Received: 17 July 2023 | Revised: 14 December 2023 | Accepted: 9 February 2024

DOI: 10.1002/ecy.4290

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Plant growth–defense trade-offs are general across interactions with fungal, insect, and mammalian consumers

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Funding information
National Science Foundation, Grant/Award Numbers: DEB-1234162, DEB-1831944

Handling Editor: Lin Meng

Abstract

Plants face trade-offs between allocating resources to growth, while also defending against herbivores or pathogens. Species differences along defense trade-off axes may promote coexistence and maintain diversity. However, few studies of plant communities have simultaneously compared defense trade-offs against an array of herbivores and pathogens for which defense investment may differ, and even fewer have been conducted in the complex natural communities in which these interactions unfold. We tested predictions about the role of defense trade-offs with competition and growth in diversity maintenance by tracking plant species abundance in a field experiment that removed individual consumer groups (mammals, arthropods, fungi) and added nutrients. Consistent with a growth–defense trade-off, plant species that increased in mass in response to nutrient addition also increased when consumers were removed. This growth–defense trade-off occurred for all consumer groups studied. Nutrient addition reduced plant species richness, which is consistent with trade-off theory. Removing foliar fungi increased plant diversity via increased species evenness, whereas removal of other consumer groups had little effect on diversity, counter to expectations. Thus, while growth–defense trade-offs are general across consumer groups, this trade-off observed in wild plant communities does not necessarily support plant diversity maintenance.

KEYWORDS

competition–defense hypothesis, diversity maintenance, fungal pathogens, growth–defense hypothesis, insect herbivory, mammalian herbivory, nutrient limitation, top-down bottom-up, trade-offs

INTRODUCTION

Determining the mechanisms behind species coexistence and diversity maintenance remains a central goal for ecologists, as the loss of biodiversity continues across all of Earth's biomes (Isbell et al., 2022; Sala et al., 2000). Species coexistence theory often requires that species have trade-offs in their ecological strategies (Chesson, 2000; HilleRisLambers et al., 2012; Mordecai, 2011). For example, plant allocation of resources toward herbivore or pathogen defense can come at a cost to growth rates or the ability to compete for limiting resources (growth–defense and competition–defense trade-offs, Endara & Coley, 2011; Herms & Mattson, 1992; Lind et al., 2013; Monson et al., 2021). Species differences along these defense trade-off surfaces can promote diversity maintenance (Holt et al., 1994; Viola et al., 2010). Despite the wide range of plant consumers, most defense trade-off tests have focused on single consumer groups. In addition, few studies have tested the generality of the growth–defense and competition–defense trade-off theories of diversity maintenance by quantifying concurrent plant diversity responses to the full range of herbivores, pathogens, and mutualists in natural systems (Seabloom et al., 2018).

Competition–defense and growth–defense trade-offs have been investigated in theoretical, laboratory, and field studies for defense against mammalian herbivores, insect herbivores, and aboveground fungal pathogens (Cappelli et al., 2022; Endara & Coley, 2011; Heckman et al., 2019; Holt et al., 1994; Lind et al., 2013; Throop & Lerdau, 2004; Viola et al., 2010). Through in situ manipulations of grassland sites, Lind et al. (2013) found that growth–defense trade-offs are more prominent than trade-offs between competition and defense among grassland plant species in response to mammalian herbivores. Microbial pathogens also can have large impacts on plant communities (Allan et al., 2010; Bever et al., 2015), and recent work by Cappelli et al. (2020) suggests that plant interactions with fungal pathogens may also be constrained by growth–defense trade-offs. All plant consumers share some common constraints (e.g., they rely on plant carbon for energy); however, herbivores and pathogens also differ in important ways such as size, reproductive rate, stoichiometric ratios and modes of feeding (Lafferty & Kuris, 2002). The identity of the consumer guild and the varying degrees of specialization across mammalian herbivores, insect herbivores, and pathogens may also drive plants to employ different defense pathways to resist consumption depending on the consumer guild (Felton & Korth, 2000; Traw & Bergelson, 2003). These differences in life history among consumer types and plant defenses may cause plant species to exhibit different defense trade-offs to herbivores versus pathogens. Alternatively, defense trade-offs may not vary among defenses against different types of consumers of photosynthetic tissue if plant investment in defense comes at the same cost to growth rates or competitive ability. Furthermore, growth–defense and competition–defense trade-offs are more important for constitutive rather than induced defense mechanisms and this potentially holds true for both herbivory and pathogens (Monson et al., 2021). Experiments comparing plant responses to both herbivores and pathogens can help to determine the variability of defense trade-offs. However, they are understudied in the context of particular plant communities relative to laboratory or theoretical spaces, and are additionally understudied in wild plant populations relative to agricultural and model systems (Kempel et al., 2011; Pieterse et al., 2012).

Consumer–resource models suggest that when consumers are reduced, poorly defended plant species may increase in abundance (Grover & Holt, 1998; Holt et al., 1994), a prediction supported in empirical tests (Lind et al., 2013; Viola et al., 2010). Similarly, nutrient competition theory (Tilman, 1982) suggests that adding nutrients will favor the population growth of fast-growing species with lower nutrient use efficiency, a prediction also empirically supported (Wedin & Tilman, 1993). By observing the covariation of plant species responses to consumer and nutrient manipulations, four potential outcomes emerge that illustrate where species might fall along growth–defense or competition–defense trade-off axes (Figure 1). A negative relationship between species responses to consumer removal and nutrient addition supports a competition–defense trade-off, in which species invest in competition at the expense of defense (or vice versa, upper-left and bottom-right quadrants, respectively; Figure 1). Alternatively, species may increase with both consumer removal and nutrient addition due to an investment trade-off between growth and defense. In this case, a species may decline in response to both consumer removal and nutrient addition (good resource competitor and well defended; bottom-left quadrant, Figure 1) or vice versa (upper-right quadrant, Figure 1).

