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Ambient changes exceed treatment effects on plant species abundance in global change experiments

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Abstract

The responses of species to environmental changes will determine future community composition and ecosystem function. Many syntheses of global change experiments examine the magnitude of treatment effect sizes, but we lack an understanding of how plant responses to treatments compare to ongoing changes in the unmanipulated (ambient or background) system. We used a database of long-term global change studies manipulating CO_2, nutrients, water, and temperature to answer three questions: (a) How do changes in plant species abundance in ambient plots relate to those in treated plots? (b) How does the magnitude of ambient change in species-level abundance over time relate to responsiveness to global change treatments? (c) Does the direction of species-level responses to

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global change treatments differ from the direction of ambient change? We estimated temporal trends in plant abundance for 791 plant species in ambient and treated plots across 16 long-term global change experiments yielding 2,116 experiment–species–treatment combinations. Surprisingly, for most species (57%) the magnitude of ambient change was greater than the magnitude of treatment effects. However, the direction of ambient change, whether a species was increasing or decreasing in abundance under ambient conditions, had no bearing on the direction of treatment effects. Although ambient communities are inherently dynamic, there is now widespread evidence that anthropogenic drivers are directionally altering plant communities in many ecosystems. Thus, global change treatment effects must be interpreted in the context of plant species trajectories that are likely driven by ongoing environmental changes.

KEYWORDS

elevated CO_2, nitrogen, phosphorus, plant community, warming, water

1 | INTRODUCTION

Plant community composition can respond to global change and mediate important long-term effects of global change on ecosystem processes (Avolio et al., 2015; Cowles, Wragg, Wright, Powers, & Tilman, 2016; Langley & Hungate, 2014; Smith, Knapp, & Collins, 2009; Zhang, Niinemets, Sheffield, & Lichstein, 2018), so understanding those changes is key for projecting future ecosystem functions. For at least five decades (Valiela, Teal, & Sass, 1975), ecologists have conducted long-term field experiments testing how plant communities will respond to environmental changes such as chemical (e.g., CO_2 and nutrient pollution) and climatic drivers (e.g., temperature and precipitation change). These experiments are often considered predictive of which species will be favored by future environmental change, “winners,” and which will not, “losers,” based on whether the specific change driver alters some measure of performance such as abundance (Craine, 2009; Dukes & Mooney, 1999; Langley & Hungate, 2014; O'Brien & Leichenko, 2003; Poorter & Navas, 2003). Accordingly, many manipulative studies collect very high-quality, detailed data on individual species abundance through time. Manipulative experiments are powerful in that plant response can be attributed to a single factor if adequate controls are included in the experimental design. However, global change experimental plots are typically small-scale, and there are limits to the number of experimental treatments that can be feasibly imposed. When analyzed individually, these experiments often yield idiosyncratic treatment effects (Zhu, Chiariello, Tobeck, Fukami, & Field, 2016) that can vary in space and though time. Treatment effects often diminish through time, a finding that has been interpreted as evidence of acclimation or negative feedbacks (Leuzinger et al., 2011; Smith et al., 2015). With the goal of generalizing global patterns, meta-analyses have summarized the results across many individual global change experiments (Andresen et al., 2016; Hedges, Gurevitch, & Curtis, 1999; Wu, Dijkstra, Koch, Peñuelas, & Hungate, 2011; Xia & Wan, 2008), and scientists have established networks of similar manipulative experiments (Borer, Grace, Harpole, MacDougall, & Seabloom, 2017). To reduce noise and complexity, such synthetic efforts often focus on effect sizes that are structured to isolate relative differences between treatments and controls (Hedges et al., 1999). Still, predicting changes in abundance of plant species or functional groups has proven exceptionally difficult (Kimball et al., 2016; Lavorel & Garnier, 2002; Meir, Mencuccini, & Dewar, 2015; Reich, Hobbie, Lee, & Pastore, 2018; Verheyen et al., 2017).

A growing body of evidence from observational studies of long-term monitoring plots, remotely sensed data, or species range shifts demonstrates that vegetation distribution is responding strongly to environmental change (Doughty et al., 2016; Franklin, Serra-Diaz, Syphard, & Regan, 2016; Jamiyansharav, Fernández-Giménez, Angerer, Yadamsuren, & Dash, 2018; Maguire, Nieto-Lugilde, Fitzpatrick, Williams, & Blois, 2015; Parmesan & Yohe, 2003; Schuster, Martinez, & Dukes, 2014; Simkin et al., 2016). While these studies capture ongoing responses to environmental change, attribution to a particular cause can be difficult (Cudlin et al., 2017), thereby complicating comparisons to manipulative studies. For instance, widely observed encroachment of woody plants into herbaceous ecosystems is commonly attributed to elevated CO_2, among other competing hypotheses (Saintilan & Rogers, 2015). However, CO_2 experiments may be ill-suited to capture landscape-scale vegetative shifts because the “island effect” inherent to plot-level studies can exclude important large-scale CO_2 feedbacks such as altered regional humidity or energy balance (de Boeck et al. (2015), Leuzinger, Fatichi, Cusens, Körner, & Niklaus, 2015).

