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DOI:
10.1002/ecy.3626

Document Version
Final published version

Link to publication record in Manchester Research Explorer

Citation for published version (APA):
Langley, J. A., Grman, E., Wilcox, K. R., Avolio, M. L., Komatsu, K. J., Collins, S. L., Koerner, S. E., Smith, M. D., Baldwin, A. H., Bowman, W., Chiariello, N., Eskelinen, A., Harmens, H., Hovenden, M., Klanderud, K., Mcculley, R. L., Onipchenko, V. G., Robinson, C. H., & Suding, K. N. (2022). Do trade-offs govern plant species' responses to different global change treatments? *Ecology*. https://doi.org/10.1002/ecy.3626

Published in:
Ecology

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Download date:28. Mar. 2024

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Received: 28 July 2021 | Accepted: 21 October 2021

DOI: 10.1002/ecy.3626

REPORTS

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Do trade-offs govern plant species' responses to different global change treatments?

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Handling Editor: Rachel M. Mitchell

Abstract

Plants are subject to trade-offs among growth strategies such that adaptations for optimal growth in one condition can preclude optimal growth in another. Thus, we predicted that a plant species that responds positively to one global change treatment would be less likely than average to respond positively to

J. Adam Langley and Emily Grman are co-first authors.

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another treatment, particularly for pairs of treatments that favor distinct traits. We examined plant species' abundances in 39 global change experiments manipulating two or more of the following: CO_2, nitrogen, phosphorus, water, temperature, or disturbance. Overall, the directional response of a species to one treatment was 13% more likely than expected to oppose its response to a another single-factor treatment. This tendency was detectable across the global data set, but held little predictive power for individual treatment combinations or within individual experiments. Although trade-offs in the ability to respond to different global change treatments exert discernible global effects, other forces obscure their influence in local communities.

KEYWORDS
data synthesis, elevated CO_2, global change experiments, herbaceous plants, irrigation, nitrogen, resource strategies, warming

INTRODUCTION

Plants face multiple simultaneous environmental and climatic changes that will intensify in the future, and predicting plant response remains a great challenge for ecologists. Researchers have tried to predict plant responses to global change based on phylogeny (Edwards et al., 2007) and traits (Lavorel & Garnier, 2002), but success has been idiosyncratic (Kimball et al., 2016). Thousands of ecosystem manipulations have tested plant responses in the field, but each experiment can manipulate only a limited number of factors, most commonly just one or two (Song et al., 2019). Finding consistent patterns in plant species' responses to different global change drivers would enhance our ability to leverage existing experimental results and extrapolate to other drivers in other ecosystems.

Plants are subject to trade-offs among strategies that may determine how they respond to environmental change (Chapin et al., 1987; Díaz et al., 2016; Grime, 1977; Tilman, 1990; Viola et al., 2010), which could lend predictability to plant responses. Because optimizing strategies for responding to one environmental condition often compromises optimizing for another, plants may exhibit differential abilities to respond to different global change drivers (Craine, 2009). For example, in late successional grasslands, a plant species may either compete well for nitrogen (N) or for light (Tilman, 1990) but not both, owing to differences in allocation required to optimize acquisition of each resource. Patterns suggestive of trade-offs have been observed in individual global change experiments. For example, in a brackish marsh, C_3 sedges responded positively to elevated carbon dioxide (CO_2), but negatively to added N, whereas the opposite was true for C_4 grasses, owing to trade-offs in plant physiology and allocation (White et al., 2012) compounded by competition between grasses and sedges (Langley & Megonigal, 2010). Therefore, the species' responses to each treatment, elevated CO_2 and N, tended to be inversely related. Similarly, plants may specialize for optimal growth at a particular level of one resource. For instance, optimizing growth at high water availability may incur a cost in terms of drought tolerance (Luo et al., 2008). If these trade-offs play a strong role in determining species' responses, we would expect species' responses to different global change treatments to oppose one another (blue circles in Figure 1) for combinations of treatments that favor distinctive, or mutually exclusive, traits.