Trade-offs can play an important role in maintaining species diversity according to equilibrium coexistence theory (Chesson, 2000; Holt et al., 1994; Mordecai, 2011; Viola et al., 2010), yet few studies have quantified both defense trade-offs and plant diversity dynamics in systems in which nutrient supply (altering the competitive environment) and consumption by multiple consumer guilds (altering the benefit of defense) are manipulated. If trade-offs are important for coexistence in a community, then reducing consumers or increasing nutrients should reduce diversity, following predictions from resource and apparent competition theory (Grover & Holt, 1998; Holt et al., 1994). Indeed, experimental reduction of pathogens or herbivores in plant communities can lead to loss of plant diversity (Allan et al., 2010; Carson & Root, 2000; Liu et al., 2022, but see Hillebrand et al., 2007), and fertilization experiments often find trends of decreasing species diversity (Seabloom, Adler, et al., 2021). What remains unclear is whether the investment in defense against herbivores compared with pathogens imposes differing trade-offs among plant species and has differing consequences for diversity. Within a single plant

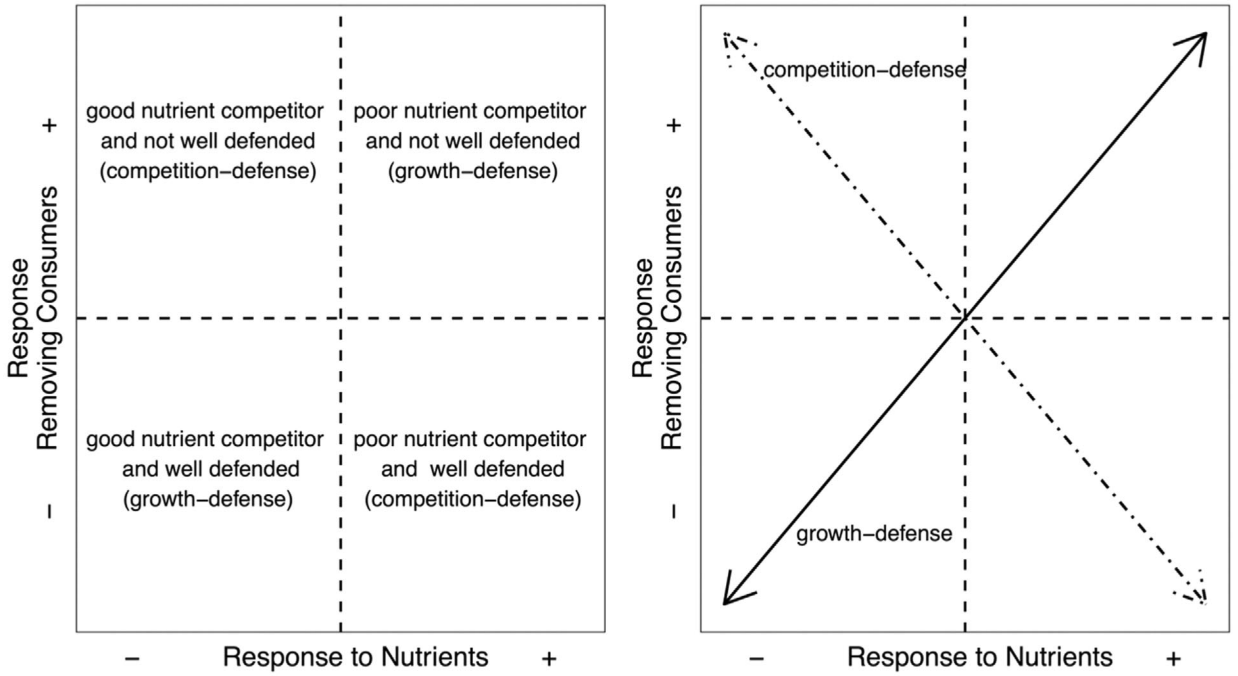

FIGURE 1 Environmental manipulations reveal defense trade-offs among grassland plant species. Shown are the hypothetical outcomes and covariation of species responses to nutrient addition and removal of consumers (e.g., removing herbivores or pathogens). Species that are good nutrient competitors will decrease in response to nutrient addition while poor nutrient competitors will increase (*x*-axis). Similarly, species that are not well defended will increase in response to removing herbivores or pathogens while well defended species will decrease in relative abundance (*y*-axis).

community, if plant species fall along a defense trade-off axis for herbivores, but not for pathogens (potentially due to a lack of differential pathogen impacts on plant species populations), then we would expect herbivore removal to influence diversity while pathogen removal would not. Additionally, if herbivore and pathogen interactions are constrained by defense trade-offs that help maintain species diversity, then removing multiple consumer groups (e.g., mammalian herbivores and fungal pathogens) is predicted to lead to greater loss of species than just removing one type of consumer following theory of niche dimensionality and the number of limiting factors in a system (Hutchinson, 1957).

To determine the generality of trade-offs between defense and competition or growth in plant communities with a wide range of plant consumer types, we quantified grassland plant species' abundance responses to reduced consumers (large mammalian herbivores, arthropods, foliar fungi, soil fungi) and added nutrients. We also measured plant diversity responses to these same consumer and nutrient treatments to test whether trade-offs affected species diversity. We specifically tested (1) whether defense trade-offs among plant species vary among large mammalian herbivores, arthropods, foliar fungi, and soil fungi, (2) if defense trade-offs vary with plant functional type, and (3) how plant species richness, evenness, and diversity respond to resource and consumer manipulations.

METHODS

Study site

This work was conducted at the University of Minnesota's Cedar Creek Ecosystem Science Reserve, Minnesota, United States (latitude 45.4 N, longitude 93.2 W), a Long-Term Ecological Research site. Cedar Creek is underlain by sandy, nitrogen-poor soils and has a mean annual precipitation of 750 mm year^{-1} and a mean annual temperature of 6°C. The sandy soils of this study site are very nutrient limited relative to other grasslands worldwide (Fay et al., 2015).