These two threads of research, manipulative global change experiments and observations of ongoing change, have addressed the same questions independently, yielding some alternative assessments of change across landscapes and projections of future plant change in isolated plots. For instance, observational studies have recorded losses of legumes but attribute the net loss to landscape fragmentation or fire suppression (Leach & Givnish, 1996) or to mammalian herbivory (Ritchie & Tilman, 1995). Meanwhile, a meta-analysis of 304 N fertilization experiments predicted that legumes will respond negatively to N addition (Xia & Wan, 2008). Coordinated studies have compared the two approaches at individual sites. A recent study of alpine tundra plant communities demonstrated good agreement between responses to ambient warming in monitored plots and to experimental warming in manipulated plots (Elmendorf et al., 2015). Yet, the prevailing evidence for plant phenology responses to warming is that experiments generally underestimate responses (Wolkovich et al., 2012). Combining approaches of experimental manipulation and observation can be powerful (de Boeck et al. 2015), but few studies have undertaken both simultaneously. Experiments often document background changes in plant species abundance in control plots—but this "ambient change" is not attributable to any manipulated variable. How does ambient change relate to measured treatment effects? To our knowledge, no multi-site studies have explicitly compared global change treatment responses to ambient change within the same experiments.

We used abundance data from 791 plant species across 16 global change experiments at least 10 years in duration to assess long-term, directional change in species-level abundance in ambient plots (referred to as "ambient change") and compared these measures to that observed in plots exposed to relatively long-term manipulative treatments: CO_2, water, nitrogen, phosphorus, or temperature. We focused on sustained, directional change in abundances. We propose that sustained, directional shifts in plant responses provide a signal of the longer-term species trajectories rather than shorter-term changes that could be cyclical (Stouffer, Wainwright, Flanagan, & Mayfield, 2018). We expect that owing to the importance of global change drivers for plant communities and the strength of treatments applied in global change experiments, treatment effects should overwhelm background trends in plant abundance. If ambient change in manipulative experiments is comparable in *magnitude* to global change treatment effects, then ambient change could have a profound influence on how we interpret experimental results. We asked three questions: (a) How do changes in plant abundance in unmanipulated "ambient" plots (ambient change) relate to that in treated plots (treatment change)? (b) How does the magnitude of ambient change relate to its responsiveness to global change (treatment effect)? (c) Does the direction of ambient change differ from the direction of treatment effect? By capitalizing on existing long-term experimental data, the answers to these questions will shape the interpretation and design of future studies.

2 | MATERIALS AND METHODS

We used species abundance data from experiments in herbaceous ecosystems including grasslands, tundra, pastures, and wetlands. Datasets for this analysis were obtained from the CoRRE (Community Responses to Resource Experiments) database (for details on data selection see https://corredata.weebly.com). The dataset includes only herbaceous communities as tree species abundance responses are extremely difficult to extrapolate from decade-scale experiments (Franklin et al., 2016). Herbaceous plant communities can reach a relatively stable state more quickly than forests following disturbances that leave soil intact, such as herbivory or fire (Koerner et al., 2014). For this analysis, we selected studies from the database that manipulated at least one global change driver for 10 or more years. The only exception was the inclusion of one 8-year dataset from the Tas-FACE study to improve representation of warming and CO_2 treatments and the southern hemisphere. We included the five treatments (elevated CO_2, nitrogen, phosphorus, water addition, and warming) that were most commonly applied. The subset included 791 species across 16 experiments at 12 sites (See metadata, Supporting information Table S1). We treated the same species at different sites independently. Our analysis only included single-factor treatments and controls.

2.1 | Assessment of species abundance change

We assessed long-term, directional change in plant abundance through time using different indices for different purposes. To capture **responsiveness** for comparisons of species-level responses *among* sites, we used the correlation coefficients (Pearson's *r*, referred to as *r*) from correlations of absolute abundance of each species versus time (year 1 = first year treatments were applied). We estimated a separate r for each species in each treatment in each experiment, pooling across replicate plots. The sign of r expresses the direction of change and standardizes trajectories on a scale from −1 to 1 that is universally comparable among species and sites, and is not influenced by magnitude of abundance or change like slopes would be (Gurevitch, Curtis, & Jones, 2001). A value of 1 indicates consistent increase in species abundance; −1 indicates consistent decrease; 0 indicates no consistent trend (refer to Supporting information Figure S1 for examples of these relationships). To account for the possibility that long-term increases or decreases in abundance were consistent but not linear, we also assessed change with Spearman's rank correlation coefficients (ρ) as an alternative estimate of responsiveness. Correlation coefficients capture the consistency of linear increase or decrease in abundance over time and across plots, but they do not capture the magnitude of change.

To estimate and compare the **magnitude** of plant abundance change *within* sites, we used linear slopes of abundance through time (**m**) using plot-level data for each timepoint. Though more complex relationships can occur, we used linear relationships because our questions centered on long-term, directional change through time. Because techniques of measuring species abundance varied among studies (gridline intercept, % cover, biomass; Supporting information Table S2), the slopes are not directly comparable across sites. The parameters we used in characterizing plant change are summarized in Table 1.

TABLE 1 Summary of parameters used in assessing change in abundance

Parameter	Description	Analysis
Linear responsiveness (r)	Correlation coefficient of species abundance through time	For global comparisons of species-level abundance change across all experiments (dependent on linear change)
Monotonic responsiveness (ρ)	Spearman's rank correlation coefficient of species abundance through time	For global comparisons of species-level abundance change across experiments (not dependent on linear change)
Magnitude of change (m)	Absolute value of slope of species abundance through time	For within-site comparisons of magnitude of change
Dynamic treatment effect	Absolute value of difference between $m_{\text{treatment}}$ and m_{ambient}	For comparisons of dynamic treatment effects to ambient change
Relative dynamic treatment effect	Ratio of dynamic treatment effect to ambient change	
Average abundance ($\bar{x}$)	Average abundance over time	For calculation of static treatment effect size
Static treatment effect	Absolute value of difference between $x_{\text{treatment}}$ and x_{ambient}	For comparisons of treatment effects to ambient change
Relative static treatment effect	Ratio of static treatment effect to ambient change	