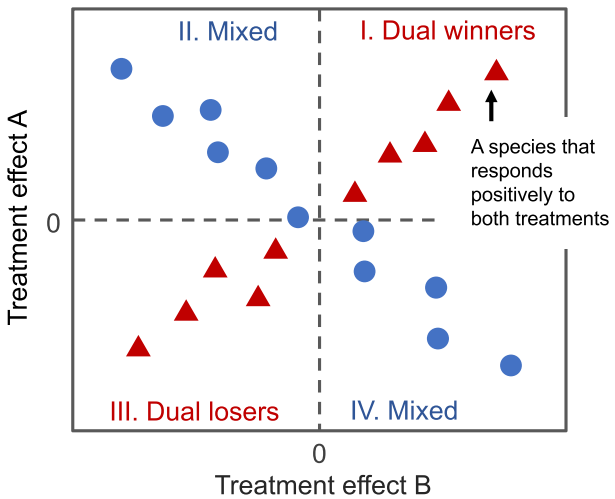


FIGURE 1 Illustration of potential species' responses to two different global change treatments. Each species (symbol) falls into one quadrant according to how it responds to the treatments: Positively to both (Quadrant I), negatively to both (Quadrant III), or positively to one and negatively to the other (Quadrants II and IV are pooled as "mixed responders")

Alternatively, plant species may not exhibit trade-offs in response to global change treatments. For instance, some plants exhibit plasticity depending on environmental conditions (Agrawal, 2001; White et al., 2012) that allows them to adapt to any change in resource availability, environmental conditions, or combination thereof (Tilman, 1982). Or, as many global change treatments increase resource availability, species adapted to high rates of resource acquisition may be expected to respond positively to any resource addition regardless of trade-offs among acquisition strategies (Chapin et al., 1987). Species that elude the constraints of trade-offs and perform well under a wide variety of environmental conditions have been referred to as "Hutchinsonian demons" (Cadotte et al., 2006; Kneitel & Chase, 2004), or "superspecies" (sensu Tilman, 1982). Such "demonic" species would be expected to increase in abundance in response to multiple environmental changes, while displacing other species that are specifically attuned to certain conditions (Mozdzer & Megonigal, 2012). Instead of being strictly shaped by trade-offs in resource acquisition or tolerance, plant communities may contain a subset of species that respond positively to most or all global change treatments and other species that respond negatively to any kind of perturbation. In this case we would observe a *positive* relationship between species' responses to different global change treatments (red triangles in Figure 1).

The degree to which species' responses to different treatments correspond may also depend on the specific combination of treatments. In global change studies, many common treatments increase resource availability (CO_2, nutrients, water), whereas drought reduces resource availability, and warming alters conditions and has equivocal influences on resource availability. Plant species may respond consistently to resource additions but respond differently to other treatment types such as disturbances. We may expect that addition of soil resources (N, P, water) would favor the same plant species, as there is some overlap in the mechanisms to acquire those different soil resources. Synthesizing across studies that examine a variety of treatment combinations will help elucidate where consistent patterns in plant response may occur.

Our goal was to answer the questions: (1) Do individual species' responses to one global change treatment relate to their responses to a second treatment? (2) Does the relationship depend on the particular treatment combination? To answer these questions, we used plant species' abundance data from 39 in situ experiments that exposed ecosystems to two or more single-factor global change treatments in separate plots. We examined the relationships between species' abundance responses to 18 different treatment combinations. If plant species' responses to different drivers tend to be inversely related, then trade-offs in the ability of a plant species to tolerate or take advantage of different global change treatments should shape future community composition. Alternatively, if species' responses to different treatments are positively related, relatively few species that respond strongly to many global change treatments will tend to dominate future communities and govern ecosystem responses to global change.

