

Is There a Temperate Bias in Our Understanding of How Climate Change Will Alter Plant-Herbivore Interactions? A Meta-analysis of Experimental Studies*

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ABSTRACT: Climate change can drive major shifts in community composition and interactions between resident species. However, the magnitude of these changes depends on the type of interactions and the biome in which they take place. We review the existing conceptual framework for how climate change will influence tropical plant-herbivore interactions and formalize a similar framework for the temperate zone. We then conduct the first biome-specific tests of how plant-herbivore interactions change in response to climate-driven changes in temperature, precipitation, ambient CO₂, and ozone. We used quantitative meta-analysis to compare predicted and observed changes in experimental studies. Empirical studies were heavily biased toward temperate systems, so testing predicted changes in tropical plant-herbivore interactions was virtually impossible. Furthermore, most studies investigated the effects of CO₂ with limited plant and herbivore species. Irrespective of location, most studies manipulated only one climate change factor despite the fact that different factors can act in synergy to alter responses of plants and herbivores. Finally, studies of belowground plant-herbivore interactions were also rare; those conducted suggest that climate change could have major effects on belowground subsystems. Our results suggest that there is a disconnection between the growing literature proposing how climate change will influence plant-herbivore interactions and the studies testing these predictions. General conclusions will also be hampered without better integration of above- and belowground systems, assessing the effects of multiple climate change factors simultaneously, and using greater diversity of species in experiments.

Keywords: climate change, plant-herbivore interactions, tropical, temperate, aboveground, belowground.

Introduction

Understanding the ecological effects of climate change is an increasingly important area of theoretical and empirical

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research (Gilman et al. 2010; Wu et al. 2011). Much recent work on climate change effects has focused on changes in species distributions (Pateman et al. 2012; Pauli et al. 2012; Amissah et al. 2014; Sheppard et al. 2014), the loss of biodiversity (Bellard et al. 2012), changes in plant phenology (Wolkovich et al. 2013), and temporal mismatches between interacting species (Singer and Parmesan 1993; Durant et al. 2007; Kudo and Ida 2013). These effects have been observed over a relatively short timescale (IPCC 2014), and it is thought that they could ultimately lead to drastic changes in interspecific interactions with community-level consequences (van der Putten et al. 2004; Tylianakis et al. 2008).

Herbivores and plants comprise the majority of terrestrial biodiversity. Their complex interactions can influence population and community dynamics (Lurgi et al. 2012) and have major effects on agricultural systems (Oerke 2006), making them central to the responses of terrestrial systems to climate change (Mulder et al. 1999). The highest diversity of herbivore species and feeding types is found in insects (class Insecta; Speight et al. 2008), which evidence to date suggests are extremely sensitive to changing climatic conditions (Bale et al. 2002). This is because there are multiple pathways by which climate change can exert effects, for example, directly via climate-driven changes in physiology and behavior or indirectly via changes in host plant characteristics or abundance (Bale et al. 2002). Understanding how plant-herbivore interactions respond to changing climates is therefore critical to improving predictions for how climate change affects ecological and agricultural systems.

A rich literature has documented the diversity of ways with which plants interact with herbivores aboveground (AG; e.g., leaf-feeders) and belowground (BG; e.g., root-feeders). AG and BG herbivores can influence each other, their host plants, and local communities and ecosystem properties (van der Putten et al. 2009). For example, BG herbivores can cause changes in leaf physiology, thereby affecting AG attackers and their predators (Soler et al.

2005; van Dam et al. 2005; Rasmann and Turlings 2007; Erb et al. 2011). The opposite is also true—AG herbivores can drive changes in root physiology and resistance (Masters 1995; Soler et al. 2005; Kaplan et al. 2008; Erb et al. 2011). Finally, recent research has revealed unexpected ways plants themselves mediate interactions between BG and AG herbivores (Bardgett and Wardle 2003; Wardle et al. 2004). Although there is mounting evidence that global climate change can alter AG interactions, how it influences BG interactions and the link between AG-BG subsystems has rarely been explored.

Because the distribution of organisms is geographically heterogeneous (Cramer et al. 2001; Walther et al. 2002), the magnitude of plant and herbivore responses to climate change and the magnitude of these effects might depend in large part on the biome in which their interactions take place (Walther et al. 2002). Although there is regional variability in model predictions, generally global increases in CO₂ will positively affect forest productivity (net primary production) and shift the species composition in the temperate zone (Reich and Frelich 2002; Reich et al. 2006; IPCC 2014). In the tropical zone, increases in CO₂ will increase net biomass but could also cause higher fire incidence that can positively affect mortality and forest turnover (Cramer et al. 2004; Malhi and Phillips 2004; Phillips et al. 2004). Trees in the tropics are likely to be negatively affected by increases in temperature (Clark et al. 2003, 2010; Feeley et al. 2007; Way and Oren 2010) and may have limited ability to alter traits in response (Drake et al. 2015). In contrast, temperate trees will grow in response to warming (Carter 1996; Rehfeldt et al. 2002) and likely have greater flexibility to alter physiological and structural traits (Drake et al. 2015). Understanding how the effects of climate change influence plant-herbivore interactions across latitudes is therefore critical to predicting species responses.