2.2 | Comparison of species responsiveness across experiments

To explore patterns of covariance among treatments in responsiveness between plant species abundance changes across the entire dataset, we used three different metrics. First, we used the responsiveness term defined above as correlation coefficient of species change through time. We correlated species responsiveness in ambient control plots (r_{ambient}) to species responsiveness in each global change treatment (r_{CO2}, r_{nitrogen}, $r_{\text{phosphorus}}$, r_{water}, and r_{warming}) for a total of 1,172 site–species–treatment combinations such that each point represents a single species. Second, to evaluate the validity of assuming linearity, we also compared across treatments using Spearman's ρ as an index of monotonic change through time (ρ_{ambient} vs. ρ_{CO2}, ρ_{nitrogen}, $\rho_{\text{phosphorus}}$, ρ_{water}, and ρ_{warming}). Finally, though we could not compare m across experiments owing to differing metrics of abundance, we did compare the magnitude of change among treatments within each individual experiment. We correlated m_{ambient} with (m_{CO2}, m_{nitrogen}, $m_{\text{phosphorus}}$, m_{water}, and m_{warming}) for each experiment.

2.3 | Comparisons of magnitude of change within experiments

We compared the strength of ambient trends to treatment effects. We estimated linear slopes of abundance by treatment year, with treatment year 1 as the first year of measurement for ambient plots (m_{ambient}) and each treatment ($m_{\text{treatment}}$) for each site. The magnitude of ambient trends was defined as the absolute value of m_{ambient} in abundance change per year.

2.4 | The magnitude of dynamic and static treatment effects

We used two methods to estimate the magnitude of treatment effects on species abundance within each site, one allowing for a *dynamic* treatment effect that may change over the course of the study (Figure 1a), and one considering a *static* treatment effect averaged over the course of the study (Figure 1b).

We estimated effects of each treatment on rate of species change for each experiment as the average absolute value of the difference between slopes (m) of treatment and control for each species. Because the units of slopes were not comparable across experiments, we relativized treatment effects for each experiment by dividing by the absolute value of the ambient slope for each species:

$$\text{Relative dynamic treatment effect} = \frac{|m_{\text{treatment}} - m_{\text{ambient}}|}{|\, m_{\text{ambient}}|}$$

This ratio reflects the relative strength of treatment in altering plant trajectories compared to ambient change. Values >1 indicate that treatment effects are stronger than ambient change.

A treatment could have a sustained effect that is not well captured by the linear slope through time. Therefore, we also estimated mean treatment effects for each site by averaging abundance across all treatment years of each experiment for each species.

As above, we divided this mean treatment effect size by the absolute value of m_{ambient} to express the treatment effect relative to the magnitude of ambient change in abundance for each species:

$$\text{Relative static treatment effect} = \frac{|\bar{x}_{\text{treatment}} - \bar{x}_{\text{ambient}}|}{|\, m_{\text{ambient}}|}$$

where $\bar{x}_{\text{treatment}}$ and $\bar{x}_{\text{ambient}}$represent mean abundance of species over the entire experiment. Here, we divided a difference in abundance by a rate of change in abundance, yielding a time expressed in years. This value can be considered the amount of time required for the magnitude of ambient change to exceed the magnitude of treatment effects.

Both relative static and dynamic treatment effects were log-normally distributed owing to some small values in the denominators, so we report medians of individual species treatment effects in characterizing the whole dataset. To avoid over-representing experiments that have more species, we also estimate mean treatment effects for each experiment. To calculate experiment means for each treatment, we used the equation: $10^{[\mathrm{mean}(\log_{10}x)]}$ where x is the treatment effect for each species. We report the mean of these site averages for each treatment (n = 3–11).

2.5 | Direction of treatment effects compared to direction of ambient change

The treatment effect assessments above compare the magnitude of change without regard for the direction. To determine whether treatment effects were likely to amplify or moderate ambient change, we took the sign of the slope from each linear relationship of species abundance through time for each experiment–treatment to represent a binary direction, either positive or negative. We used Fisher's exact tests to determine whether the direction of the static treatment effect (+ or −) was related to the direction of ambient change (+ or −).

2.6 | Robustness

To assess the robustness of the patterns, we restricted the dataset in three ways and re-performed some of the above analyses. First, to determine how important experimental duration was for the patterns, we curtailed each dataset (to include only the first 5 years), from the full-length dataset (from 8 to 31 years in duration). Second, we restricted analyses to species that constituted more than 1% and more than 5% of total plant abundance to determine whether abundant and rarer plants responded differently. Third, we restricted analyses to plant species for which abundance in ambient plots exhibited a slope with $p < 0.05$ to focus on species that exhibit consistent ambient change. We further restricted them to $p < 0.001$ to account for the possibility that multiple comparisons lead to spuriously significant results. Rather than using these P-values for hypothesis testing, we used them as arbitrary demarcations to subset species that exhibit consistent ($p < 0.05$) or highly consistent ($p < 0.001$) directional, ambient change across plots and through time. All data filtering, summarizing and statistical calculations were performed in JMP Pro 13 (SAS Institute).

