Determinants of community compositional change are equally affected by global change

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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 (3) 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

**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 losses. 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
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 nonresource 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 I 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
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

| 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 | | | |
| CO₂ | 7 | 4 | |
| Drought | 3 | 2 | |
| Irrigation | 12 | 9 | |
| N | 32 | 15 | |
| P | 9 | 4 | |
| Precipitation variability | 8 | 4 | |
| Multiple resource treatments—60 total control treatment comparisons | | | |
| 3 resources | 1 | 1 | CO₂, irrigation and N |
| Irrigation + CO₂ | 1 | 1 | |
| Multiple nutrients | 51 | 10 | Includes some combination of N, P, K and other micronutrients |
| N + CO₂ | 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 | 7 | 7 | |
| Resource and nonresource treatments—57 total control treatment comparisons | | | |
| CO₂ + 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 | |
| Multiple resources + temperature | 6 | 3 | Resources include some combination of CO₂, 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.

*Single 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.
adjust time. We used the Benjamini–Hochberg correction to the proportion of significant versus non-significant changes. To assess whether some types of community change processes investigated (e.g., evenness before species gains) for each control–treatment comparison. With this averaged data, we performed 10 tests to investigate whether Glass's \( D \) differed from zero and used Benjamini–Hochberg adjustment to correct for 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 \([219 \times 4\) 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.
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 $-12^\circ$C to $22^\circ$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 $r < 0.39$. 

**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).
DETERMINANTS OF COMMUNITY COMPOSITIONAL CHANGE ARE EQUALLY AFFECTED BY GLOBAL CHANGE

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 $\text{CO}_2$ (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 likely 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

| Community change measure | Chi-square | Degrees of freedom | Adj. $p$ 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.
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 co-manipulated, 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 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.
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

**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.
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 treated 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 comanipulated, 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/ld54a326d6420a678b1553d493bc1a) 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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Supplemental Files

Table S1. Experiments used in this study. For the treatment column, shown in parentheses is what is added: CO2 (ppm), N (g m\(^{-2}\)), P (g m\(^{-2}\)), K (g m\(^{-2}\)), water (% of annual precipitation), heat (°C).