METHODS

Data sets for this analysis were obtained from the CoRRE (Community Responses to Resource Experiments) database (corredata.weebly.com) (Komatsu et al., 2019). The database includes communities dominated by herbaceous species, as tree species' abundance responses are extremely difficult to extrapolate from decade-scale experiments (Franklin et al., 2016). For this analysis, we selected studies from the database that individually manipulated at least two global change drivers for three or more years. We included eight treatments that were commonly imposed with other treatments in the same experiment: elevated CO_2, nitrogen addition, phosphorus addition, multiple nutrient addition, water addition, drought, warming, and disturbance. To create a disturbance category with replication robust enough to include in our analyses, we lumped burning, mowing, and clipping on the basis that each treatment removes plant biomass, though we acknowledge that these disturbances differ in many other ways. Our analysis included only single-factor treatments (e.g., warming or nitrogen) from experiments manipulating multiple factors and did not include combined treatments (e.g., treatments manipulating both warming and nitrogen).

Treatment effects

For each experiment, we estimated mean abundance across all years for each species in the control (C) and treatment (T) plots from raw abundances for each plot in each treatment year. Methods of assessing abundance varied among studies including percent cover, point intercept, and biomass. To assess treatment effects across sites we estimated an effect size, E, as $(T - C)/(T + C)$, where T is the mean species' abundance in the treatment and C is that of the control. Metrics with only the control abundance in the denominator, such as log response ratio or percent simulation, are incalculable for many rare species. In contrast, E allows us to assess treatment effects when species are gained or lost because of treatments (i.e., where species are absent in the treatment or control

plots). It ranges from −1 to 1, where negative values represent reduced abundance in the treatment compared to control, and positive the opposite (for distribution of E by treatment see Appendix S1: Figure S1). For species that occur in both treatment and control plots, E is perfectly correlated with other treatment effect metrics (Spearman's rho = 1 for log response ratio and percent stimulation; Appendix S1: Figure S2) and our results are very similar to those using log response ratio (see Supplement).

In many (32%) cases, species occurred in one treatment group (T or C) but not the others. These results could arise from treatment effects on plant presence or from stochasticity in distribution of rare species. To account for both possibilities, we ran the analyses on two different versions of the data set. We first ran the analyses with the full data set to include potentially important treatment effects on rare species. Then, we ran the analyses with a restricted data set, excluding species that were absent from either all control plots or all treatment plots for each treatment type at a site.

We categorized species in terms of their responses to the two treatments (Figure 1). Species with positive responses to one treatment but negative responses to another fell into Quadrants II and IV (mixed responders), suggesting trade-offs. Species with positive responses to both treatments (dual winners) or negative responses to both treatments (dual losers) fell into Quadrants I and III, respectively. We calculated the proportion of species in each group (dual winners, dual losers, and mixed) for each pair of treatments in each study. One species in one experiment could account for more than one data point, if the experiment applied more than two treatments. Because most of our results rely on the number of species falling into the different quadrants, results are identical between log response ratio and E when omitting species absent from either all treatment or all control plots.

Null model

All methods of assessing treatment effects compare response variables in treatment groups to that in the controls. Because each treatment effect from different treatments within a given experiment is referenced to the same control value, comparing treatment effects to one another incurs some degree of mathematical dependence. For instance, if we estimate E (or any other effect-size metric) for an experiment that manipulates both warming and N addition, the same control value is used in the calculation of both treatment effects. As a result, variability across control values tends to yield a positive relationship between the two treatment effects. To account for this mathematical dependency, we constructed a null model to determine if our estimated relationships between treatment effects differed from what one would expect with the same numerical properties of the data set but with no relationship between treatment effects. To do this, we randomly reshuffled the treatment assignments among all control and treatment plots within each experiment. For instance, if in a given experiment, Plot 1 was a control, Plot 2 was fertilized, and Plot 3 was warmed, we randomized such that one permutation of the null data set may have Plot 1 as warmed, 2 as fertilized and 3 as control such that any real relationship among treatment effects would be eliminated. We generated 999 pemutations of these null data sets and calculated species' abundances, effect sizes, and the proportion of species falling into each quadrant (Figure 1) for each permutation as described above for the actual data.