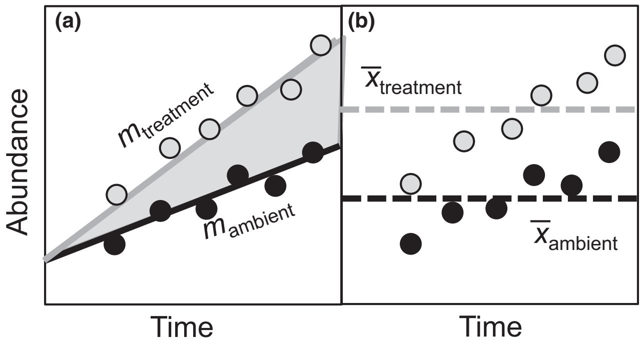

FIGURE 1 Stylized data illustrating estimation of treatment effects. The dynamic treatment effect (a) is the difference in linear trend attributable to the treatment, and the static treatment effect (b) is the difference in mean abundance over the course of the experiment. For clarity, symbols here represent treatment means, though individual plot data were used for the analyses

3 | RESULTS

3.1 | Assessment of ambient change and how it relates to change in treated plots

The distribution of r_{ambient} across species was flatter than a normal distribution (Shapiro–Wilk W test, $p < 0.001$, Figure 2, left panel). That pattern became more pronounced when the dataset was restricted to abundant (>1% relative abundance) species (Figure 2, right panel), indicating more consistent ambient change in species that play larger roles in ecosystems. Changes in plant species abundances under each treatment were closely related to changes in abundances in ambient controls (Figure 3). In other words, when species were increasing (or decreasing) in abundance over time in ambient plots, they were often also increasing (or decreasing) in abundance over time in treatment plots. These patterns could be driven by rare species, which may not strongly influence ecosystem processes. Therefore, we tested the robustness of these patterns by restricting the database to only abundant species, by species that show consistent directional change, and by curtailing the duration of studies. Restricting the analysis to include only species that

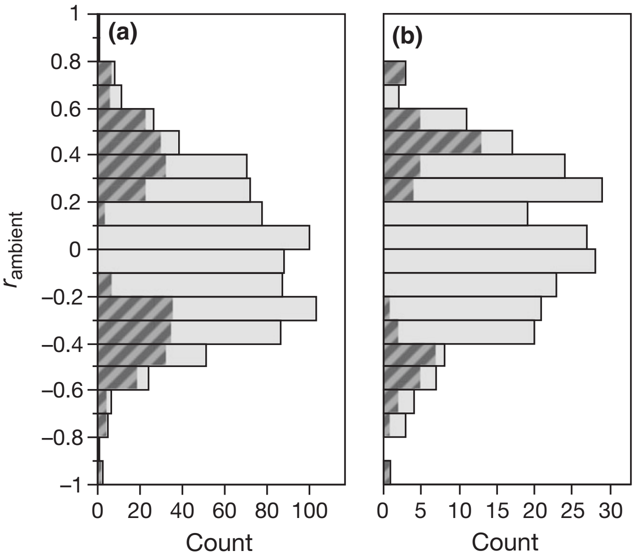

FIGURE 2 Distribution of long-term ambient changes in species abundance (r_{ambient} = correlation coefficient for species abundance vs. time). On the left (a), the full dataset is shown and hatched bars represent the site-species that exhibited consistent, directional change (slope $p < 0.05$ for correlations between abundance and year) under ambient conditions. On the right (b), the dataset is restricted to include only abundant species (>1% relative abundance), and hatched bars represent site-species that were exhibited highly consistent, directional change ($p < 0.001$)

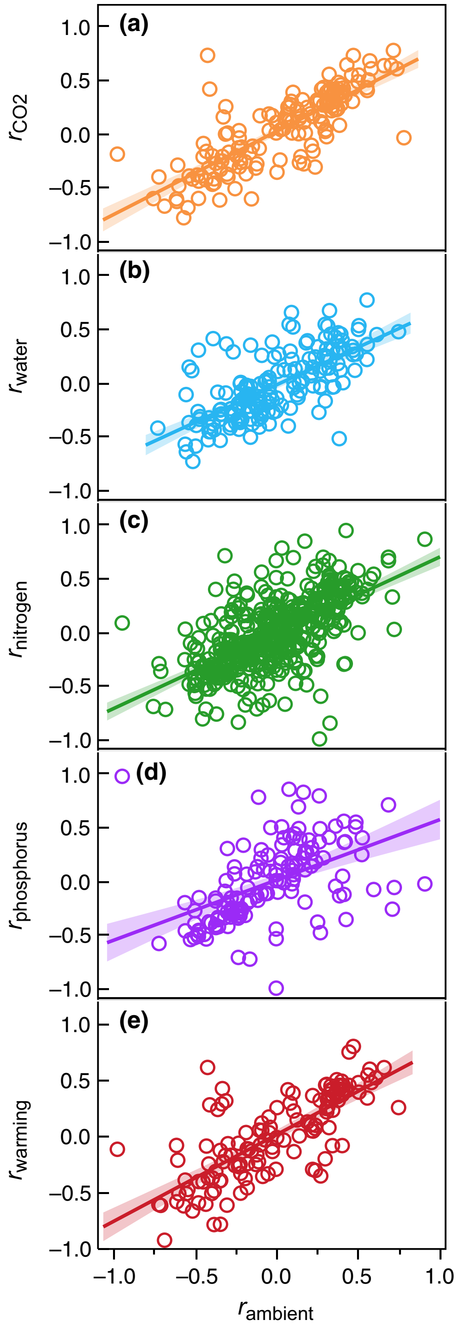

FIGURE 3 Scatterplots of the relationship between $r_{ambient}$ and $r_{treatment}$ across all species separated by treatment. All $p < 0.0001$; (a) $r_{CO2} = 0.773 * r_{ambient} + 0.014$; (b) $r_{water} = 0.697 * r_{ambient} - 0.026$; (c) $r_{nitrogen} = 0.703 * r_{ambient} - 0.014$; (d) $r_{phosphorus} = 0.559 * r_{ambient} + 0.004$; (e) $r_{warming} = 0.770 * r_{ambient} + 0.007$ $r_{ambient}$ = the correlation coefficient of ambient plant abundance versus time $r_{treatment}$ = the correlation coefficient of treatment plant abundance versus time [Colour figure can be viewed at wileyonlinelibrary.com]