Predictions about the outcome of plant-herbivore interactions under climate change have been based primarily on expected changes in plant nutritional content. Following Bryant's (1983) hypothesized "carbon-nutrient balance," Coley (1998) outlined a framework for how climate change should influence plant-herbivore interactions in the tropics. She argued that the increase in atmospheric CO₂ would result in increased mean carbon storage in soil organic matter (Schimel et al. 1994), ultimately leading to higher carbon absorption and lower concentrations of leaf nitrogen, that is, nitrogen dilution (Fajer 1989; Coley 1998). Consequently, tropical plants would shift to having leaves with reduced nutritional quality (Fajer 1989; Coley 1998), reduced concentrations of nitrogen-based defenses, and elevated carbon-based defenses (Coley 1998). Herbivores would increase their per capita consumption rates due in part to increased CO₂ and the effects of reduced

precipitation, ultimately leading to lower plant growth rates (Coley 1998).

Despite almost 20 years having past since Coley put this comprehensive framework forward, a similar one for temperate plant-herbivore interactions has yet to emerge. Here we draw on prior empirical and theoretical work to develop a series of predictions for how climate change will influence plants, herbivores, and their interactions in temperate regions comparable to those put forward by Coley for the tropics. The complete framework can be found in figure 1, but we briefly summarize it here. We hypothesize that if the climate in temperate regions changes as predicted (IPCC 2014), plants will have elevated levels of carbon-based defenses (Bryant et al. 1987; Gebauer et al. 1998; Bidart-Bouzat and Imeh-Nathaniel 2008). This will decrease leaf nutritional quality via the nitrogen dilution effect (Bryant et al. 1983). If as predicted increases in atmospheric CO₂ enhance reproduction and the development of herbivores, then herbivory in the temperate zone should increase with elevated CO₂ (Lincoln et al. 1993; Bezemer and Jones 1998). Drought would negatively affect plants by impeding the conductance or absorption of nutrients, thus decreasing plant growth and nutritional quality (Mattson and Haack 1987; Bartels and Sunkar 2005; Jactel et al. 2012; He and Dijkstra 2014). As growth declines, moderate drought will result in greater investment in physical and chemical N- and C-based defenses as a result of the increased levels of available carbon and nitrogen (Mattson and Haack 1987; Jactel et al. 2012). Thus, drought-stressed plants should be more attractive or acceptable to insects, causing herbivory to increase (Mattson and Haack 1987; Jactel et al. 2012). Because many plant and insect physiological processes are temperature dependent, an increase in temperature should stimulate plant growth, leaf nutritional quality, and ultimately herbivory (Bale et al. 2002; Bidart-Bouzat and Imeh-Nathaniel 2008; Wu et al. 2011). However, the effect of temperature on plant defenses will vary depending on the type of chemical produced (Bidart-Bouzat and Imeh-Nathaniel 2008). For example, N-containing compounds and some volatile organic compounds will be enhanced by increasing temperature (Sallas et al. 2003; Loreto et al. 2006), while some phenolic compounds will decrease (Kuokkanen et al. 2001). Ozone (O₃) causes stress in plant cells that results in decreased respiration and plant growth (Grantz et al. 2006; Lindroth 2010); it also reduces absorption and allocation of nutrients (Lindroth 2010). These physiological changes stimulate the induction of metabolic pathways that cause an increase in carbon-based defenses, resulting in decreased rates of herbivory (Sandermann 1996; Bidart-Bouzat and Imeh-Nathaniel 2008; Lindroth 2010).

