrammed in Figure S1). We fit Gaussian GAMs using the `mgcv::gam()` function (Wood, 2011). GAMs offer the flexibility needed to detect change over time because they allow for nonlinear relationships between response and predictor variables without needing to specify the exact functional relationship. For each treatment in an experiment, we fit two GAMs. The first GAM included an interaction term that fits separate lines for each treatment and control comparison. The second GAM was fitted without the interaction term, where the modelled relationship is just cumulative change as a function of time in both treated and control plots. Both GAMs included a random effect for plot ID to account for spatial variation among plots. We then compared the two models using a likelihood ratio test (function `anova()`) to determine which of the two models is best supported by the data. A significant p value ($p < 0.05$) means that treatment and control plots have different temporal trends of cumulative change over time. We used the Benjamini–Hochberg correction to adjust p values from the GAM analysis for multiple hypothesis testing for each dataset using `p.adjust()` in R. Each dataset was corrected for five comparisons (the number of community change processes investigated) multiplied by the number of treatments; if an experiment had three treatments, we corrected for 15 multiple comparisons. To assess whether some types of GCD treatments were more likely to result in significant community changes than others, we performed an equal proportion analysis using `prop.test()` to compare the proportion of significant versus non-significant

changes among community change processes across manipulation types (e.g., resources vs. nonresources) and different GCDs applied alone. We used Benjamini–Hochberg adjustment to correct for 10 multiple comparisons in the test of equal proportions analysis.

The GAM analysis determined whether a GCD treatment affected a community change process, but it did not quantify the magnitude of effect. To examine the magnitude of difference in community change between treatment and control plots, we used Glass's D . Glass's D is the average of the treatment minus the average of the control in a given year, divided by the standard deviation of the control in that year. We chose Glass's D because it allows for differences between the standard deviation of control and treated plots (McGaw & Glass, 1980), compared with Cohen's D and Hedges's G which assumes that the standard deviation of control and treatment groups are similar. A positive value of Glass's D indicates that the treated plots have greater community changes than the controls, and a negative number indicates the treatments had smaller community changes than the controls. We averaged Glass's D across all years of control–treatment comparisons to have 219 datapoints, one for each control–treatment comparison. With this averaged data, we performed t tests to investigate whether Glass's D differed from zero and used Benjamini–Hochberg adjustment to correct for 60 multiple comparisons. For many GCD treatments, there were cases where the treatments were less than the controls and vice versa which could result in no net change. Therefore, we repeated these analyses using the absolute value of Glass's D .

Next, we assessed whether there was an order to community change (e.g., evenness changes occur before species are gained or lost). We did not include richness change in this analysis because changes in richness are the result of unbalanced gains and losses. For this analysis, we used 343 (out of a possible 876 [219×4 measures]) control–treatment community change measure comparisons where cumulative change differed significantly as determined by the GAM analysis when adjusted for multiple comparisons. For each community change process, we determined the year in which the treatment and control were most different based on the maximum Glass's D across all years of an experiment. We then assigned a sequence of community changes according to the year in which maximum change occurred. For example, if the maximum difference between control and treated plots for evenness change occurred in Year 3 and the maximum difference in species gains occurred in Year 5, then evenness change occurred before species gains. In the case of ties, rank was assigned randomly. We then tallied the number of times an order of change was observed (e.g., evenness before species gains) for each control–treatment comparison. We performed a chi-square analysis to determine whether there were any differences in the frequency with which measures of community change occurred first.