contributed over 1% and 5% of plant abundance (29.1% and 9.4% of all species) yielded stronger patterns (R^2 across treatments = 0.61 and 0.60, Table 2). For species that experienced consistent, directional change under ambient conditions (31.9% of linear trends had a $p < 0.05$; 10.0% had $p < 0.001$), the relationship between $r_{ambient}$ and $r_{treatment}$ was also strong (mean R^2 across treatments = 0.66 for $p < 0.05$ and $R^2 = 0.82$ for $p < 0.001$). Curtailing the duration of the datasets to five years generally weakened the relationships (mean $R^2 = 0.33$). Using Spearman's rank correlation coefficients to characterize abundance change through time yielded $\rho_{ambient}$ that were very closely related to $r_{ambient}$ ($R^2 = 0.92$) indicating that assuming linearity in abundance change did not greatly affect the analysis.

The degree of covariation among $r_{treatment}$ and $r_{ambient}$ depended on treatment. Elevated CO_2 had the highest agreement with ambient; $r_{ambient}$ predicted 65% of the variability in r_{CO2}. Species responsiveness in phosphorus treatments ($r_{phosphorus}$) was the lowest at 24%. The degree of covariation among $r_{treatment}$ and $r_{ambient}$ also varied sharply by experiment (Supporting information Figure S2). For instance, responsiveness at Smithsonian Ecological Research Center (SERC), a coastal wetland, strongly covaried across treatments ($R^2 = 0.90$). Niwot Ridge (alpine tundra) had much lower average correlations of $r_{treatment}$ with $r_{ambient}$ ($R^2 = 0.11$). Though, we could directly not compare $m_{ambient}$ to $m_{treatment}$ across the entire dataset, and we did so within individual experiments. Here, too, there was high agreement (Supporting information Figure S3, across all experiment–treatment combinations average $R^2 = 0.59$).

3.2 | Magnitude and direction of treatment effects compared to ambient change

We compared rate of abundance change in ambient plots ($|m_{ambient}|$) to the treatment effect on that rate of change ($|m_{treatment} - m_{ambient}|$). Relativizing treatment effects to ambient change allowed us to assess patterns across the entire dataset. Across all experiments, the median species had a relative dynamic treatment effect of 0.83 (N = 1,058), and 57% of species had a value less than 1. The means across treatments did not differ from each other (Figure 4a, n = 3–11, one-way ANOVA, $p = 0.438$), nor did any differ from 1 (95% confidence intervals enveloped 1). When the dataset was restricted to abundant species (>1% or >5% relative abundance averaged over entire experiment) or to cases in which ambient change was consistent ($p < 0.05$ or $p < 0.001$), the magnitude of relative dynamic treatment effects was similar but generally decreased (Table 3).

We also used a second method of assessing the relative strength of ambient change by estimating the difference in average abundance over the study period for each species from that in ambient ($\bar{x}_{treatment} - \bar{x}_{ambient}$). We divided this metric, an abundance, by change in ambient abundance through time, a rate ($m_{ambient}$), to yield the length of time required for ambient change to exceed the magnitude of static treatment effects (Figure 4b). The median across all species was 4.3 yr. Relative static treatment effect did not vary significantly among treatments (one-way ANOVA, $p = 0.137$, n = 3–11).

Species directions (increasing or decreasing in abundance) in all treatments agreed with directions in ambient plots for 81% of cases. Still, we tested the tendency of the direction of *treatment effects* (whether the treatment increased to decreased abundance *relative* to ambient) to agree with the direction of ambient change. The direction of ambient change had no bearing on direction of static treatment effects for any treatment (Fisher's exact test, two tail, all

TABLE 2 R^2 of $r_{ambient}$ with each $r_{treatment}$ across all studies and for various subsets of the data

R^2 with $r_{ambient}$	N	Full	Curtailed	>1%	>5%	$p < 0.05$	$p < 0.001$
r_{CO2}	155	0.65	0.47	0.80	0.74	0.84	0.87
r_{H2O}	173	0.48	0.42	0.63	0.60	0.67	0.75
$r_{nitrogen}$	380	0.40	0.34	0.38	0.48	0.57	0.79
$r_{phosphorus}$	330	0.24	0.26	0.53	0.66	0.37	0.92
$r_{warming}$	134	0.57	0.33	0.70	0.53	0.84	0.78

Notes. Covariation was stronger for the full duration of the study rather than datasets curtailed to years 1–5, and tended to increase when the dataset was restricted to abundant (>1% and >5% relative abundance) and consistently changing ($p < 0.05$ and $p < 0.001$) species.

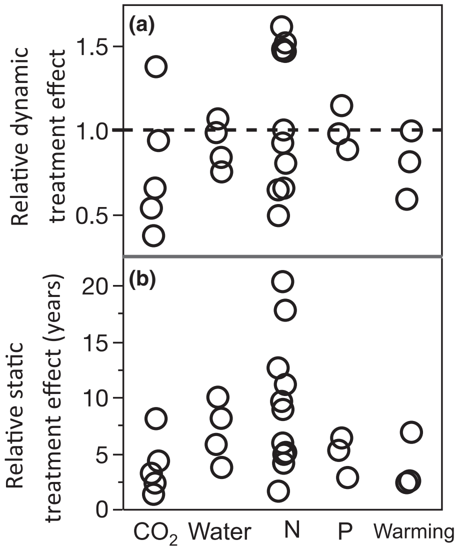

FIGURE 4 (a) Means of the relative dynamic treatment effect for each treatment. Each circle represents one experiment. Effects <1 are smaller than ambient change. (b) The relative static treatment effect expressed in years required for ambient change to exceed the static treatment effect in magnitude for an average species in each experiment. Values represent means for each experiment (n = 3–11)

$p > 0.1$). Overall, treatments were just as likely to amplify (51% of cases) as antagonize the (49% of cases) ambient trends (Figure 5). We reran this test on each subset of the dataset described above. In no case did the direction of treatment effects depend on the direction of ambient change (Fisher's exact test, two tail, all $p > 0.1$).