The work described here was conducted in an old field abandoned from agriculture in 1956, approximately 50 years prior to the start of the current study. Most plants in this system are perennial and changes in biomass are predominantly due to vegetative growth. The community is dominated by C4 and C3 grasses, forbs, and legumes with a mean aboveground biomass of approximately 200 g m^{-2} (Zaret et al., 2023). Plant communities at this site experience high levels of pathogen damage relative to other grasslands around the world and arthropod herbivory damage to plant tissues has also been documented in the field (Ebeling et al., 2021). Previous work in a nearby field by Mitchell et al. (2002) found that plant species are commonly infected by *Colletotrichum* sp. (fungal leaf spot), *Erysiphe cichoracearum* (powdery mildew), and *Uromyces* sp. (fungal rust). Plant species in this system are also host to a diverse assemblage of arthropods, with herbivores representing 62% of the taxa (Borer et al., 2012). Mammalian herbivores are also common at the study site including *Odocoileus virginianus* (White-tailed Deer) and *Sylvilagus floridanus* (Eastern Cottontail).

Pesticide treatments

In 2008, we established an experiment with six food web manipulation treatments: Control, Soil Fungicide, Foliar Fungicide, Insecticide, Fence, and All Removal (fencing plus all the pesticide treatments). Each treatment was randomly assigned to 3 m × 3 m plots, replicated across eight blocks ($N = 48$). Pesticide treatments were applied regularly throughout the growing season (mid-April to end of September each year) with monthly applications for the Soil Fungicide treatment using Ridomil Gold SL (Syngenta Crop Protection, Inc., Greensboro, NC, USA), and biweekly applications for the Foliar Fungicide using Quilt (Syngenta Crop Protection, Inc., Greensboro, NC, USA) and Insecticide using Marathon II (OHP, Inc., Mainland, PA, USA). Two times a season Malathion was applied as the Insecticide treatment instead of Marathon II to prevent resistance to the pesticide in the arthropod community. For the Fence and All Removal treatments, large mammalian herbivores were excluded by a 2 m wire fence that surrounded the plot with a mesh size of 5 cm × 10 cm.

Previous work from this study site has found that the pesticide treatments significantly reduce foliar pathogen incidence and insect herbivory in the field (Borer et al., 2015) and a greenhouse study revealed that in the absence of consumers the pesticides do not impact plant growth (Seabloom et al., 2017). Additionally, in the absence of arthropods or foliar fungi (via pesticide treatments) plant community biomass increases significantly (Kohli et al., 2019; Seabloom et al., 2017; Zaret et al., 2022). Collectively these studies suggest that arthropod and fungal communities impose net antagonistic rather than net mutualistic effects on the plant community.

Nutrient addition treatment

Starting in 2019, a nutrient addition treatment was added to the consumer removal experiment. Experimental plots were divided into two subplots (1.5 m × 3 m plots), with one of the subplots being randomly assigned to the nutrient addition treatment and one remaining under ambient nutrient conditions. The subplots receiving nutrient addition were fertilized with nitrogen, phosphorus, potassium, and micronutrients once a year in early spring before the growing season (early April). The annual fertilizer application was composed of 10 g N m^2/year as timed-release urea [$(NH_2)_2CO$], 10 g P m^2/year as triple-superphosphate [$Ca(H_2PO_4)_2$], 10 g K m^2/year as potassium sulfate [K_2SO_4] and 100 g m^2/year of a micronutrient mix of Ca (6%), Fe (17%), S (12%), Mg (3%), Mn (2.5%), Cu (1%), Zn (1%), B (0.1%), and Mo (0.05%). Nutrients were applied annually every spring except the micronutrient mix, which was only applied in the first year to avoid toxicity. This exact fertilization regime has been demonstrated to overcome nutrient limitation in many grasslands worldwide including our study site (Seabloom, Borer, et al., 2021). To avoid lateral nutrient leakage, plots were trenched to a depth of 30 cm and sampling of the plant community occurred at least 0.25 m away from the trenched area.

For the purposes of this study, we excluded from analyses those plots that crossed nutrient addition with consumer removal treatments because our goal was to identify how plant species respond to nutrient addition and consumer removal independently rather than testing how nutrients modify consumer removal impacts on plant species. For analyses, eight fertilized Control plots (no pesticides or fencing) and 48 unfertilized plots consisting of Control, Foliar Fungicide, Soil Fungicide, Insecticide, Fence, or All Removal were included, resulting in a total of 56 plots.

Measuring species abundances

To determine the abundance of plant species in the various treatments of the consumer removal experiment, aboveground biomass was harvested and sorted to species identity at peak biomass (late August) in 2019, 2020, and 2021. In each experimental plot, aboveground biomass was clipped in two 0.1 m × 1 m strips. The biomass was then sorted to species, dried to a constant mass, and weighed to the nearest 0.001 g. To minimize the effects of destructive sampling, the location of the aboveground biomass harvest was moved every year within each experimental plot. There were 38 plant species identified across the 3 years of data collection at this experimental site, and each species was assigned to one of four functional groups: C3 grasses, C4 grasses, Forbs (nonleguminous herbaceous plants), or Legumes. There was also one woody species in this experiment (*Rhus glabra*).

Quantifying species response to treatments

The proportional response of species abundances to experimental treatments was determined using the log response ratio (LRR) as log(Biomass_{xt}/Biomass_{xc}) where Biomass_{xt} is the biomass of species × in treatment *t* (either nutrient addition, Foliar Fungicide, Soil Fungicide, Insecticide, Fence, or All Removal treatment) and Biomass_{xc} is the biomass of that same species in the corresponding Control plot in a given experimental block. LRRs for each species in a given treatment were then averaged across experimental blocks giving an estimate of each species average response to treatments in a given sampling year as the final units of observation in our analysis.