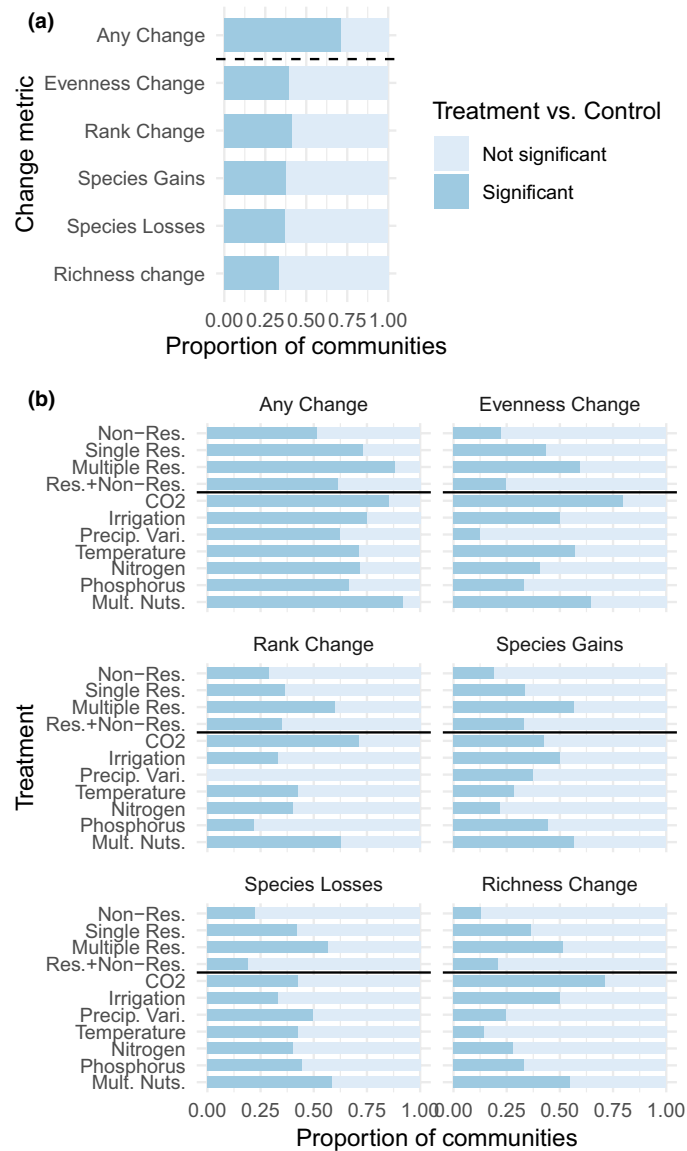


FIGURE 1 In response to all global change driver (GCD) treatments, the proportion of communities where processes of community change were significantly different between treatment and control plots. (a) Overall for any process (top row) and for all processes of community change alone ($n = 219$). (b) Global change drivers grouped into manipulation type and GCD treatments for those treatments with enough replication (see Table 1 for sample sizes)

Finally, to further evaluate whether environmental and ecosystem properties affected the magnitude of change of each community change process, we conducted multiple linear regressions on Glass's D (averaged over all years of the control–treatment comparisons, $n = 219$), using Benjamini–Hochberg adjustment to correct for five multiple comparisons. We used five site-level predictors: above-ground net primary production (ANPP; ranged from 66 to 1415 g m⁻²), mean annual temperature (MAT; ranged from -12°C to 22°C), mean annual precipitation (MAP; ranged from 229 to 1526 mm), rarified regional species richness (SR) (regional SR; ranged from three to 60 species) and site evenness (ranged from 0.11 to 0.71), as presented in Komatsu et al., (2019). Briefly, ANPP estimates were provided by principal investigators at each

site or estimated as the mean ANPP across all control plots in all years from contributed ANPP data from each experiment. MAT and MAP were obtained from WorldClim (www.worldclim.org). Rarified regional SR for a site was based on the total number of species observed over the course of the experiment in the control plots only. Site evenness was the average evenness of all control plots of a site across all years of the experiment measured using the Evar measure (Smith & Wilson, 1996). Sites with low evenness are dominated by a few species, and sites with high evenness are not as strongly dominated. Prior to the regression analysis, we first standardised predictor variables by subtracting the mean across all sites and dividing by the standard deviation. Correlations among predictor variables were all $r < 0.39$,

except ANPP and MAT ($r = 0.57$), and variance inflation factors were all <2 , indicating no serious collinearity (Quinn & Keough, 2002). We also investigated correlations between site predictors and changes in community change processes using Pearson's correlation coefficient and used Benjamini–Hochberg adjustment to correct for 25 multiple comparisons. The magnitude of GCD treatment never affected the magnitude of response (Figure S2), which was also found in two other studies using this same dataset, that the amount of N or water added was not correlated with the magnitude of effect on richness and community composition (Komatsu et al., 2019) or ANPP (Avolio et al., 2020).