4 | DISCUSSION

4.1 | Covariation of plant abundance change in ambient and treated plots

The direction and consistency of change in plant species abundance in ambient plots was very closely related to that in treated plots. Strong covariation was apparent across the entire database. However, it was stronger for abundant species, suggesting that the abundance of key species under any treatment is more closely related to ambient trends than for rarer species, perhaps because of noisier data for rare species. Cases in which a treatment tended to change the trajectory of a plant that was consistently increasing or decreasing in ambient abundance were few. This finding challenges the notion that global change treatments select for "winner" and "loser" species (Langley & Hungate, 2014; Poorter & Navas, 2003). In other words, plant species are changing in abundance in global change experiments, but the change is most strongly driven by factors that affect both ambient and treatment plots.

The level of covariation between ambient plant abundance and treated plant abundance depended on experiment and treatment. Species changes in elevated CO_2 were more closely related ambient species changes than those under N and P addition (Table 2). This finding is consistent with results of experimental work showing that nutrient addition induces stronger effects on community composition than elevated CO_2 (Isbell et al., 2013). The differences in covariation across experiments could arise partly from the strength of applied treatments (e.g., the N addition rate in fertilized plots). Experiments also vary in the importance of external factors that can drive strong covariation among ambient and treated plots. For instance, in the tidal marsh at SERC, patterns in plant species abundance are driven largely by flooding frequency. Variability in flooding frequency through time is largely determined by decadal-scale oscillations in local sea level. Recently, an interval of high sea level has diminished the abundance of drought-sensitive, high-marsh grasses like *Spartina patens* (Supporting information Figure S1), overwhelming strong global change treatment effects observed during intervals with lower sea levels (Langley & Megonigal, 2010). At the other end of the spectrum, low covariance between $r_{ambient}$ and $r_{treatment}$ indicates that treatment levels are relatively strong compared to background drivers. For instance, Niwot is a site with low ambient resource supply coupled with strong selection for slow growth, and high microsite heterogeneity may result in low rates of change in response to current environmental change (Spasojevic, Bowman, Humphries, Seastedt, & Suding, 2013). There, relatively strong environmental treatments surpass thresholds in intensity and favor establishment and population growth of more responsive species (Suding, Farrer, King, Kueppers, & Spasojevic, 2015; Theodose & Bowman, 1997).

4.2 | The magnitude of ambient change

That change in species abundance of plants in ambient plots is closely related to that in treatments argues that ambient change is an

TABLE 3 Relative dynamic and relative static treatment effects for each subset

Treatment	Full	Curtailed	>1%	>5%	$p < 0.05$	$p < 0.001$
Relative dynamic treatment effects						
CO_2	0.8 (0.2)	0.8 (0.1)	0.6 (0.2)	0.6 (0.2)	0.5 (0.1)	0.4 (0.2)
Water	0.9 (0.1)	0.9 (0.1)	0.9 (0.2)	1.1 (0.4)	0.5 (0.1)	0.6 (0.3)
N	1.1 (0.1)	1.2 (0.2)	1.3 (0.2)	1.2 (0.2)	0.8 (0.1)	0.5 (0.1)
P	1.0 (0.1)	1.0 (0.2)	0.6 (0.1)	1.6 (1.2)	0.5 (0.2)	0.2 (0.1)
Warming	0.8 (0.1)	0.8 (0.1)	0.6 (0.1)	0.4 (0.0)	0.4 (0.0)	0.2 (0.1)
Relative static treatment effect						
CO_2	3.8 (1.2)	2.0 (0.1)	3.5 (1.2)	4.4 (2.0)	1.7 (0.4)	1.4 (0.5)
Water	6.9 (1.4)	2.1 (0.2)	6.2 (1.3)	6.8 (2.1)	3.4 (0.8)	3.6 (1.2)
N	9.3 (1.8)	2.6 (0.4)	10.1 (1.7)	10.8 (1.8)	4.8 (1.0)	3.4 (0.8)
P	4.8 (1.0)	2.1 (0.2)	3.8 (1.2)	9.9 (6.8)	2.9 (1.1)	2.2 (1.0)
Warming	3.9 (1.5)	1.9 (0.0)	2.8 (0.8)	4.5 (1.7)	1.4 (0.4)	1.3 (0.4)

Notes. For relative dynamic treatment effects, the magnitude of ambient change for each species is set to 1. Relative static treatment effects are expressed in years of ambient change required to overcome the treatment effect on a species averaged over the course of the study. Values represent experimental means with standard error in parentheses (n = 3–11).