Here we conduct the first biome-specific tests of predicted changes in plant-herbivore interactions resulting

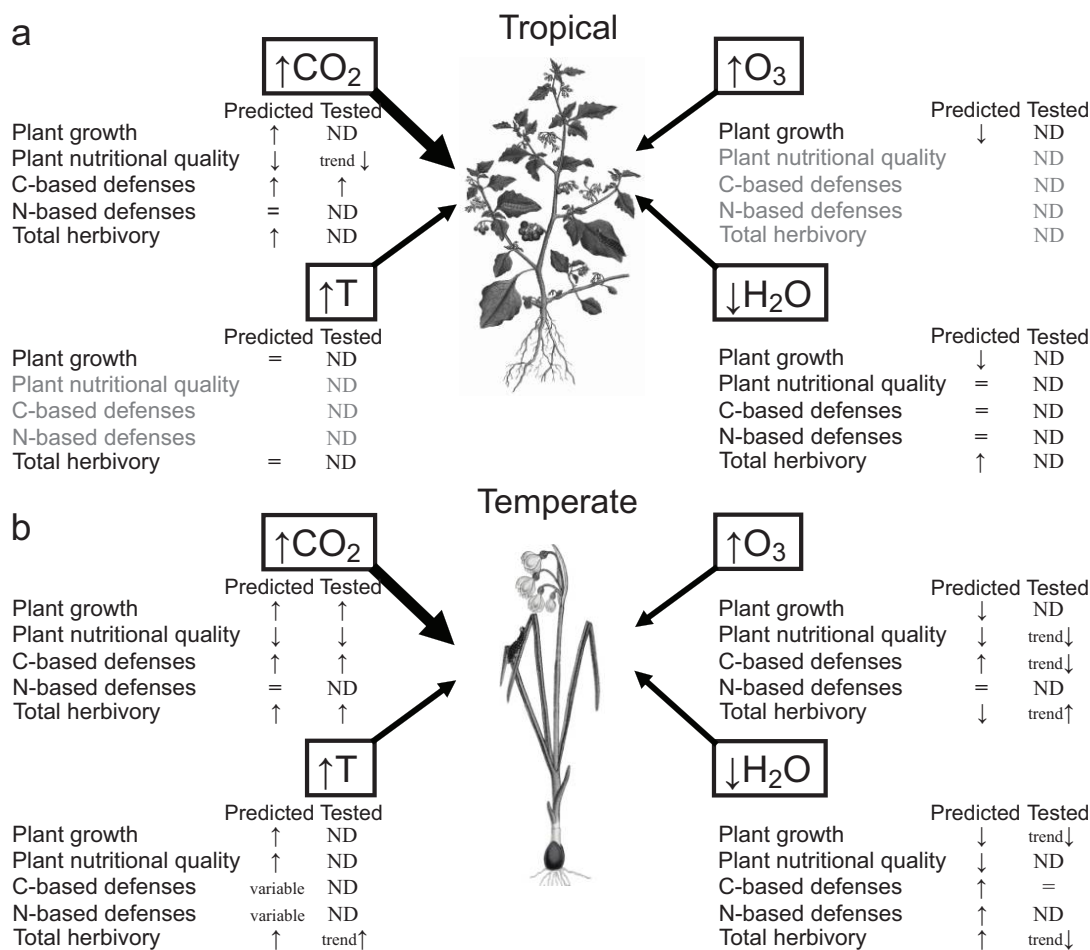


Figure 1: Framework for predicted trends and results of how climate change will affect plants and plant-herbivore interactions for tropical (a) and temperate (b) species and support for these predictions based on meta-analyses. In both frameworks, plant growth is quantified as aboveground biomass, nutritional quality is the concentration of N in leaves, and total herbivory is the amount of biomass consumed by herbivores. The environmental changes whose impact we evaluated are increases in carbon dioxide (CO₂), air temperature (T), and ozone levels (O₃) and decreases in precipitation (H₂O). Symbols represent increased production (↑) or decreased production (↓). ND = not enough data to test a prediction; trend = nonsignificant trends. Gray indicates that there are no predictions to test.

from climate change. Previous reviews of herbivory and climate have mostly been qualitative, focused on temperate species, and investigated the effects of rising CO₂ levels. We take a step forward by using a meta-analysis of experimental studies, for which we reviewed more than 5,000 published articles, to quantify the responses of tropical and temperate plant species, their AG and BG subsystems, and both natural and agricultural systems. We then used data on the magnitude of the effects observed, variation in sample sizes, and the statistical power of individual studies to address the following questions: (1) How do different components of plant-herbivore interactions respond to experimental manipulation of climate change?

(2) Do these patterns differ between tropical and temperate systems? (3) How do AG and BG plant-herbivore subsystems differ in their responses to manipulations of climate change variables?

Methods

Meta-analysis: Data Collection

We began by searching for articles in the Web of Science (ISI) in April 2014. We compiled all articles published between 1900 and 2013 that resulted from searches using the terms “climate change or global change,” “plant,” “herbi-

vor* or insect,” “interaction,” “aboveground,” “belowground,” “response*,” and “defenses” in different combinations. Data from book chapters and graduate theses as well as unpublished data were not included in our analyses.