Analysis of species' responses to pairs of treatments

We assessed whether the distribution of plant species across the four possible quadrants of response (Figure 1) differed from expected distributions when there is no relationship between treatment effects (i.e., from the

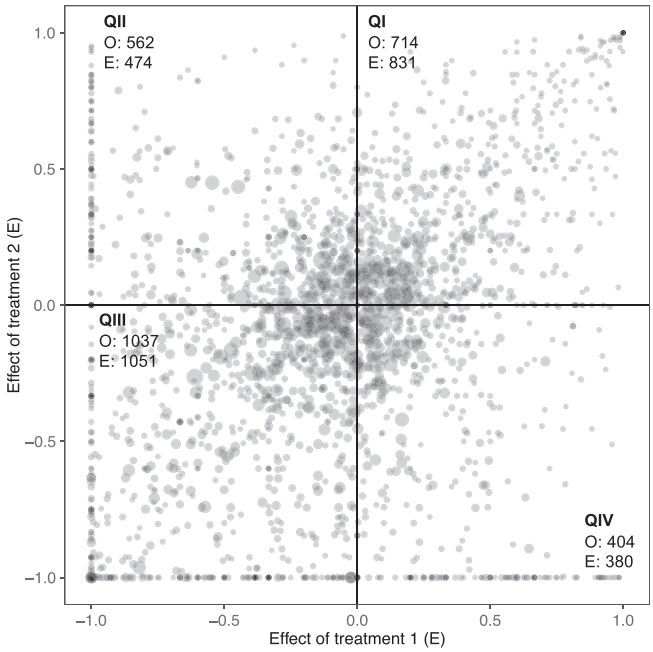


FIGURE 2 Species' responses to pairs of treatments. Each point represents a species in one treatment combination in one experiment. Point size indicates the species' relative abundance in the control plots. Points are transparent, and high densities of symbols darken for visibility of overlapping points. Text indicates the number of species in that quadrant across all studies and treatment combinations, both observed (O) and expected (E) from the simulated data

simulated communities). A positive difference between the observed proportion and the mean proportion in the simulated communities (observed – expected proportion >0) indicates that a study had more species in a quadrant than would be expected if there were no relationship among treatment effects.

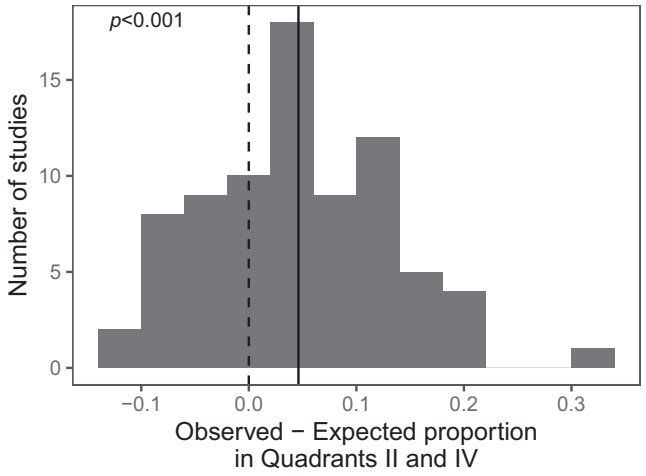


FIGURE 3 Difference in proportion of mixed responders (species in Quadrants II and IV; see Figure 1) between the observed and simulated communities, for all 78 studies in our data set. Observations right of the dashed line at zero indicate studies and treatment combinations in which more than the expected proportion of species responded positively to one treatment and negatively to the other. The solid vertical line indicates the mean difference across all 78 studies

To test whether the proportion differed from the expectation for individual treatment combinations in individual studies, we compared the distribution of permuted proportions to the observed proportions of mixed responders and calculated a two-tailed p value based on whether the observed value was more extreme than 95% of the 999 permuted values. To test whether the observed proportion differed from the expectation across all studies and all treatment combinations, we conducted a paired-sample t-test across all 78 experiment–treatment combinations.