| Experiment Location          | Experiment Name | Treatments | Details | Key Publication | Species Data Collection Method | Notes |
|-----------------------------|-----------------|------------|---------|-----------------|--------------------------------|-------|
| Angelo Coast Range Reserve, CA, USA | Watering | 1. Water (20) added in winter  2. Water (20) added in spring | 7 years; 6 replicates | Suttle et al. 2007, Science, 315: 640-642 | 24 pin counts in 6 0.25 m\(^{2}\) plots |       |
| Arctic LTER, Toolik Field Station, AK, USA | Moist Acidic Tundra (MAT2) | 1. N (10) and P (5) | 17 years; 4 replicates | Hobbie et al. 2005, Journal of Ecology 93: 77-782 | Species cover estimate in 8 1-m\(^{2}\) plots to the nearest 1% |       |
| Arctic LTER, Toolik Field Station, AK, USA | Moist Non-acidic Tundra (MNT) | 1. N (10) and P (5) | 16 years; 4 replicates | Gough and Hobbie 2003, Oikos 103: 204-216 | Species cover estimate in 8 1-m\(^{2}\) plots to the nearest 1% |       |
| Allegan State Game Area, MI, USA | Experiment 1 | 1. N (20.1) patchy distribution  2. N (20.1) uniform distribution  3. Seeds of 46 native species added  4. Seeds + N patchy  5. Seeds + N uniform | 5 years; 8 replicates | Gross et al. 2005, Ecology 86: 476-486 | ANPP by species clipped in 12 0.25 m\(^{2}\) plots. Species ANPP is then summed across all plots |       |
| Ecological-Botanical Garden, University of Bayreuth, Germany | Event2 | 1. Reduced rainfall variability  2. Increased rainfall variability (early drought)  3. Increased | 5 years; 5 replicates | Khan et al. 2018 Ecosystems 21: 1306-1321 | ANPP sorted to species in two 0.1m\(^{2}\) plots |       |
| Location                        | Treatment       | Experiment Parameters | Management Details                                                                                                                                 |
|--------------------------------|-----------------|-----------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------|
| Health and Safety Laboratory, Derbyshire, UK | Precipitation & warming (PQ) | 1. Heated (3)  
2. Drought (20)  
3. Water (20)  
4. Heat + Drought  
5. Heat + Water | 13 years; 5 replicates  
Fridley et al. 2007, Global Change Biology 17: 2002-2011  
25 pin hits in a 6.25 m² plot |
| Carpenteria Salt Marsh Reserve, CA, USA | Salt Marsh | 1. N (164), P (84), K (41) | 7 years; 10 replicates  
Pennings and Simpson 2008, Plant Ecology 196: 245-250  
Percent cover estimated to nearest 1% in 0.25 m²  
Replicated in six different plant community types, in the first year the treatments were N (84); P(42), K(21) |
| Cedar Creek LTER, Cedar Creek Ecosystem Science Reserve, MN, USA | BioCON | 1. CO2 (160) elevated  
2. N (4) added  
3. CO2 + N | 14 years; 12 replicates  
Reich et al. Nature, 2001, 410: 809-812  
ANPP by species clipped at 10 cm by 100 cm strip  
Only included plots with all 16-species planted |
| Cedar Creek LTER, Cedar Creek Ecosystem Science Reserve, MN, USA | E001 | 1. Micronutrients [P (4.5), K (6.1), epsom salts and lime] added  
2. N (9.52) added +micronutrients  
3. N (27.2) +micronutrients | 24-30 years (depending on the field); 5 or 6 replicates depending on the field  
Tilman Ecological Monographs, 1987, 57: 189-214  
ANPP by species clipped at 10 cm by 3 m strip  
Replicated in 3 fields of different successional ages and one never-plowed oak savanna. |
| Cedar Creek LTER, Cedar Creek Ecosystem Science Reserve, MN, USA | E002 | 1. Micronutrients [P (4.5), K (6.1), epsom salts and lime] added  
2. N (9.52) added +micronutrients  
3. N (27.2) +micronutrients | 10 years; 6 replicates  
Tilman Ecological Monographs, 1987, 57: 189-214  
ANPP by species clipped at 10 cm by 3 m strip  
Replicated across 3 fields of different successional ages. All plots were disturbed by disking before the start of the experiment. |
| Culardoch Experimental | Culardoch | 1. N (10)  
2. N (20) | 5 years; 6  
Britton and Fisher 2007;  
Cover estimated to |
| Site, Eastern Highlands, Scotland | 3. N (50) 4. Clip (12% ANPP removed in August) 5. N10 + clip 6. N20 + clip 7. N50 + clip | replicates | Journal of Applied Ecology 44: 135-135 | 1% in a 0.25 m² quadrat |
| Restoration Ecological Research Station, Duolon County, China | Nitrogen and Water Manipulation Experiment | 1. N (10) 2. Water (50) 3. N + Water | 6 years, 7 replicates (in the first year there were only 5 replicates) | Xu et al. 2012, PlosOne, 7: e39762 | Species cover to nearest 1% in permanent 1 m² plot |
| Inner Mongolia Grassland Research Station, China | Nitrogen Experiment | 1. P+K [P (1.55), K (3.95)] 2. N (5.6) + P+K 3. N (11.2) + P+K 4. N (22.4) + P+K 5. N (39.2) + P+K 6. N (56) +P+K | 8 years; 6 replicates | Yu et al. 2010, Ecology Letters, 13:1390-1399 | ANPP to species collected in 1 m² |
| Jasper Ridge Biological Preserve, CA, USA | Jasper Ridge Global Change Experiment | 1. N (7) 2. Water (50%) 3. Heat (1.5) 4. CO2 (300) 5. N + Water 6. N + Heat 7. N + CO2 8. Water + Heat 9. Water + CO2 10. Heat + CO2 11. N + Water + Heat 12. N + Water + CO2 13. Water + Heat + CO2 14. N + Heat + CO2 15. N + Water + Heat + CO2 | 14 years; 6 replicates | Zhu et al. 2016 PNAS 113: 10589-10594 | 10 pin hits in a 0.5 m² area |