For one of the resulting studies to be included in our meta-analysis, it had to meet three criteria. First, the studies had to have both control and treatment levels (i.e., ambient conditions vs. experimental increases or decreases in a climatic variable). Second, studies had to be based on unique data sets; when studies by the same author(s) used subsets of the same data set in separate articles, only the most comprehensive study was included. Third, studies had to provide sufficient statistical information to allow the calculation of effect sizes. We calculated effect sizes using means, sample sizes, standard errors, or standard deviations extracted from control and experimental groups. For several publications there were discrepancies in the sample sizes reported in the methods, figures, and tables; to standardize, we used the ones reported in the methods. Since a large proportion of the studies presented the data graphically, we obtained the numeric values for responses directly from the figures.

We then used the statistical software MetaWin 2.1 to calculate effect sizes (Rosenberg et al. 2007) in each study. We calculate the effect sizes of each climate change factor only when a focal species had at least three measurements. These measurements could be from the same study but with different species or from different studies with the same species. For studies where multiple measurements were recorded (e.g., monthly, yearly), only the first or last measurements were used to calculate effect sizes. The measurement had to have the most complete statistical information.

We assigned the articles to categories for analysis based on the climate change factors manipulated, the plant species studied, the subsystem in which the experiment and measurements took place, and the plant response measured. The climate factors considered were levels of carbon dioxide (CO₂) and ozone (O₃), air temperature (*T*), and precipitation, both increases (iH₂O) and decreases (dH₂O). Plant species were divided into four groups: (1) crops, that is, all species produced in agricultural systems; (2) grasses, that is, all grass species independent of their geographic origin; (3) temperate species, that is, all species from temperate regions; and tropical species, that is, all species from the tropical zone. The two subsystems considered were AG (any insect feeding on leaves, with measurements of AG plant responses to herbivory) and BG (nematodes or insects feeding on roots, with measurements of BG plant responses). Plant responses measured were final AG or BG biomass, plant nutrients (i.e., nitrogen, carbohydrate, and sugar content, C:N ratio), and plant defenses (i.e., carbon-based defenses, nitrogen-based defenses, physical defenses). Finally,

we used the change in herbivore body mass and rate of plant consumption in each climate change treatment to quantify the impact of climate change on the interactions between plants and herbivores.

Meta-analysis: Statistical Analyses and Tests for Publication Bias

Because the majority of the studies reported a pair of means and variance and had small sample sizes (Rosenberg et al. 2007), we used Hedges’s *d* (eq. [1]) to measure the effect size (Osenberg et al. 1999; Koricheva et al. 2013). It uses the treatment and control estimated means (\bar{Y}_1 and \bar{Y}_2) and their associated sample sizes (n_1 and n_2) and standard deviations (s_1^2 and s_2^2 ; Koricheva et al. 2013) to calculate the difference between the two groups, *d*, as

$$d = \frac{\bar{Y}_1 - \bar{Y}_2}{\sqrt{\frac{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2}{n_1 + n_2 - 2}}} \left(1 - \frac{3}{4(n_1 + n_2 - 2) - 1} \right). \quad (1)$$

It has the advantage of not being biased by unequal sampling variances in the paired groups and includes a correction factor for small sample sizes (Rosenberg et al. 2007).

The influence of climate change factors on plants and plant-herbivore interaction traits was quantified by calculating the effect size for each of the pairwise comparisons (i.e., control vs. experimental treatment). The mean effect sizes were computed and compared using MetaWin 2.1 (Rosenberg et al. 2007). A positive effect size indicates that a given climate change factor enhances the response of a given plant trait (Rosenberg et al. 2007; Koricheva et al. 2013), while a negative effect size indicates a detrimental effect on the performance of the trait. A climate change factor effect was considered statistically significant if the 95% confidence interval (CI) of the trait’s mean effect size did not include 0 (Rosenberg et al. 2007; Koricheva et al. 2013), with 95% CIs calculated as mean \pm 1.96 standard deviation/sqrt (sample size). Comparisons of climate change effects on plants and plant-herbivore interactions both within and among factors was explored by calculating the between-group heterogeneity (Q_b), which we then compared using a χ^2 test statistic (Koricheva et al. 2013) to determine whether there were significant differences between effect sizes for different climate change factors. In sum, all analyses were performed to determine whether the observed variance in effect size was significantly different from that expected by sampling error (Koricheva et al. 2013).