If species were absent from either a Control or experimental treatment plot, the LRR would be undefined; however, the absence or presence of species in these plots is likely to be meaningful (representing the local extinction or invasion of species in response to treatments). Therefore we replaced these zero values with a small value (0.01 g, one-half of the minimum observed biomass in the study) in order for LRRs to be defined when species were absent from corresponding treatment or Control plots used in LRR calculations (Lind et al., 2013; Seabloom et al., 2018; Viola et al., 2010). We tested the sensitivity of adding the 0.01 g values and the results were not different when we did not replace zero values (the direction and significance of standardized major axis [SMA] relationships were the same).

To quantify the distribution and frequency of defense trade-offs and plant species responses, we followed methods from Lind et al. (2013), assigning categorical responses to plant species in a given sampling year for each consumer removal treatment. Categories were assigned as follows: no response, consumer only, nutrient only, or trade-off (species responded independently to both consumer removal and nutrient addition treatments). These categories were assigned to species based on their LRR values in a given sampling year and consumer removal treatment. We used a doubling/halving threshold in which no response was categorized as $-0.693 < \text{LRR} < 0.693$ such that species were conservatively categorized as responsive if the treatments caused species to be at least doubled or reduced to half their untreated abundance. We then assigned species in the trade-off category into "growth–defense" for species if responses were positively correlated or "competition–defense" if responses were negatively correlated (Figure 1). To determine the sensitivity of our conclusions, we also evaluated the frequency of defense trade-offs at a greater LRR threshold of ±1.386 reflecting a quadrupling change of species abundances relative to Control.

Statistical analysis

All analyses were done using the R statistical program version 4.2.1 (R Core Team, 2022). To look at the relationship between species responses to consumer removal and nutrient addition, we used SMA estimation using the *smatr* package (Warton et al., 2012). SMA is similar to regression, however SMA does not assume predictive relationships between two variables (i.e., independent and dependent variables in regression) and is therefore appropriate when looking at the relationship of two variables that may be influenced by the same processes (e.g., plant defense trade-offs). The initial goal of using SMA was to determine whether species responses to consumer removal and nutrient addition were positively associated (in support of growth–defense trade-off; Figure 1) or negatively associated (in support of competition–defense trade-off; Figure 1). The significance of whether slopes from SMA differed from zero among the various consumer removal treatments is reported in Tables 1 and 2. In the case in which growth–defense trade-offs were observed (i.e., SMA slope was significantly greater than zero), we also assessed whether plants overall were more responsive to nutrient addition or consumer removal treatments by testing whether slopes from SMA differed from one using the "slope.test" function in the *smatr* package.

TABLE 1 SMA parameters for the relationship between consumer removal and nutrient addition for various consumer removal methods.

Treatment	SMA slope	R^2	*p*-value
Foliar Fungicide	1.067	0.31	<0.001
Soil Fungicide	0.893	0.19	<0.001
Insecticide	0.929	0.17	<0.001
Fence	0.984	0.12	0.003
All Removal	0.857	0.3	<0.001

Note: All Removal is a combination of all the pesticide treatments and the Fence treatment.

Abbreviation: SMA, standardized major axis.

TABLE 2 SMA parameters for the relationship between consumer removal and nutrient addition for plant functional groups.

Treatment	SMA slope	R^2	*p*-value
C3 Grass	0.842	0.37	<0.001
C4 Grass	1.262	0.17	0.007
Forbs	0.918	0.15	<0.001
Legumes	0.752	0.7	<0.001

Abbreviation: SMA, standardized major axis.

To answer the main questions of this study, we used likelihood ratio tests (built into the "sma" function in the *smatr* package) to determine whether the slopes of the SMA estimation varied across (1) different consumer removal treatments, and (2) different plant functional groups. To account for the temporal structure of our three-year data set, we also performed a likelihood ratio test to determine whether the slopes of the SMA estimation varied across years of sampling. Following the categorization of species responses (see the previous *Methods* section) and to test whether the frequency of growth–defense versus competition–defense trade-offs differed among species, we performed a X^2 test with the null expectation that species exhibit growth–defense and competition–defense trade-offs equally across the 38 species sampled here.

Using the same species abundance data derived from harvested biomass, we calculated species richness, evenness, and the Inverse Simpson Index of diversity using the *vegan* package (Oksanen et al., 2013). The Inverse Simpson Index is equivalent to the Effective Number of Species based on the Probability of Interspecific Encounter ($\mathrm{ENS}_{\mathrm{PIE}}$) and has the utility of partitioning out diversity into its components, Species Richness and Simpson's Evenness, by the equation:

$$\begin{aligned}&\text{Inverse Simpson Index of Diversity}\\&\quad=\text{Species Richness}\times\text{Simpson's Evenness}.\end{aligned}$$

To determine the impact of consumer removal and nutrient addition on these diversity metrics, we constructed linear mixed effects models using the "lme" function in the *nlme* R package (Pinheiro et al., 2017). Consumer removal and nutrient addition were treated as fixed effects, and year and experimental block were treated as random effects (with the experimental block nested within year) to account for the temporal and spatial structure of the data set. Species Evenness and the Inverse Simpson Index metrics were log-transformed for the linear mixed effects models to meet assumptions of normality.

RESULTS

Prevalence of plant defense trade-offs across consumer types

The slopes of the relationship between species responses to consumer removal and nutrient addition were significantly positive for all five consumer groups (Table 1, Figure 2). In addition, all five of the SMA slopes (Foliar Fungicide, Soil Fungicide, Insecticide, Fence, and All Removal treatments) did not differ (Likelihood ratio statistic $= 2.808$, $df = 4$, $p = 0.590$). Individual species did not differ in their responses along the consumer removal and nutrient addition trade-off axes for different types of consumer removal treatments (no significant interaction between species and type of consumer removal when looking at the response to treatments $p > 0.05$). Additionally, the SMA slopes did not differ from one (Likelihood ratio statistic $= 4.328$, $df = 5$, $p = 0.503$), showing that all treatments induced similar effects. The community-level response to consumer removal and nutrient addition had a positive slope for all 3 years of sampling (Appendix S1: Figure S1). However, slopes varied among sampling years (Likelihood ratio statistic $= 10.79$, $df = 2$, $p = 0.005$) with 2020 having the highest slope and 2021 having the lowest (Appendix S1: Figure S1).