RESULTS

In 156 out of 219 control–treatment comparisons, at least one process underlying temporal community change—change in richness and evenness, a shift in species ranks (i.e., reordering), or gains or losses of species—significantly differed between treatment and control plots (71%; Figure 1a). Additionally, all processes of community change were equally likely to be affected by GCD treatments ($p = 0.478$, $\chi^2 = 3.496$, $df = 4$). When we grouped all GCDs into manipulation type (e.g., resources vs. nonresources), all five community change processes were less likely to be affected by nonresources manipulations or nonresources and resources in combination, except for rank changes. Additionally, multiple resources more often resulted in at least one mechanism of community change than a single resource being manipulated alone (Table 2 and Figure 1b). When further subsetting the data to compare across individual GCD treatments, we found all processes of community composition change were equally sensitive to all treatments investigated here (Table 2 and Figure 1b). Overall, adding multiple nutrients resulted in at least one community

change process being significantly affected in 92% of comparisons, followed by CO₂ (86%), irrigation (75%), N (74%), temperature (71%), phosphorus (67%) and precipitation variability (63%; Figure 1b). When rare species were removed (those with less than 0.1% relative cover), the results remained similar, suggesting rare species did not drive community responses to GCD treatments (Figure S3).

When focusing on magnitude of the difference between the control and treatment for each process, we found, on average, GCD treatments resulted in higher richness and evenness change and species losses (Figure 2). Rank changes and species gains were split between being higher in treatments compared to controls and vice versa, resulting in no net directional differences between treatments and controls. With respect to manipulation type, we found that nonresource manipulations did not affect the magnitude of community change processes. In contrast, single resource manipulations resulted in greater evenness changes and species losses, while multiple resource manipulation resulted in greater evenness and richness change and species losses. When resources and nonresources were coapplied in a treatment, there were greater richness and evenness changes and species losses. For individual GCD treatments, only multiple nutrient additions resulted in greater evenness and richness changes (Figure 2). All other GCDs treatments did not affect the magnitude of any community change processes. When using the same data, but analysing absolute values of magnitude, we found that overwhelmingly, GCD treatments affected community change processes (Figure S4).

We found no evidence of a predictable progression to community change (Figure 3); all four processes, evenness, rank change and species gains and losses, were equally like to occur first for the communities examined ($p = 0.856$, $\chi^2 = 0.773$, $df = 3$). Evenness and rank changes alone were the most common community changes,

TABLE 2 We performed an equal proportion analysis to assess whether different manipulation types ($n = 219$) or GCD treatments ($n = 126$) were equally likely to affect each measure of community change

	Community change measure	Chi-square	Degrees of freedom	Adj. <i>p</i> value
Manipulation type	Richness change	19.11	3	0.003
	Evenness change	19.14	3	0.003
	Rank change	12.10	3	0.070
	Species gains	14.52	3	0.023
	Species losses	21.10	3	0.001
GCD treatment	Richness change	12.15	6	0.587
	Evenness change	12.59	6	0.501
	Rank change	17.54	6	0.075
	Species gains	10.74	6	0.956
	Species losses	4.32	6	1.00

Note: Data are plotted in Figure 3. Shown are the Benjamini–Hochberg adjusted *p* values for 10 comparisons. Bolded values are significant at $p < 0.05$.

GCD, global change driver.