| Kellogg Successional | 1. Tilled in 1989 | 22 or 24 | Huberty et al. | ANPP to |
| Location | Treatment Details | Years | Replicates | Journal Reference | Species Collection Details |
|----------|-------------------|-------|------------|-------------------|---------------------------|
| LTER, Kellogg Biological Station, MI, USA | plots (T7) | 2. N (12.3) added 3. N + Tilling (depending on the treatment); 6 replicates | 1998 Journal of Ecology 86:794-803 | species collected in 1 m² |
| Kluane Area, Yukon Territory, Canada | BFFert | 1. N (17.5), P (5), K (1.5) 2. Fence to remove herbivores 3. NPK+Fence | Turkington et al. 2002, Journal of Ecology 90: 325-337 | 205 pin hits in an 25 m² plot |
| Kluane Area5, Yukon Territory, Canada | KGFert | 1. N (17.5), P (5.8), K (5.8) added 2. Fungicide (Benlate) added 3. NPK + fungicide | McLaren and Turkington 2010 Journal of Ecology, 98: 459-469 | 100 pin hits in a 1 m² plot |
| Konza LTER, Konza Prairie Biological Station, KS, USA | Belowground Plot Experiment | 1. unburned N (10) added 2. unburned P (1) added 3. unburned N+P 4. burned 5. burned N (10) 6. burned P (1) 7. burned N+P | Callaham et al. 2003. Soil Biology & Biochemistry, 35: 1079-1093 | Percent cover estimated using Daubenmire method adding a <1% category in a 10 m² plot (1986-1998) and average from two 0.5 m² (1999 onwards) |
| Konza LTER, Konza Prairie Biological Station, KS, USA | Irrigation Plots | 1. water added to maintain soil saturation (~30) | Wilcox et al. 2016 Ecology 97:561-568. | Species cover estimated by Dabenmire cover and then converted to percent in a 10 m² plot Replicated in uplands and lowlands, located in annually burned watershed |
| Konza LTER, Konza Prairie Biological Station, KS, USA | Phosphorus plots | 1. P (2.5) added 2. P (5) 3. P (10) 4. N (10) added 5. N (10) + P (2.5) | Avolio et al. 2014, Journal of Ecology, 102: 1649-1660 | Species estimated to nearest 1% cover in four 0.25 m² plots Located in biennially burned watershed |
| Study Location | Experiment Details | Number of Replicates | Data Source | Species Estimation | Notes |
|----------------|--------------------|----------------------|-------------|--------------------|-------|
| Konza LTER, Konza Prairie Biological Station, KS, USA | Rainfall Manipulation Plots | 1. Heated (1) 2. Fewer, Larger Rainfall Events 3. Fewer Larger rainfall events + heat | 11 years; 6 replicates | Knapp et al. Science 2002, 298:2202-2205 | Species estimated to nearest 1% in four 1 m² plots. Located in annually burned watershed |
| Konza LTER, Konza Prairie Biological Station, KS, USA | Restoration Heterogeneity Plots | 1. N (5) added 2. Stone added to make soil shallow 3. N + Stone | 6 years; 4 replicates | Baer et al. Ecological Monographs 2017, 86: 94-106. | Species estimated to nearest 1% cover in two 0.25 m² plots |
| University of Kansas Field Station, Lawrence, KS, USA | Experiment 6 | 1. N (4) 2. N (8) 3. N (16) 4. P (8) 5. N4 + P 6. N8 + P 7. N16 + P | 11 years; 6 replicates | Foster et al. 2011, Journal of Ecology 99: 473-481 | For species with abundance > 1%, cover estimated to nearest 1% cover in two 1 m² plots. For species with under 1% cover, estimated to nearest 0.01% |
| Archbold Biological Station’s Buck Island Ranch (formerly Macarthur Agro-Ecological Research Center), FL, USA | Fireplots | 1. N (5) added 2. P (5) added 3. N+P (5) 4. Burned in Summer 5. Burned in Summer + N (5) added 6. Burned in Summer + P (2) added 7. Burned in Summer + N+P 8. Unburned 9. Unburned + N (5) added | 6 years; 4 replicates | Boughton et al. 2017, J of Plant Ecology 11: 576-584 | Species cover estimated with a modified Daubenmire scale in a 10 m² plot. Control plots are burned in the winter |
| Location                                      | Plot Code | Treatment | Design | Data Length | Experiment References | Methodology | Notes |
|-----------------------------------------------|-----------|-----------|--------|-------------|------------------------|-------------|-------|
| Northern Great Basin Experimental Range, Oregon, USA | gb        | Unburned + P (2) added Unburned + N+P | 1. Increased precipitation variability (early season) 2. Increased precipitation variability (late season) | 6 years; 4 replicates | Bates et al. 2006, Journal of Arid Environments 64: 670-697 | Plant cover estimated using Daubenmire method in 0.2 m² plot |
| Wichita State Ninnescah Reserve, KS, USA | HerbDiv | N (12), P (3.3), K (8) Aboveground fence Aboveground fence + NPK Insecticide Insecticide + NPK Aboveground fence + insecticide Aboveground fence + insecticide + NPK Belowground fence + aboveground fence + insecticide Belowground fence + aboveground fence + insecticide + NPK | 5 years; 8 replicates | Russell and Houseman 2018, Journal of Plant Ecology 12: 531-541 | Species cover estimated in to 0.01% 7.5 m² plots |
| Niwot LTER, Niwot Ridge, CO, USA | 246Nfert | N (2) N (4) N (6) | 8 years; 5 replicates | Bowman et al. 2006, Ecological Applications 16: 1183-1193 | 100 pin hits in a 1 m² plot |