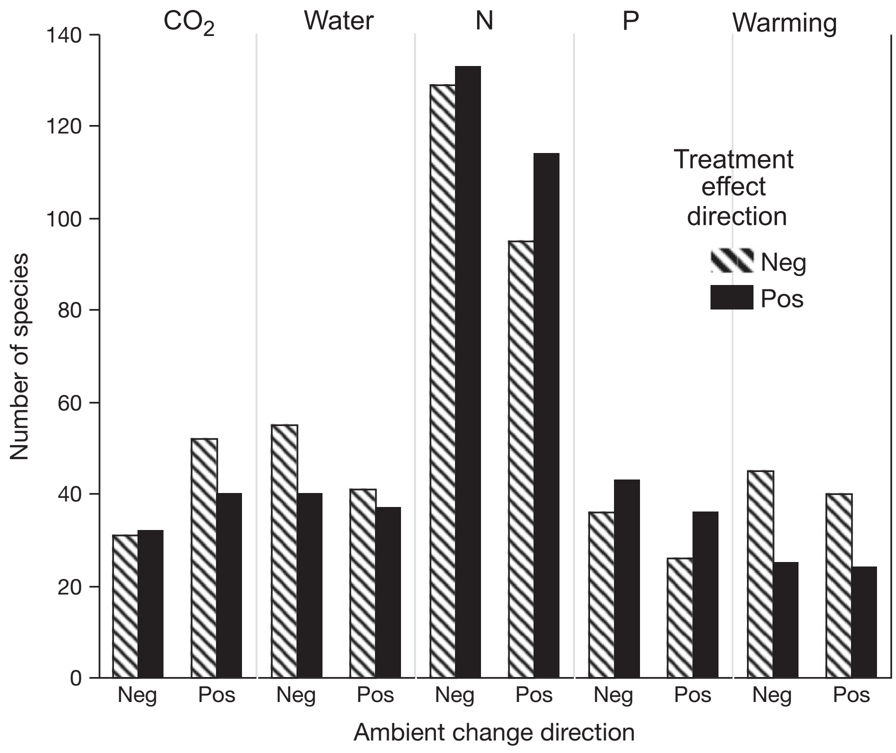

FIGURE 5 The distribution of species across the four possible categories of directional effects for each treatment. The direction of ambient change was not related to the direction of static treatment effect for any treatment (Fisher's exact test, two tail, all $p > 0.1$)

important force, so we compared ambient change to treatment effects quantitatively. The magnitude of ambient change was surprisingly large relative to the magnitude of treatment effects regardless of the approach for assessing treatment effects. The relative dynamic treatment effect was generally similar to, but smaller on average than, the magnitude to ambient change (Figure 4a). A second approach of assessing treatment effects, relative static treatment effects, showed similar results. By this estimate, treatment effects on the average species were equivalent to only 4.3 years of ambient change in species abundance. This amount of time is astonishingly short given that most global change experiments apply treatments at levels that target multiple decades or centuries into the future (Lin, Xia, & Wan, 2010). Both metrics agreed with the covariance analysis, such that the soil resource treatments (nitrogen, phosphorus, and water) tended to yield larger effects than elevated CO_2 or warming (Figure 4a,b). We conclude that ambient change, whatever drives it, is of similar magnitude or even exceeds the magnitude of treatment effects for most species and that we may be underestimating the relative importance of inertia already present community trajectories.

4.3 | Drivers of ambient change

The implications of strong ambient change depend on what factors are driving it. Changes in species abundance in ambient plots could result from (a) natural (non-anthropogenic) phenomena, (b) anthropogenic drivers, or (c) experimental artifacts. First, plant communities change through time due to natural population cycles, such as those driven by non-anthropogenic climactic variability, succession, recovery from disturbance, competitive dynamics, demographic stochasticity, mast seeding, or herbivore boom–bust cycles (Fuhlendorf & Smeins, 1997; Foster & Gross, 1998; Ostfeld & Keesing, 2000; De Mazancourt *et al*., 2013; Stouffer et al., 2018). The sites included herein are dominated by herbaceous plants, many of which have shorter-term population cycles than woody species and would likely exhibit more rapid responses to climatic variability. The long duration of the studies should minimize the effect of short-term (<5-year) cycles on linear increases or decreases in plant abundance, though the effects of long-term succession or recovery from disturbance may still be important at some sites (Foster & Gross, 1998).

Alternatively, anthropogenic changes, related to climate, biogeochemistry, invasion, or disturbance, may have long-term (>decades) directional influence on species abundance, given the long-term trajectories of directional change in these drivers. Elevated CO_2 is the most homogenous driver of environmental change globally. Climatic changes such as warming and altered precipitation can drive rapid changes in plant communities (Gottfried et al., 2012; Kelly & Goulden, 2008), and such effects are apparent in observational studies (Parmesan & Yohe, 2003). Chemical changes like nitrogen deposition are known to have strong influences on species abundances (De Schrijver et al., 2011; Pennings et al., 2005; Stevens, Dise, Mountford, & Gowing, 2004). Exotic species invasion has been changing plant abundance for a century (Hejda, Pyšek, & Jarošík, 2009). It may be the case that the most important drivers of ambient change are also some of the factors being manipulated in the global change experiments.

These first two possibilities can be difficult to disentangle, as they may not be mutually exclusive. That is, the driver of ambient change could be a natural cycle that is intensifying. Revisiting the example from SERC, flooding frequency is the dominant driver of ambient change (Langley & Hungate, 2014; Langley, Mozdzer, Shepard, Hagerty, & Megonigal, 2013), and it varies with natural cycles. However, anthropogenic climatic change has likely contributed to increased flooding frequency at this site in recent decades. Similarly, droughts can reshape communities naturally. Many regions around the world, especially in grasslands, are expected to have, and may already be experiencing, increasing frequency of severe drought (Spinoni, Naumann, Carrao, Barbosa, & Vogt, 2014). Therefore, determining if the driver of ambient change is natural or anthropogenic depends on attribution of abiotic global changes themselves.