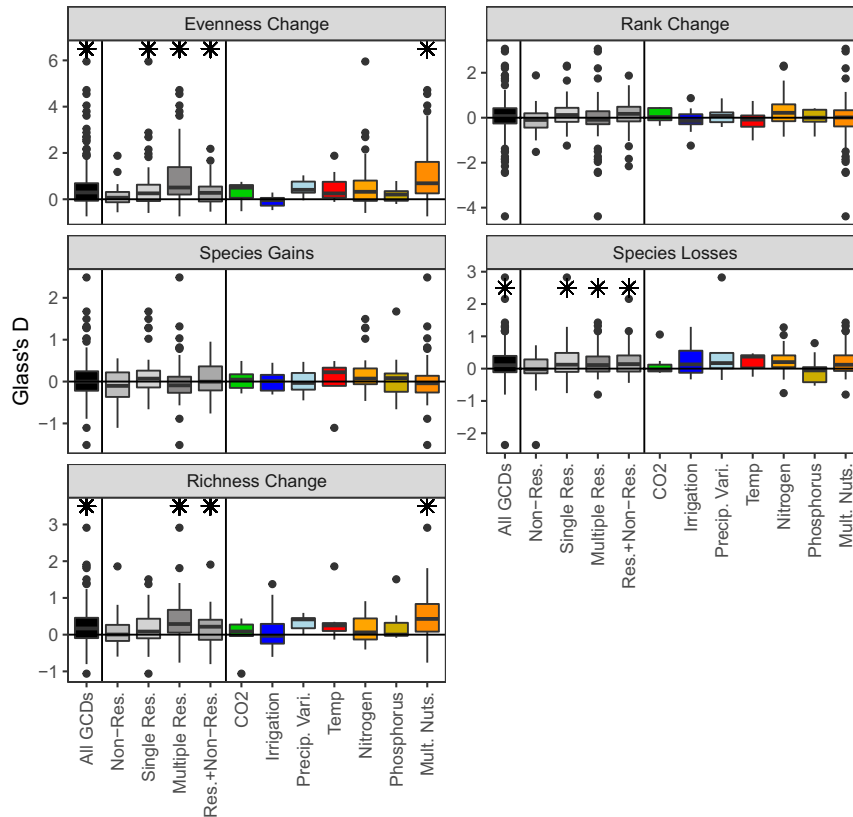


FIGURE 2 The magnitude of difference between treatment and control plots (measured with Glass's D) for each community change measure. Shown in black are all global change drivers (GCDs) together ($n = 219$), in grey are the GCDs grouped into manipulation types and then in colour are each GCD treatment for which we have enough replicates separately (see Table 1 for the number of replicates in the manipulation and GCD type categories). An asterisk denotes significant difference from zero, suggesting an overall magnitude change (either increase or decrease). See Figure S4 for a similar analysis on the absolute value of Glass's D

followed by gains only, and then by losses followed by gains. We also considered whether losses preceded gains or vice versa. Gains without losses occurred 27 times and losses without gains occurred 26 times. Gains followed by losses occurred 25 times, and losses followed by gains 31 occurred times.

Finally, we found few effects of environmental or ecosystem properties (ANPP, MAP, MAT, regional SR and site evenness) on the magnitude of community change (Figure 4). Together, the site properties explained less than 5% variation for each community change process, with the exception of evenness change and species gains, for which 8% and 11% of the variation was explained, respectively. Evenness changes were greater in sites with higher MAP and lower site evenness. Species gains were greater in sites with a higher regional SR. None of these ecosystem properties affected the magnitude of richness and rank changes and species losses.

DISCUSSION

It has long been known that plant communities are inherently dynamic and change over time (Cowles, 1899; Gleason, 1926), and more recently, plant community

change with GCDs has been shown to be the norm (Komatsu et al., 2019). We found that GCD treatments equally affected all five processes of temporal community composition change but that there was no consistency in the order of community changes. In other words, contrary to what was hypothesised by the Hierarchical Response Framework (Smith et al., 2009), reordering within the extant community did not typically precede species gains or losses. We found similar frequency of significant changes among the five processes of community composition change, suggesting that all measures are similarly sensitive to GCDs. Species gains were as common as species losses, and the understudied process of shift in species ranks (reordering) was also equally common. These findings highlight the importance of studying all the ways communities can change and that there is no one 'best' measure. We generally found multiple resource treatments had the greatest effects on community change processes, in terms of frequency and magnitude of changes in these processes. In contrast, when resources and nonresources were comanipulated, the effects of the resource manipulations on the different processes were diminished. We also found that species gains were higher in more speciose ecosystems. However, the five ecosystem and environmental properties that we