RESULTS

We observed more dual winners (Quadrant I) and dual losers (Quadrant III) than mixed responders (Quadrants II and IV) for the simulated data (Figure 2) owing to the mathematical dependency of the treatment effects. When accounting for this pattern in the simulated data, the number of mixed responders in the actual data was 13% greater than expected (966 species observed, 854 expected). This greater-than-expected proportion of

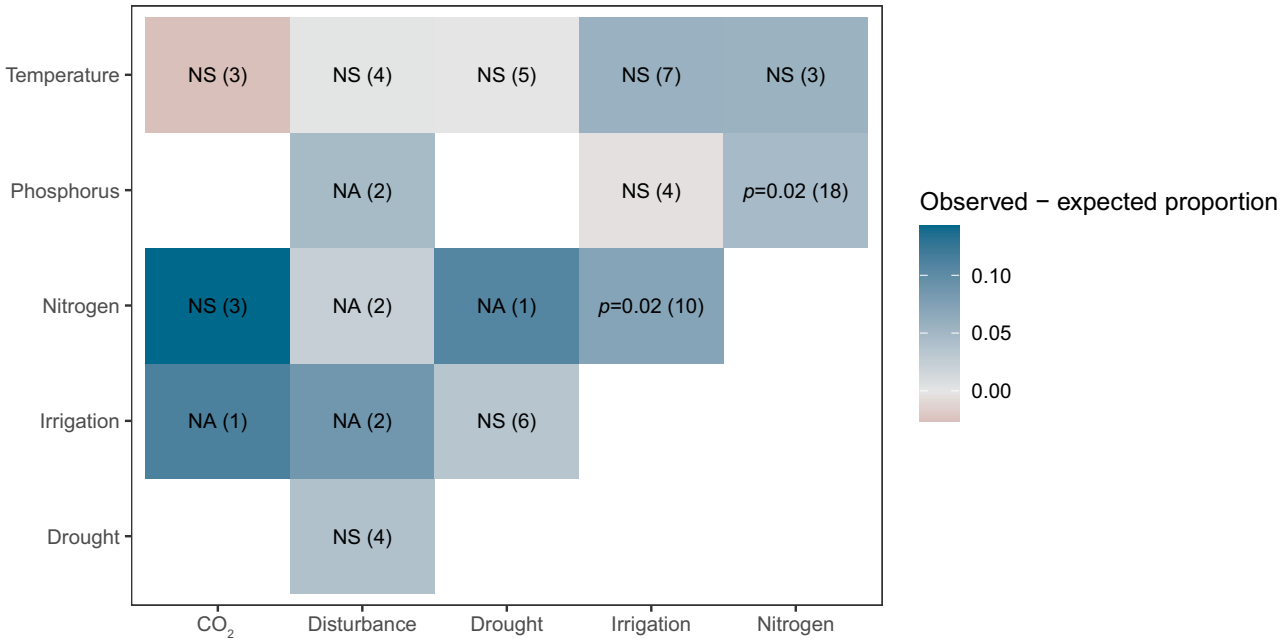


FIGURE 4 The proportion of mixed responders (species increasing in one treatment and decreasing in another) for key treatment combinations, above what was observed in the simulated communities. Blue cells indicate higher-than-expected proportions of mixed responders for that treatment combination, suggestive of trade-offs. Gray cells indicate treatment combinations where the distribution of species did not differ from the distribution observed in the simulated communities. Number of studies for each treatment combination are in parentheses. t-test results ($p < 0.1$ or NS if nonsignificant) are also shown in the cells if there were >2 studies. NA indicates that combination lacked enough studies to analyze

species responding positively to one treatment but negatively to another was statistically significant across all studies and all treatment combinations (Figure 3; $t = 4.82$, df = 77, $p < 0.001$; Appendix S1: Figure S4). The number of dual winners was 14% lower than expected ($t = -4.36$, df = 77, $p < 0.001$), and the number of dual losers matched expectations ($t = 1.15$, df = 77, $p = 0.3$). Subsetting the data to exclude species that were absent in treatment or control plots did not change the results (mixed responders were 13% greater than expected and dual winners were 15% lower than expected, Appendix S1: Figure S3).

There tended to be more mixed responders than expected across most treatment combinations (blue patches in Figure 4 and Appendix S1: Figure S5), again suggestive of trade-offs in species' ability to respond. Of the 11 treatment combinations that had enough replicates to do *t*-tests, only two individual treatment combinations were significant: N × Irrigation and N × P. We detected a far higher proportion than expected in one treatment combination where we expected strong trade-offs (N × CO_2), but this was not significant ($p = 0.3$). We detected fewer mixed responders than expected for one treatment combination (CO_2 × Temperature; pink patch in Figure 4) but this was also nonsignificant ($p = 0.1$).