Finally, experimental artifacts and observational error may also contribute to ambient change. Plot studies incur artifacts such as physical disturbance, chamber effects, and proximity among treatments. For instance, increasing growth of nitrophilic species in N-fertilized plots could allow them to establish in nearby control plots. Any effects that influence all plots would increase rates of change in ambient plots as well as covariation among treatments, and may partly explain the correlations we observe across ambient and treatment plots (Figure 3) and relatively weak treatment effects (Figure 4). On the other hand, the timing, levels and combinations of global change treatments may engender artifacts that tend to cause overestimation of plant responses to global change treatments. Treatment application typically occurs more quickly than real perturbations. For instance, nearly all elevated CO_2 experiments elevate CO_2 abruptly, even though the CO_2 rise simulated occurs over decades or centuries. Moreover, treatment applications may be more extreme than are likely to occur in real ecosystems. A recent catchment-level fertilization experiment found no effects on plant communities despite large effects often reported in plot-level studies. The authors attributed the disparity to unrealistically high levels of N addition in plot-level studies (Johnson, Warren, Deegan, & Mozdzer, 2016). Additionally, if measurement methodology (such as misidentification of species) varied through time, it could result in spurious covariation in plant abundance change between ambient and treated plots in our study. Though perhaps present in some cases, experimental artifacts are unlikely to explain the consistent importance of ambient change across these diverse studies.

4.4 | Implications

Like studies that monitor unmanipulated plots (Verheyen et al., 2017), long-term global change experiments can provide important information on background plant community change, and have the advantage of comparing it to the change caused by treatments. We found that changes in plant species abundance through time in ambient plots were stronger on average than the changes attributed to experimental treatment effects. These unexpectedly large changes in plant species abundances in unmanipulated plots merit further exploration. The implications of these findings for ecological communities and ecosystem processes depend on what is driving ambient change, though we did not directly address attribution in this analysis. Ambient changes detected in these experiments could be driven by (a) natural phenomena, (b) anthropogenic factors, or (3) experimental artifacts.

A preponderance of evidence suggests that ongoing climate change is dramatically altering terrestrial plant communities (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Parmesan & Hanley, 2015; Parmesan & Yohe, 2003; Rosenzweig et al., 2008). If, for instance, an experimental site were already experiencing warming, might additional, experimentally imposed warming only marginally increase the already existing rate of change in species abundances? Or, alternatively, would this cause an even greater treatment effect? Here we found that ambient changes in plant abundance often exceed treatment effects. The most important drivers of this strong ambient change are likely some of the same factors that global change experiments manipulate. For example, ambient $[CO_2]$ is now roughly 50% higher than it was in preindustrial times. Rising atmospheric CO_2

could alter plant abundance in ambient plots. Over long intervals, ambient change driven by CO_2 may ultimately reduce the measured difference between ambient and elevated CO_2 plots (Drake, 2014) given that the treatment difference is consistent CO_2 responsiveness saturates at higher [CO_2]. That treatment effect direction was unrelated to ambient change direction (Figure 5) argues that the primary drivers of ambient change frequently differ from the manipulated factors. The unmanipulated drivers of change may interact with manipulated factors in unpredictable ways.

Because we did not herein attribute ambient change to particular drivers, it remains to be more fully explored how plant species changes under a particular ongoing global change compare to responses under those same manipulated factors. Such comparisons would be complicated for several reasons. More than one driver may contribute to ambient change at most sites. In the present study, we did not have the replication across experiments necessary to include analysis of multifactor treatments. The most important driver(s) would have to be mimicked at realistic levels, and there would need to be sufficient time for experimental effects to manifest. Experiments involving antecedent conditions (e.g., preindustrial [CO_2]) could be useful in linking ongoing ambient change to experimentally manipulated drivers (Concilio, Nippert, Ehrenfeucht, Cherwin, & Seastedt, 2016).

Despite uncertainty in attribution of plant abundance changes, we suggest that our findings have implications for the design and interpretation of global change experiments. Ongoing global change studies should assess and report the change in ambient plots. Strict focus on treatment effect sizes may overlook background changes, which are often stronger than treatment effects. Long-term studies, especially those that measure community composition frequently, are best able to assess ambient change. Global change studies may have a variety of different goals. To directly address the importance of global change relative to dynamic plant communities, some new global change experiments should locate treatments along invasion fronts, in pollution hotspots, and near thresholds of abiotic change such as rising seas, for it is in these places, where rapid community shifts are already occurring, that the influence of additional global change drivers will be most important to capture.

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AUTHOR CONTRIBUTIONS

Adam Langley is a C2E member, provided raw data, developed research questions, analyzed data, and wrote paper. Samantha Chapman developed research questions, analyzed data, and contributed to paper writing. Meghan L. Avolio and Kimberly J. La Pierre are members and leaders of C2E, analyzed CoRRE Database, provided raw data, developed research questions, and contributed to data analyses and paper writing. William D. Bowman and David S. Johnson are C2E Members, provided raw data, developed research questions, and contributed to data analyses and paper writing. Kevin R. Wilcox is a member and leader of C2E, contributed to data analyses and paper writing. Forest Isbell is a C2E member, provided raw data and contributed to data analyses and paper writing. Alan K. Knapp, Bryan L Foster, Mark J Hovenden, J Patrick Megonigal, Paul CD Newton, Kenwyn B Suttle, and David Tilman provided raw data and contributed to paper writing. Chrsitopher J Lortie is a C2E member and contributed to paper writing. Sally E. Koerner and Peter B Reich are C2E members, provided raw data, and contributed to paper writing. Melinda D Smith is a C2E member, contributed to data analyses and paper writing.

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SUPPORTING INFORMATION

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

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