| Niwot LTER, Dry Meadow | N (25) | 11 years; 5 | Bowman et al. | 100 pin hits in Replicated in |
| Location                          | Experiment/Project                           | Treatment Details                                                                 | Year | Publications / Notes                                                                 |
|----------------------------------|-----------------------------------------------|------------------------------------------------------------------------------------|------|-------------------------------------------------------------------------------------|
| Niwot Ridge, CO, USA             | NXP                                           | 1. P (25) 2. N + P                                                                 |      | 1993, Ecology 74: 2085-2097                                                         |
|                                  |                                               | a wet and dry community types                                                      |      |                                                                                     |
| Niwot LTER, Niwot Ridge, CO, USA | International Tundra Experiment (ITEX)        | 1. Heat added (1) 2. N (28 or 10) 3. Heat + N 4. Snow (116) added 5. Snow + Heat (1) 6. Snow + N (28 or 10) 7. Snow + Heat + N | 10 year; 6 replicates | Farrer et al 2014, Global Change Biology 20: 1238-1250 Line intercept with 100 hits in a 1 m² plots. 28 g N added from 2006-2010, then 10 g m⁻² N |
| Plum Island LTER, Plum Island Estuary, MA, USA | TIDE                                          | 1. N (37.5)                                                                        | 7 years; 6 replicates | Johnson et al. 2016 Ecological Applications 26: 2647-2659. Percent cover to 1% in a 1-m² plot |
| San Claudio, Argentina           | Lucero                                        | 1. N (20)                                                                          | 6 years; 6 replicates | Tognetti 2010 PhD Dissertation. Facultad de Agronomía Universidad de Buenos Aires. Percent cover to 5% in 2.64 m² plot |
| Smithsonian Environmental Research Center, MD, USA | CO2 and Nitrogen Experiment                   | 1. N (25) added 2. CO2 (340) elevated 3. N + CO2                                  | 10 years; 5 replicates | Langley and Megonigal 2010, Nature 466: 96-99 ANPP sorted to species in 5 0.25 cm² plots |
| Smithsonian Environmental Research Center, MD, USA | Tidal Marsh CO2 Experiment                    | 1. CO2 (340)                                                                        | 18-26 depending on the community; 10 replicates | Arp et al. 1993. Vegetatio 104/105: 133-143 Number of species counted in 5 100 cm² plots Replicated in three community types dominated by different species |
| Sevilleta LTER, Sevilleta         | Extreme Drought in Grassland                  | 1. Drought (66) 2. Precipitation variability                                      | 5 years; 10 replicates | Fernandes et al. 2018. Environmental Cover converted from ANPP Replicated in two community |
| Location | Experiment/Climate Change | Treatments | Duration | Authors | Reference | Data/Species | Notes |
|----------|---------------------------|------------|----------|---------|-----------|--------------|-------|
| National Wildlife Refuge, NM, USA | Experiment (EDGE) | (monsoon rains applied later) | 9 years, 10 replicates | Ladwig et al. 2012 | Microbiology 20: 259-269 | data to 0.5% | types dominated by different species |
| Sevilleta LTER, Sevilleta National Wildlife Refuge, NM, USA | N Fert | 1. N (10) added | | | | | |
| | | 2. Water (50) added | | | | | |
| | | 3. Heat (1) added | | | | | |
| | | 4. N + Water | | | | | |
| | | 5. Water + Heat | | | | | |
| | | 6. N + Heat | | | | | |
| | | 7. N + Heat + Water | | | | | |
| Sevilleta LTER, Sevilleta National Wildlife Refuge, NM, USA | Warming – El Nino – Nitrogen Experiment (WENNDEx) | 1. N (2) added | 6 years, 5 replicates | Collins et al. 2017 | Oecologia 169: 177-185 | ANPP by species in 4 1 m² plots |
| | | 2. Water (50) added | | | | | |
| | | 3. Heat (1) added | | | | | |
| | | 4. N + Water | | | | | |
| | | 5. Water + Heat | | | | | |
| | | 6. N + Heat | | | | | |
| | | 7. N + Heat + Water | | | | | |
| Spindletop Research Farm, KY, USA | University of Kentucky Climate Change Study | 1. Heat (3) | 5 years; 5 replicates | McCulley et al. 2014, | Frontiers in Chemistry, 2: art98 | Cover in two 1 m² plots estimated to nearest 1% |
| | | 2. Water (30) | | | | | |
| | | 3. Heat + Water | | | | | |
| Sedgwick Reserve, CA, USA | Nitrogen | 1. N (4) | 5 years; 5 replicates | Seabloom et al. 2003, | PNAS 100: 13384-13389 | ANPP to species in two 0.1 x 1 m strips |
| | | 2. Seed addition (annual species to perennial communities, perennial species to annual communities) | | | | | |
| | | 3. N + Seed addition | | | | | |
| Sedgwick Reserve, CA, USA | Water | 1. Water (34.1) | 5 years; 5 replicates | Seabloom et al. 2003, | PNAS 100: 13384-13389 | ANPP to species in two 0.1 x 1 m strips |
| | | 2. Seed addition (annual species to perennial communities) | | | | | |