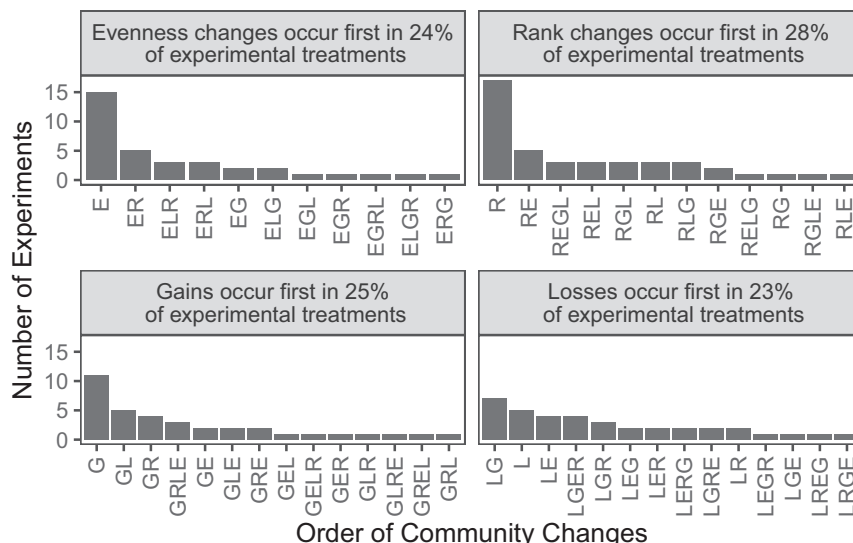


FIGURE 3 The order of community changes (E = evenness, R = rank, G = gain and L = loss) in treatments that resulted in significant community change differences between treatment and control plots, grouped by which measure of community change occurred first. Single letters indicate that only that community change measure changed significantly between treatment and control plots. Multiple letters indicate the sequence of community changes. For example, EGR indicates that evenness changed first, species gains second and rank changes third

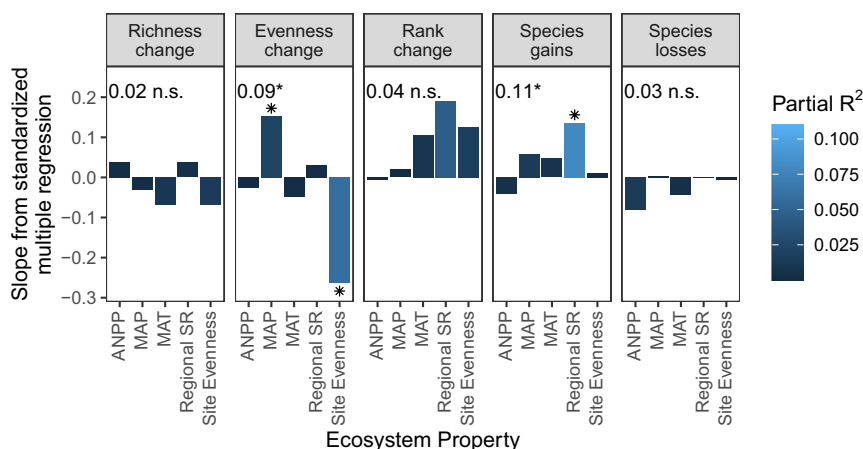


FIGURE 4 Strength of relationships (effect size from standardised multiple regression) between the magnitude of differences between control and treated plots for all measures of community change (calculated with Glass's *D*) and environmental and ecosystem properties: above-ground net primary production (ANPP), mean annual precipitation (MAP), mean annual temperature (MAT), regional species richness (SR) and site evenness. There were 219 points in each multiple regression. Lighter coloured bars indicate higher partial R^2 of the ecosystem property with the aspect of community change. Model R^2 and significance are shown in the top left of each panel; * $p < 0.05$. All correlations are shown in Figure S5

tested (MAT, MAP, ANPP, regional SR and site evenness) did not consistently affect the various ways communities can change. Our synthesis of GCD studies demonstrates the complex nature of community changes in response to resources and nonresource manipulations over time.