Of the 354 responses used in the analysis (e.g., comparison of species response to consumer removal and nutrient addition across the five consumer removal treatments and 3 years of study), a trade-off (independent species response to both consumer removal and nutrient addition) was observed 193 times making it the most common response of species across years of study and various consumer removal treatments (Figure 3). Among the 193 trade-off observations, growth–defense trade-offs (positive correlations for species response to consumer removal and nutrient addition, $N = 135$) were more frequent than competition–defense (negative correlation, $N = 58$) responses, ($X^2 = 18.607$, $df = 1$, $p < 0.001$, Figure 3). Growth–defense trade-offs were also consistently more frequent than competition–defense trade-offs within each of the five consumer removal treatments (Foliar Fungicide, Soil Fungicide, Insecticide, Fence, All Removal; Appendix S1: Figure S2) matching results from the SMA analysis. These results were robust when we increased the LRR threshold to a more conservative value of ±1.386 (Appendix S1: Figure S3).

Defense trade-offs across plant functional groups

All four plant functional groups (C3 grasses, C4 grasses, forbs, legumes) showed consistently positive slopes for the relationship between response to consumer removal and nutrient addition (Table 2, Figure 4). These positive slope estimates only marginally differed among functional groups (Likelihood ratio statistic $= 7.547$, $df = 3$, $p = 0.056$) with C4 grasses having the highest positive slope estimate and legumes having the lowest positive slope estimate (Table 2).

Species responses to consumer removal differed among functional groups ($F = 5.328$, $df = 3$, $p = 0.001$) as well as for nutrient addition ($F = 3.100$, $df = 3$, $p = 0.027$). On average across all consumer removal treatments, reducing

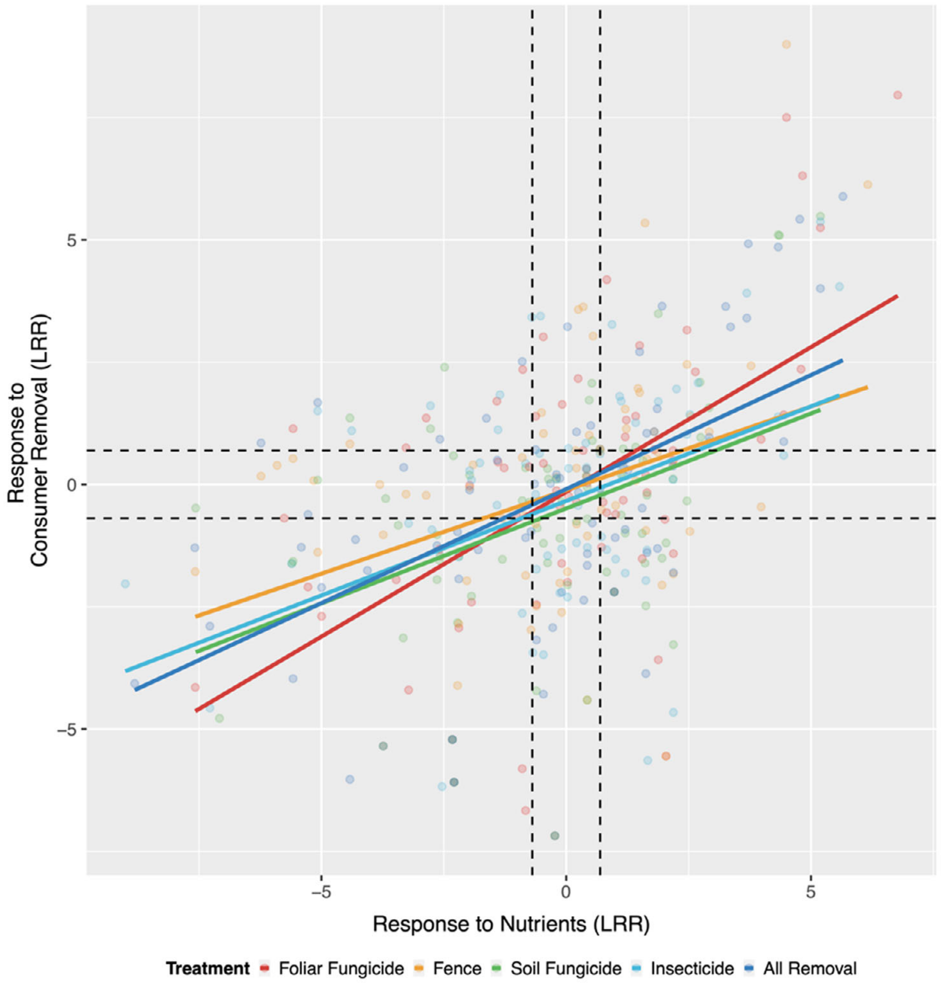

FIGURE 2 Species responses to consumer removal and nutrient addition. Lines represent a standardized major axis regression (output in Table 1). Data points represent 3 years of data in which each point is a species response to one of the five consumer removal treatments and nutrient addition. Dashed lines represent response thresholds for each axis where LRR > 0.693 (doubling) or < −0.693 (halving) is required for species to be considered responsive to treatments.

consumers caused legumes to increase in abundance while decreasing the abundance of C4 grasses and forbs (Appendix S1: Figure S4). Adding nutrients caused forbs to decrease and C3 grasses marginally increased (Appendix S1: Figure S4). Functional group response to consumer removal did not vary across the different types of consumer removal (nonsignificant interaction between functional groups and type of consumer removal treatment, df = 12, $F = 0.194$, $p = 0.9986$).