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| Australian Federal Department of Defense Pontville Small Arms Range Complex, Tasmania | TasFACE Global Change Impacts Experiment | 1. Heat (2)  
2. CO2 (150)  
3. Heat + CO2 | 7 years; 6 replicates | Hovenden et al. 2006, Australian Journal of Botany 54: 1-10 | Number of individuals in a 1.5 m² plot | perennial communities, perennial species to annual communities)  
3. Fenced to remove herbivory by gophers  
4. Water + Seed Addition  
5. Water + Fencing  
6. Seed Addition + Fencing  
7. Water + Seed addition + Fencing |
Table S2. Rank-abundance curve-based measures of community change. $S_{\text{tot}}$ is the total number of species in the community across the two time points being compared. See Avolio et al. (2019) for more details on all the community change measures.

| Community Change Measure | Equation | Range |
|--------------------------|----------|-------|
| Richness (S) change      | $(S_{t+1} - S_t)/S_{\text{tot}}$ | -1 to 1, depending on whether species are lost or gained over the time interval |
| Evenness (E) change      | $E_{t+1} - E_t$ | -1 to 1, depending on whether evenness decreases or increases |
| Rank (R) change          | $\sum_{i}^{N} \left( \frac{|R_{i,t+1} - R_{i,t}|}{S_{\text{tot}}} \right) / S_{\text{tot}}$ | 0-0.5, at 0.5 there is the maximum rank changes in the community |
| Species gains (G)        | $G/S_{\text{tot}}$ | 0-1, proportion of species that are gained |
| Species losses (L)       | $L/S_{\text{tot}}$ | 0-1, proportion of species that are lost |
Table S3. Funding sources for experiments used in this study.