There are many ways to study community changes. While it is becoming increasingly agreed upon that richness may be a particularly poor measure for studying community change (Magurran, 2016), there is no consensus as to the best approach, and several methods have been suggested (e.g., Hillebrand et al., 2018; McGill et al.,

2015). In this paper, we focus on the five fundamental ways community composition can change between two time points and quantified these changes using community change measures based on RACs (Avolio et al., 2015). We found that in 71% of control–treatment comparisons, at least one process of community change was significantly impacted by a GCD treatment; however, no one process of community change was more likely to occur than any other. Thus, studies that only focus on changes in richness or turnover (loss and gain of species) would miss the equally important processes of reordering and changes in evenness. Further, Avolio et al., (2019) found

that reordering was more strongly correlated with multivariate measures of community composition changes than changes in richness, evenness and species gains and losses when analysing the codyn dataset (Collins et al., 2017). Going forward, we suggest more studies examine all five processes of community change.

Global change is multifaceted and includes change in both plant resources and nonresources, such as temperature. Together, GCDs can be additive (i.e., not interact), antagonistic (dampen one another's effects) or synergistic (amplify one another's effects). When manipulated in isolation, nonresource manipulations in our database (including herbivory, burning and temperature) generally resulted in fewer community processes changing, and changes were lower in magnitude compared with responses to resource treatments. These nonresource treatments can influence resources indirectly. The combination of resource and nonresource manipulations also had fewer effects on the community change processes that were of lower magnitude than those resulting from resource manipulations alone, suggesting that nonresource manipulations dampen the effects of resource treatments. In a global grasslands study, the effect of adding nutrients was diminished in the presence of grazing (Borer et al., 2014), which was attributed to herbivores alleviating the light limitation caused by nutrient additions. Most of our nonresource treatments were disturbances that remove biomass, such as herbivory or burning, and may result in diminishing the competitive effects of dominant species, as suggested by the intermediate disturbance hypothesis (Connell, 1978). Unfortunately, we do not have enough replication of the nonresource treatments except for temperature to further explore differences between temperature and disturbances. Additionally, although our study was unable to differentiate between additive or synergistic interactions, we did find that multiple resource manipulations more frequently resulted in changes in community processes and these changes were of a greater magnitude for evenness changes, compared with single resource additions. Using the CoRRE dataset, Komatsu et al., (2019) also found treatments that manipulated multiple resources had the greatest effect on a multivariate-based measure of community composition. In an annual grassland, multiple resource additions typically had additive effects (Zavaleta et al., 2003), resulting in greater community changes than a single resource treatment alone, probably because N and P are often colimiting (Harpole et al., 2011). While there are several examples of combinations of resources either dampening or amplifying effects (Langley & Hungate, 2014), our study suggested that dampening effects are less common, in contrast to what has been found in other studies (e.g., Leuzinger et al., 2011).

Comparing across GCD treatments, we found that all processes of community composition change were equally sensitive to all types of GCD treatments. However, when comparing the magnitude of a GCD treatment's effects on processes of community change,