Plant community diversity responses to consumer removal and nutrient treatments

Nutrient addition significantly decreased species richness (Appendix S1: Table S1; Figure 5), significantly increased evenness (Appendix S1: Table S2; Figure 5), and had no effect on Inverse Simpson diversity (Appendix S1: Table S3). On average across all consumer removal treatments there were no impacts on any metric of diversity (Figure 5; Appendix S1: Tables S1–S3). The individual consumer removal treatments also did not significantly impact species richness (Appendix S1: Table S1) or evenness (Appendix S1: Table S2), although the Foliar Fungicide marginally increased species evenness (df = 115, $t = 1.911$, $p = 0.0585$). Additionally, the Foliar Fungicide significantly increased Inverse Simpson diversity, primarily via increased species evenness, while no other consumer removal treatments impacted Inverse Simpson diversity (Appendix S1: Table S3, Figure S5).

DISCUSSION

Trade-offs in ecological strategies play a central role in the theory of species coexistence. However, it remains unclear how prevalent and variable defense trade-offs are

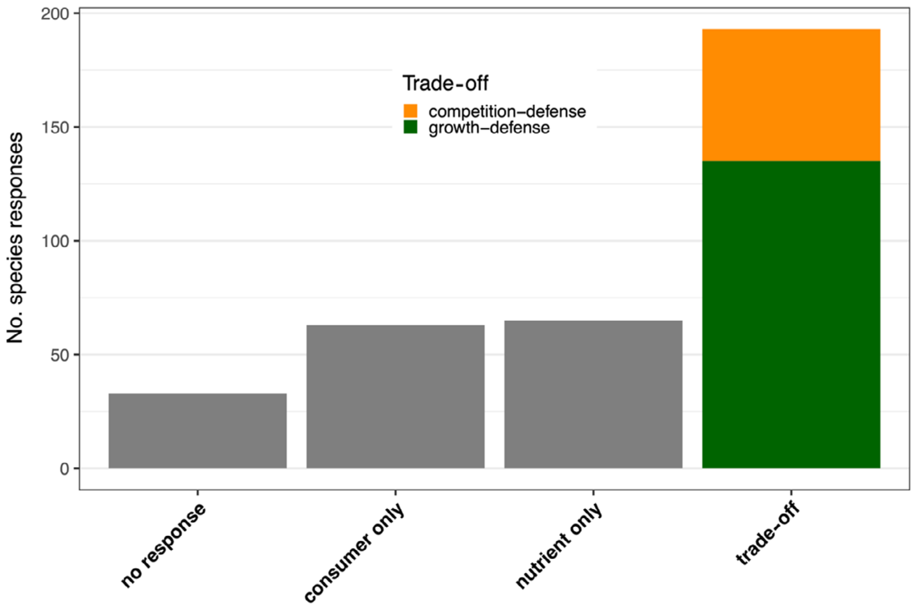

FIGURE 3 Frequency of species responses and nonresponses to nutrient addition and consumer removal treatments from 3 years of sampling. Species responses to each of the consumer removal treatments are included (Foliar Fungicide, Soil Fungicide, Insecticide, Fence, All Removal). "No response" was categorized as −0.693 < LRR < 0.693. Species were assigned to the "trade-off" if responses were positively correlated (growth–defense) or negatively correlated (competition–defense). The total number of observations is 354 (the same data points shown in Figure 1). Species responses are separated by individual consumer removal treatment, in Appendix S1: Figure S2.

in naturally occurring plant communities, whether trade-offs differ in response to different consumers, or whether observed trade-offs are consistent with theoretical predictions for coexistence. We show that mammalian herbivores, arthropods, foliar fungi, and soil fungi all impose quantitatively similar growth–defense trade-offs across plant species, and these trade-offs are consistent among years and grassland plant functional groups. In contrast, both the magnitude and direction of changes in plant diversity depended on the type of consumer or nutrient manipulation. In general, we did not find clear evidence that defense trade-offs play a role in maintaining diversity. Our experiment demonstrates that in the context of plant community dynamics, plant life history strategies and plant interactions with the consumer food web predominantly fall along a single continuum of growth–defense trade-offs across a diversity of plant forms and consumer types ranging from microbes in the soil to large mammalian herbivores.

Despite differences in the spatial scales, temporal scales, and energy use efficiencies for herbivores versus pathogens (Lafferty & Kuris, 2002), our findings unify the theory of plant defense trade-offs across kingdoms and for above and belowground food webs. Previous field experiments have tested for competition–defense and growth–defense trade-offs in terrestrial systems (Lind et al., 2013; Viola et al., 2010) and have focused on herbivores and foliar fungi (Cappelli et al., 2020; Heckman et al., 2019). Notably, our work adds to the support from these field studies that defense trade-offs can be detected in diverse plant communities where multiple species are concurrently responding to changes in the environment (e.g., perturbations to food webs or changes in nutrient supply). In addition to supporting previous independent findings that plant growth–defense trade-offs arise for herbivory and foliar fungal disease (Cappelli et al., 2020; Lind et al., 2013), our work reveals that plant interactions with soil fungi are constrained by a growth–defense trade-off. These findings align with previous theoretical work that has extended ecological models of plant communities and ecosystem processes to include pathogens and shown parallels between herbivore and pathogen controls on plant communities (Borer et al., 2022; Mordecai, 2011; Seabloom et al., 2015). As terrestrial ecosystems potentially experience a gain of primary consumers due to human activities (e.g., introducing grazers or spread of pathogens), our work predicts that plant composition will shift toward more strongly defended species that are also slow growing regardless of whether the gain of a consumer is a plant pathogen or herbivore.