We also observed more mixed responders than expected for 56 of 78 treatment combinations in individual studies (Appendix S1: Figure S6); 49 when omitting species absent from either all treatment or all control plots (Appendix S1: Figure S7). However, we found no significant deviations from the proportions expected in individual studies, though we did find marginally significant trends ($0.05 < p < 0.10$) in seven cases, all in the same direction as the overall trend (Appendix S1: Figure S6).

DISCUSSION

We addressed the question, do individual species' responses to one global change treatment relate to their responses to a second treatment? After accounting for mathematical dependency among treatment effects across the entire data set, we found that species exhibited more mixed responses (negative to one driver and positive to the other, Quadrants II and IV from Figure 1) to different treatments than would be expected if there were no relationship among treatment responses. The excess of mixed responders was afforded by a deficit of dual winners, not dual losers. Lower occurrence of dual winners than expected indicates that "demonic" species (responding positively to multiple drivers) should be relatively less common compared to other categories of response. These patterns are consistent with trade-offs influencing plant responses to different global change drivers, especially for plants that respond positively to at least one treatment. However, we found little evidence of a strong influence of trade-offs for individual treatment combinations or within individual experiments. Although trade-offs may have a detectable influence in shaping plant responses on average across many global change experiments, they do not confer explanatory power in the responses of individual communities.

Extending from this first result, we asked if the nature of the relationship among treatment responses depended on the particular treatments imposed. We pooled across experiments that tested the same two drivers, and found two combinations exhibited strong evidence of trade-offs, N × Irrigation and N × P (Figure 4). These are two treatment combinations for which we did not expect strong trade-offs as some of the same plant strategies (greater allocation to absorptive rooting and mycorrhizal surface area) should afford enhanced ability to acquire water and nutrients. Still, at a finer scale, trade-offs can exist among specializations for N, P, or water acquisition. For instance, deeper rooting may favor water acquisition, whereas shallower roots should enhance N acquisition (Kulmatiski et al., 2020). Moreover, mycorrhizal status may reflect a specialty for P versus N acquisition (Read & Perez-Moreno, 2003). These trade-offs could counteract and override a simpler above vs. belowground allocation trade-off. We observed evidence for trade-offs in the CO_2 × N treatment combination, as expected, but had low cross-experiment replication (Figure 4). More perplexing was the lack of stronger negative relationships within certain opposing treatment combinations such as drought vs. irrigation (Figure 4). One would expect the plant species that take advantage of added water to differ in growth response from those that can tolerate drought. Perhaps variation along other dimensions of plant strategy supersede the expected trade-off (Viola et al., 2010).

Although the existence of trade-offs between resource acquisition and tolerance of conditions has a solid foundation in plant physiology and is broadly accepted in plant ecology (Bazzaz & Bazzaz, 1996; Chapin et al., 1987; Craine, 2009; Tilman, 2000), these trade-offs are not easily demonstrable experimentally. For instance, optimizing xylem vessel elements for high transpiration rates, which are associated with rapid growth, should render plants more susceptible to cavitation during drought (Tyree & Ewers, 1991). This physiological constraint should engender trade-offs between growth rate in wet conditions and ability to tolerate drought. However,

comparison of grasses revealed no evidence for a trade-off (Fernández & Reynolds, 2000). In fact, the relationship between xylem safety and efficiency appears weak across species globally (Gleason et al., 2016). Such trade-offs that arise from physical and biological constraints must act on some level but do not strongly influence plant response to global change treatments.