we found differences among GCD treatments. Multiple nutrients additions resulted in a greater magnitude of evenness and richness changes compared with controls. Because we took the absolute value of richness and evenness change, we only have insight into the magnitude not direction of these changes. It is established that multiple nutrients reduce plant diversity by reducing niches (Harpole & Tilman, 2007) or by changing the nature of the limiting factor (Jentsch & White, 2019), and perhaps this is the mechanism behind these findings. We also found that broadly, GCD treatments resulted in greater changes in evenness, richness and species losses overall. This was not the case for species gains and reordering, which, while very different in magnitude from the controls, were equally likely to be greater or lesser than the controls. Thus, while GCD treatments equally result in altered species gains and losses, species losses were consistently greater in treated plots, while species gains did not have a consistent directionality. We found no evidence of an ordered progression to community change. Changes in evenness, ranks, gains and losses were all roughly equally likely to precede each other. We also found that losses and gains co-occurred as frequently as losses without gains and gains without losses. Thus, we did not find any evidence that a loss must precede a gain or a gain must then result in a loss, as would be predicted if communities were saturated. That communities are not saturated with regard to plant richness has been a conclusion in invasion biology (Ladouceur et al., 2020; Sax et al., 2007; Stohlgren et al., 2008; Turnbull et al., 2000) and is supported by our study. It is easier to conceptualise how GCDs can result in a species being lost from a treated plot than how a single species might immigrate into a treated plot because dispersal is not targeted to treatment or control plots. Resource additions should also eliminate niches, although a species establishing in a plot can be impacted by GCD treatments that make conditions more favourable to the immigrating species. We need to further study into what might determine differential patterns in species gains in response to GCDs. Towards this end, Kaarlejärvi et al., (2017) had success by incorporating species traits into models to predict when a species would immigrate into a treatment plot, but much more needs to be learned with respect to what allows for immigration to occur.

We studied the effects of five ecosystem properties on the observed variation in community changes, and our models explained very little variation among sites. First, we found that MAT and ANPP were not important in determining the magnitude of GCD treatment effect on any of the processes of community change. Sites that had lower evenness, indicating they are dominated by a few species, saw greater changes in evenness. Additionally, sites with greater MAP had more changes in evenness, perhaps because these sites had greater dominance. This suggests that dominant species exert control on community change (Hillebrand

et al., 2008) but do not determine how much a community will change. We saw more gains at sites with a higher regional species pool. This also makes intuitive sense, where there is a higher number of species dispersing into a plot, there are greater chances for species gains (Willems & Bik, 1998). A study of grassland responses to fertilisation found that the size of the species pool was negatively related to turnover (Hodapp et al., 2018); however, they did not tease apart gains and losses. Global change treatments have pervasive effects of processes of community composition change, which based on the variables we examine appear to be minimally impacted by local environmental conditions.

Perhaps the biggest conclusion we can draw from this analysis is that the only consistency in community responses to GCD treatments is that communities are changing. Only 29% of all 219 GCD treatments examined here resulted in no community change relative to the controls in the five processes of community change. Further, only 12% of communities did not change when multiple resources were manipulated, which is likely indicative of global plant community responses to on-going global change as GCDs do not occur in isolation. We found communities are consistently changing through all five key processes but that there were no common responses to the type of the GCD treatment and the progression in which the processes occur is not predictable. There are several unexplored mechanisms that, when studied, might lead to more generalisable findings, such as species response traits to the GCDs (Suding et al., 2008) and the traits and control of the dominant species (Avolio et al., 2019b). While not directly addressed here, changes in communities are linked to changes in ecosystem functioning (Avolio et al., 2014; Isbell et al., 2013; Langley & Hungate, 2014; Smith et al., 2009; Tilman et al., 2014), and thus, ecosystem level effects should be expected as well. Community composition changes are complex, and multiple measures of the processes underlying change are necessary to have an in-depth understanding of what is determining community responses to GCDs. Simply put, no one measure of community change will rule them all.

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CONFLICT OF INTEREST

All authors report no conflict of interest.

AUTHOR CONTRIBUTIONS

MLA and KJK assembled the CoRRE database. MLA, KJK, KRW, EG, ATT and SEK analysed the data. MLA wrote the paper along with SLC. All other co-authors either provided data or attended a working group where the paper was developed. All co-authors contributed to the data analysis methods and edited the paper.

PEER REVIEW


The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13824>.

DATA AVAILABILITY STATEMENT

All data is available in the Environmental Data Initiative (EDI: <https://doi.org/10.6073/pasta/1d54a326d6420a678b1553d493bfca1a>) and all code and analyses are in github (<https://github.com/mavolio/CoRRE-Community-Change-Paper>).


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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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