In our study, the growth–defense trade-off potentially can be seen as a different axis of resource competition where the species that exhibited high growth rates (positive response to nutrient addition) may be better competitors for light, which becomes an important resource when nutrient competition is alleviated (Borer et al.,

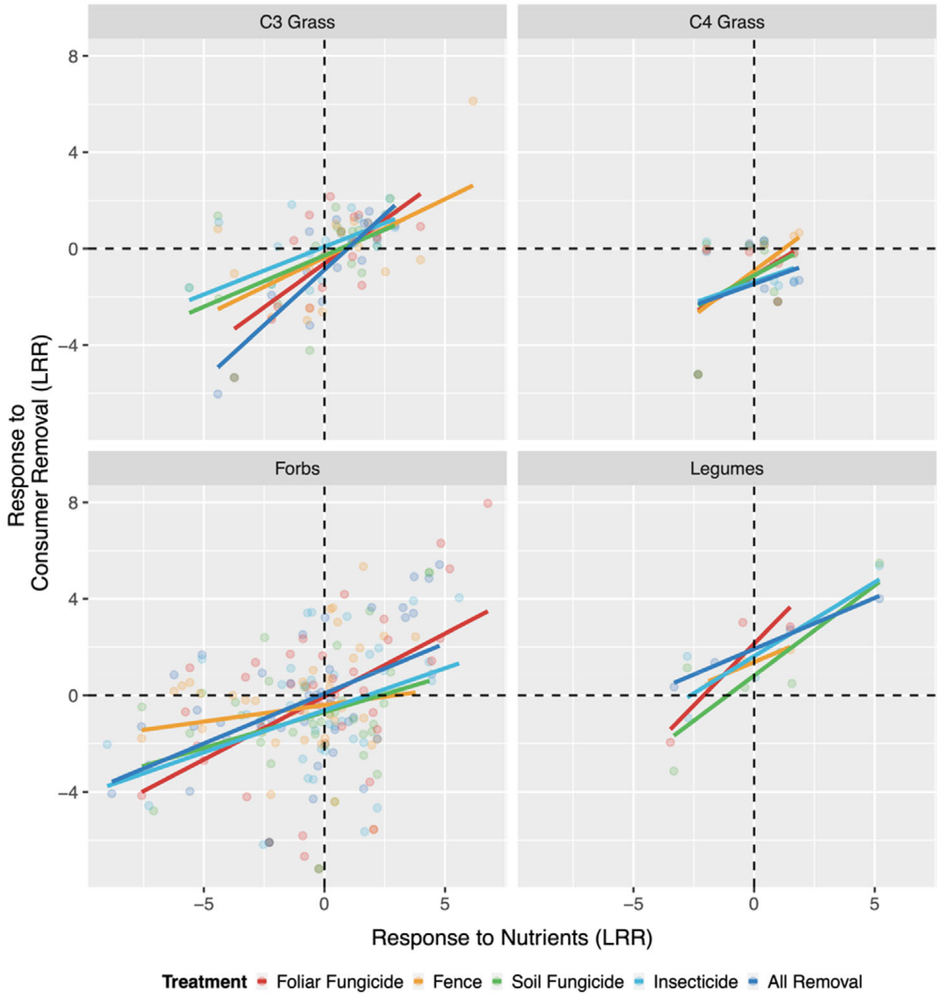

FIGURE 4 Species responses to consumer removal and nutrient addition broken down by functional group. Dashed lines represent response thresholds for each axis where LRR > 0.693 (doubling) or < −0.693 (halving) is required for species to be considered responsive to treatments.

2014; Dybzinski & Tilman, 2007; Eskelinen et al., 2022). Previous work in this experiment found that more biomass is allocated above than belowground following nutrient addition pointing to a potential shift in competition for light (Zaret et al., 2023). Overall forbs had the largest range of responses to consumer and nutrient manipulations and C4 grasses the least (Figure 4). However, we found no differences among different plant forms for defense trade-offs (forbs, N-fixing legumes, and plants differing in their photosynthetic pathway all fell along a growth–defense trade-off axis). It is possible that plant functional groups and individual species may separate out more along plant trade-off axes that include light competition, nutrient competition, and plant defense. Future work that integrates additional axes of resource competition will provide a stronger understanding of how plants invest energy toward defense from herbivores and pathogens, while concurrently competing for belowground and aboveground resources.

If species coexist due to differing allocations of growth limiting resources to defense, then removing consumers or adding nutrients are both predicted to reduce diversity (Chesson, 2000; Holt et al., 1994; Viola et al., 2010). Our nutrient addition treatment partially followed this expectation by reducing species richness; however, evenness increased, canceling out any impact on our abundance-weighted measure of diversity. Thus, nutrient addition created communities composed of relatively few species of similar abundance. Findings from a 40-year study in nearby old fields found similar patterns (Seabloom, Borer, et al., 2021), suggesting that this loss of species due to nutrient addition is not temporary.

In contrast with predictions, reducing foliar fungi caused an increase in Inverse Simpson diversity while none of the other consumer groups impacted plant diversity. This is surprising given that plant species had a wide range of both positive and negative responses to the Soil Fungicide, Insecticide, Fence, and All Removal