Resource trade-offs, which likely exist, may be obscured by other types of trade-offs or other experimental noise. Patterns of community structure across a global scale result from multidimensional axes of competing trade-offs (Hutchinson, 1961), wherein the dominant axes likely involve large-scale strategies of dispersal and perhaps not smaller-scale strategies of resource acquisition (Kneitel & Chase, 2004). The generally weak, largely resource-based trade-offs uncovered herein may give way to larger-scale trade-offs such as competition–colonization trade-offs (Cadotte et al., 2006), growth–defense trade-offs (Lind et al., 2013), competition–defense trade-offs (Viola et al., 2010), or trade-offs between different types of colonization (Yu & Wilson, 2001) that may not be manifested on plot-scale experiments.

Furthermore, patterns in plant abundance arising from trade-offs in resource acquisition or condition tolerance may be negated by other forces in ecosystems. Revisiting the marsh example described in the introduction detected the largest deviation from expected patterns and showed evidence of trade-offs at the SERC site, though it was individually nonsignificant (Figure S6). This marsh has low herbivore pressure and does not exhibit long-term patterns of plant succession, obviating nonresource trade-offs such as the colonization–competition trade-off or the growth–defense trade-off that may hold great importance elsewhere. Therefore, resource trade-offs should be strong here, and early evidence indicated they were (Langley & Megonigal, 2010). However, this site is subject to more frequent flooding from accelerating rates of sea-level rise that strongly controls plant community composition (Langley & Hungate, 2014). Trade-offs among plant resource acquisition strategies were manifested by the few dominant species responding very differently to the addition of different resources, but ultimately those trade-offs have been overwhelmed by an unmanipulated factor—increased flooding. This example from a tractably depauperate community illustrates how resource trade-offs can hold importance under certain situations, or over short periods of time, but may not shape communities in the longer term, particularly when subject to strong change in other background variables. Indeed, strong background change has been observed across many of these same studies (Langley et al., 2018), and can obscure the influence of underlying resource trade-offs.

Deciphering evidence of trade-offs is complicated by the mathematical dependence between treatment effects (Appendix S1: Figure S8), because all treatment responses are compared to the same control values to estimate treatment effects. One control plot that has low abundance of a species, perhaps just by chance, will yield greater treatment effects for the treatment plots that are referenced to it. Had we not accounted for this inherent covariation with the null model, we would have concluded that treatment effects were all positively related (Appendix S1: Figure S8, Table S3). Studies that have not accounted for mathematical dependence of treatment effects (Lind et al., 2013; Viola et al., 2010) should be reanalyzed by comparing results to null expectations.

Our study suggests that resource trade-offs shape plant responses to global change treatments but exert a generally weak influence within individual sites, even for pairs of treatments expected to favor different species. Specialization in resource acquisition strategies among species is not as important as we expected for determining plant responses to different global change treatments. Continued increases of resource availability, expected with widespread global change drivers such as CO_2 enrichment and N deposition, should further weaken trade-offs that do exist. For instance, atmospheric CO_2 has already reached higher concentrations than Earth has experienced for millions of years. Further increases that treatments impose will have diminishing effects, even for relatively CO_2-sensitive plants. Perhaps preindustrial resource levels, which were likely more strongly limiting, would yield stronger resource trade-offs. Nonetheless, these findings help place resource- and condition-driven trade-offs into the context of other forces acting to control plant community shifts in the context of current global change.

ACKNOWLEDGMENTS

This work was conducted as a part of a LTER Synthesis Group funded by NSF grants EF-0553768 to M. Avolio and K. Komatsu, and DEB 1545288 through the LTER Network Communications Office and the National Center for Ecological Analysis and Synthesis, UCSB to K. Komatsu, M. Avolio, and K. Wilcox. JA Langley acknowledges support from the NSF LTREB Program (DEB-0950080, DEB-1457100, and DEB-1557009).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Langley et al., 2021) are available in Dryad (https://doi.org/10.5061/dryad.rfj6q57c1). Code (Wilcoxkr, 2021) is available on Zenodo (https://doi.org/10.5281/zenodo.5748312).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Langley, J. Adam, Emily Grman, Kevin R. Wilcox, Meghan L. Avolio, Kimberly J. Komatsu, Scott L. Collins, Sally E. Koerner, et al. 2022. "Do Trade-Offs Govern Plant Species' Responses to Different Global Change Treatments?."*Ecology* e3626. https://doi.org/10.1002/ecy.3626