| Site                                | Experiment | Funding Source                                                                 |
|-------------------------------------|------------|-------------------------------------------------------------------------------|
| Arctic LTER                         |            | U.S. National Science Foundation DEB-1637459, 1026843, 9810222; OPP 9902695, 9902721 |
| Cedar Creek LTER                    |            | U.S. National Science Foundation DEB -1831944                                 |
| Cedar Creek LTER                    | BioCON     | National Science Foundation (NSF) Long-Term Ecological Research (DEB-0620652, DEB-1234162, DEB-1831944), Long-Term Research in Environmental Biology (DEB-1242531, DEB-1753859), Biological Integration Institutes (NSF-DBI-2021898), Ecosystem Sciences (NSF DEB- 1120064) and MRI (DBI-1725683) Programs; as well as the U.S. Department of Energy Programs for Ecosystem Research (DE-FG02-96ER62291). |
| Ecological-Botanical Garden, University of Bayreuth, Germany | Event2     | German Federal Ministry of Education and Research, SUSALPS grant numbers 031B0027C and 031B0516C |
| Culardoch Experimental Site, Eastern Highlands, Scotland | Culardoch  | Scottish Government Rural and Environment Science and Analytical Services Strategic Research Programme |
| Kellogg LTER and Michigan State AgBioResearch |            | U.S. National Science Foundation DEB-1832042                                 |
| Konza Prairie LTER                  |            | U.S. National Science Foundation DEB-1440484                                  |
| Konza Prairie LTER                  | RaMPs      | U.S. National Science Foundation DEB-1257174                                  |
| Konza Prairie LTER                  | RHPs       | U.S. National Science Foundation DEB-1147439                                  |
| Niwot Ridge LTER                    |            | U.S. National Science Foundation DEB-1637686                                  |
| Plum Island Ecosystem LTER          | TIDE       | U.S. National Science Foundation DEB 0213767, DEB 0816963, DEB 1354494, DEB 1719621, OCE 0423565, OCE 1058747, OCE 1238212, OCE 1637630, DEB 1902712 |
| Sevilleta LTER                      |            | U.S. National Science Foundation DEB-                                         |
| Location                                                                 | Project/Experiment                                                                 | Funding/Support                                                                 |
|----------------------------------------------------------------------------|-------------------------------------------------------------------------------------|---------------------------------------------------------------------------------|
| Smithsonian Environmental Research Center                                  |                                                                                     | U.S. National Science Foundation DEB-0950080, DEB-1457100, DEB-1557009; U.S. Department of Energy DE-SC0008339; U.S. Geological Survey G10AC00675; Smithsonian Institution |
| Kluane Lake                                                               | KG Fert                                                                             | NSERC Discovery Grant to R. Turkington                                           |
| Macarthur Agro-Ecological Research Center                                 | Fireplots                                                                           | Archbold Biological Station                                                     |
| Restoration Ecological Research Station, Duolon County, China              | Nitrogen and Water Manipulation Experiment                                           | National Natural Science Foundation of China 31370009                            |
| Inner Mongolia Grassland Research Station, China                           | Nitrogen Experiment                                                                 | National Natural Science Foundation of China 31270476                            |
| San Claudio, Argentina                                                    | Lucero                                                                              | PIP-CONICET 2331, PICT 20-32083, UBACYT G-024 and G-046                          |
| Spindletop Research Farm, KY, USA                                        | University of Kentucky Climate Change Experiment                                     | U.S. Department of Energy 08-SC-NICCR-1073                                       |
Figure S1. Graphical overview of analyses performed in this paper. Shown in one control and treatment plots, however, in each experiment there are at least four replicates of each treatment and the GAM analysis fits the best curve for all replicates.
Figure S2. We investigated the relationship between magnitude of treatment and the community response for nitrogen, phosphorus, temperature, water and CO2 additions. We used cor.test and corrected for multiple hypothesis testing. We found no effect of treatment amount on any measure of community response. Shown are r-values in the upper corner. For CO2 amount added in ppm, for irrigation it is mm, for nitrogen and phosphorus it is g, and for temperature is °C.
Figure S3. With rare species removed, the proportion of communities with significantly different community change between treated and control for all measures (top row) or each measure separately to any GCD treatment. Communities were subset so rare species were removed and the GAM analyses were repeated. A species was considered rare if it’s average relative cover across all control plots over time was less than 0.1%; this resulted in a substantial reduction in the dataset. Overall the results are very similar to the results based on the whole community (Figure 1A).
Figure S4. Absolute value Glass’s D for each community change measure using all control-treatment comparisons. Shown in black are all GCD treatments together, binned into manipulation type in gray (e.g. resource vs. non-resource) and then in color each GCD treatment separately. An asterisk denotes significant difference from zero.
Figure S5. Correlations between community change measures and environmental and ecosystem properties, which do not take into account correlations among predictor values like the multiple regressions shown in Figure 4. Pearson correlation coefficients are shown in the top-right of each panel; correlation lines are only added for significant relationships, n = 219.