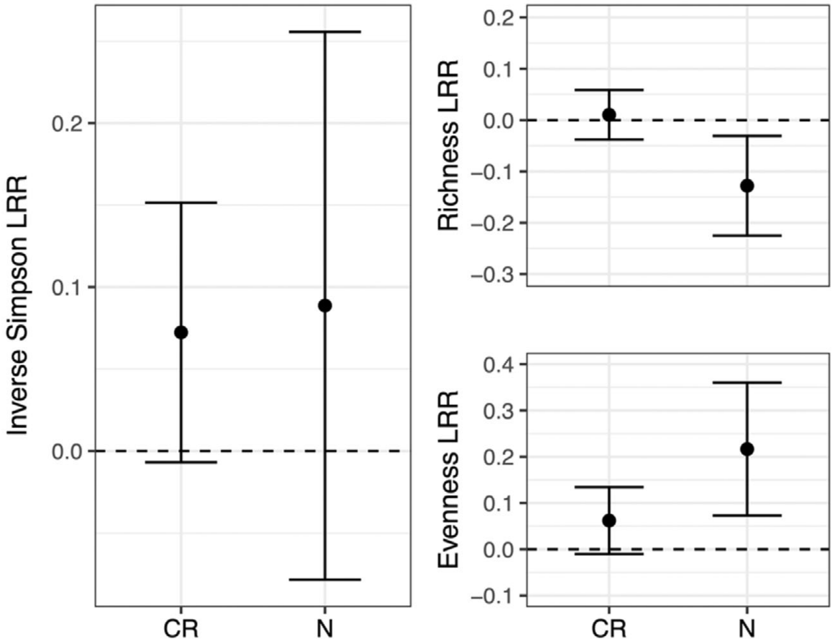

FIGURE 5 Plant diversity responses to nutrient addition (N) and consumer removal treatments (CR, average of all experimental removal treatments combined). Nutrients decreased richness but increased evenness resulting in no change in diversity (Inverse Simpson diversity metric). On average across all consumer removal treatments there was no change in richness, evenness, or diversity. For detailed outputs of model results, including individual consumer removal treatment responses see Appendix S1: Tables S1–S3 and Figure S5.

treatments (Figure 2; Appendix S1: Figure S2). The lack of decline in species diversity following the removal of consumers could be due to a few factors. First, and previously mentioned, the role of consumers in maintaining diversity may depend on other factors, such as the impact of consumption on light availability (Borer et al., 2014; Eskelinen et al., 2022). While we did not measure light availability, a previous study by Wilfahrt et al. (2020) found that foliar fungicide application can reduce light availability in grassland species. Foliar fungi may maintain higher light availability and diversity either by changing plant composition to favor poor light competitors or by infection-induced changes to leaf and canopy structure (e.g., leaf wilting altering light availability). Additionally, theory has shown that trade-offs may not always be sufficient to enable coexistence (Chesson & Kuang, 2008; Grover & Holt, 1998). Specifically, rather than promoting coexistence, consumers can promote exclusion if they do not differentially impact species (Chesson & Kuang, 2008). For foliar fungi, generalist pathogens could be agents that do not differentially impact species thereby suppressing diversity by limiting both rare and abundant species. However, we found that reducing foliar fungi caused some species to increase and others to decrease (variation in responses among species; Figure 2) showing that foliar fungi do impact species differentially in this system. Nonetheless, the counteracting roles of nutrients and pathogens on plant diversity documented here may have idiosyncratic impacts on the plant communities that cannot be determined when we consider the independent effects of nutrients or foliar fungi alone.

An area of study that we do not consider here, which is important to understanding the generality of our results, is the context dependency of plant defense strategies. The resource availability hypothesis (Endara & Coley, 2011) and nitrogen-disease hypothesis (Dordas, 2008) suggest that consumer impacts on plants may depend on the amount of resources within an ecosystem. Under higher resource scenarios, consumers are predicted to have modified impacts on plant hosts due to a variety of mechanisms ranging from modified susceptibility or immunity in plants to herbivory or infection (Smith, 2007) as well as microbes and herbivores changing consumption strategies and preference among hosts under increased nutrients (Peters et al., 2006). Previous work in this system shows amplified foliar fungal and arthropod impacts on plant biomass in fertilized plots (Zaret et al., 2023), suggesting that a shift toward poorly defended species following nutrient addition (reflecting the growth–defense trade-off) has implications for ecosystem processes such as carbon cycling. Studies integrating defense trade-offs and ecosystem processes in the context of global changes such as increasing nutrient supplies would help clarify this knowledge gap.

CONCLUSION

While a growth–defense trade-off in plants has been shown across different locations and for different consumer types, our work demonstrates that in the context of a diverse plant community, there is a general growth–defense trade-off among plant species interactions with a wide range of consumer types. Plant consumers span multiple kingdoms with very different consumption strategies, suggesting the likelihood of distinct plant defense trade-off axes among consumer guilds. However, our findings suggest the principles of defense trade-offs arising from plant chemical work and coexistence theory apply similarly within complex plant communities for mammalian herbivores, insect herbivores, foliar fungi, and soil fungi.

AUTHOR CONTRIBUTIONS

EB, ES, and LK coordinated the consumer reduction experiment. MZ, ES, and LK conceived this study. MZ and others collected data. MZ analyzed data with inputs from EB, ES, and LK. MZ wrote the first draft of the manuscript. All authors contributed substantially to manuscript revisions.

ACKNOWLEDGMENTS

Thank you to Jon Anderson, Troy Mielke, Anita Krause, Dan Bahauddin, Susan Barrott, and Cedar Creek summer interns who all aided in the logistics, maintenance, and data collection of this experiment. We also thank Sarah Hobbie for feedback on this work. This work was supported by grants from the US National Science Foundation Long-Term Ecological Research Program (LTER), including DEB-1234162 and DEB-1831944. Funding from UMN EEB and Cedar Creek supported MZ.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Kinkel, 2022) are available in the Environmental Data Initiative repository at https://doi.org/10.6073/pasta/6642a7601ddc7e24f44aea39684d8ab4. Code (Zaret, 2024) is available in Zenodo at https://doi.org/10.5281/zenodo.10778124.

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SUPPORTING INFORMATION

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

How to cite this article: Zaret, Max, Linda Kinkel, Elizabeth T. Borer, and Eric W. Seabloom. 2024. "Plant Growth–Defense Trade-Offs are General across Interactions with Fungal, Insect, and Mammalian Consumers." *Ecology* 105(5): e4290. https://doi.org/10.1002/ecy.4290