Publication bias occurs when the effect sizes included in the meta-analysis generate false conclusions compared

with those obtained when the effect sizes come from studies with appropriate statistical tests (Koricheva et al. 2013). Because of the wide range of sample sizes in the studies we reviewed, we initially used the funnel plot method to test for publication bias (Rosenberg et al. 2007; Koricheva et al. 2013) by plotting the effect sizes of different climate change factors on plant and plant-herbivore interactions against sample size. We also tested for a relationship between these with Spearman rank correlations. In the absence of bias, the plots should show symmetry around the mean effect size for each group, and effect sizes should not correlate with sample sizes (Rosenberg et al. 2007; Koricheva et al. 2013).

Results

The initial literature search resulted in 5,644 publications, of which only 120 published between 1993 and 2013 met our criteria. The full data set is deposited in the Dryad Digital Repository (<http://dx.doi.org/10.5061/dryad.dn048>; Mundim and Bruna 2016). Of the 120 papers, 80 evaluated the effect of one climate change factor, 39 evaluated the effect of two, and only one evaluated the combined effects of three factors in the same experiment. Funnel plots of effect size versus sample size for all plant and plant-herbivore interaction traits measured indicate a possible selection bias favoring studies with small sample sizes over those with larger ones (fig. A1). However, studies with small sample sizes showed more variation around the mean effect size (fig. A1), and because Spearman's rank correlations showed no significant relationships (except for sugars and carbohydrates; table A1), the bias in the meta-analysis is negligible.

What Components of Climate Change and Plant-Herbivore Interactions Are Being Investigated?

There were 92 studies that measured AG traits after AG herbivory, while only one study considered AG traits after BG herbivory. Eleven studies considered AG traits in the absence of herbivores. No study measured BG traits after exclusively AG herbivory, two studies measured BG traits after BG herbivory, and one study measured BG traits in the absence of herbivores. Only 13 studies evaluated AG-BG linkages by measuring traits in both subsystems after AG and/or BG herbivory (fig. 2b).

The most frequently evaluated climate change factor was increasing CO₂ ($n = 101$), followed by decreased precipitation and increasing levels of ozone ($n = 17$ and $n = 16$, respectively; fig. 2a). It is therefore not surprising that the most common experimental frameworks were large open-top chambers (e.g., Gao et al. 2008), small outdoor chambers (e.g., Flynn et al. 2006), and free-air CO₂ enrich-

ment experiments (e.g., Hillstrom et al. 2010; 22.5%, 20%, and 18.33% of studies, respectively).

Only four publications investigated tropical species (see fig. 2c, 2d), while 61 studies were conducted with temperate taxa. Crop species were used in 44 studies, while 11 studies used grasses and their herbivores as the model systems (fig. 2c). In total, the studies we reviewed investigated the responses of 106 plant species: 18 crop species, 22 grasses, 54 temperate plants, and 12 tropical plants. The most frequently studied species were *Populus tremuloides* (7.37%), *Gossypium hirsutum* (6.84%), *Betula papyrifera* (4.74%), and *Acer saccharum* (3.68%). No tropical species was included in more than two studies.

Effect of Climate Change on Plant Growth, Nutritional Quality, Defenses, and Interactions

When considering responses for all species combined, the effect size of the CO₂ influence on AG biomass was positive and significant (i.e., did not cross the zero line), while the ones from changes in precipitation (i.e., dH₂O and iH₂O) were significant but negative. The between-factor heterogeneity (Q_b) shows that the CO₂ effect differs significantly from dH₂O and iH₂O, but precipitation effects did not differ among themselves (fig. 3a). In contrast, the effect size of the CO₂ influence on BG biomass was positive and significant, while the effect sizes of precipitation changes were not significant (fig. 3b). However, their between-factor heterogeneity was equivalent (table 1).

Nitrogen content was reported as a measure of plant nutritional quality in 41.86% of the studies reviewed. When considering all species, CO₂ had a negative effect on N content. This effect was significantly different from the ones from precipitation changes, which had positive and significant effects on N content but did not differ in magnitude (table 1; fig. 3c). Moreover, CO₂ had a positive effect on C:N ratio, while precipitation changes had no effect on C:N ratio (fig. 3d). In addition, CO₂ significantly increased the concentration of sugar and carbohydrates in leaves (fig. 3e, 3f).

Our analyses also indicate that, across all species, the heterogeneity of CO₂ effects on C-based defenses was significantly different from those of other factors (table 1). Across species as well as within the majority of species groups, increases in CO₂ significantly increase the concentrations of C-based defenses (fig. 3g). CO₂ also increased concentrations of physical defenses across all species (fig. 3i) but had no significant effect on N-based ones (fig. 3h).

There was no significant difference in the effect of different climate change factors on herbivore body mass or on the rate of plant consumption (table 1; fig. 4a, 4b). Her-

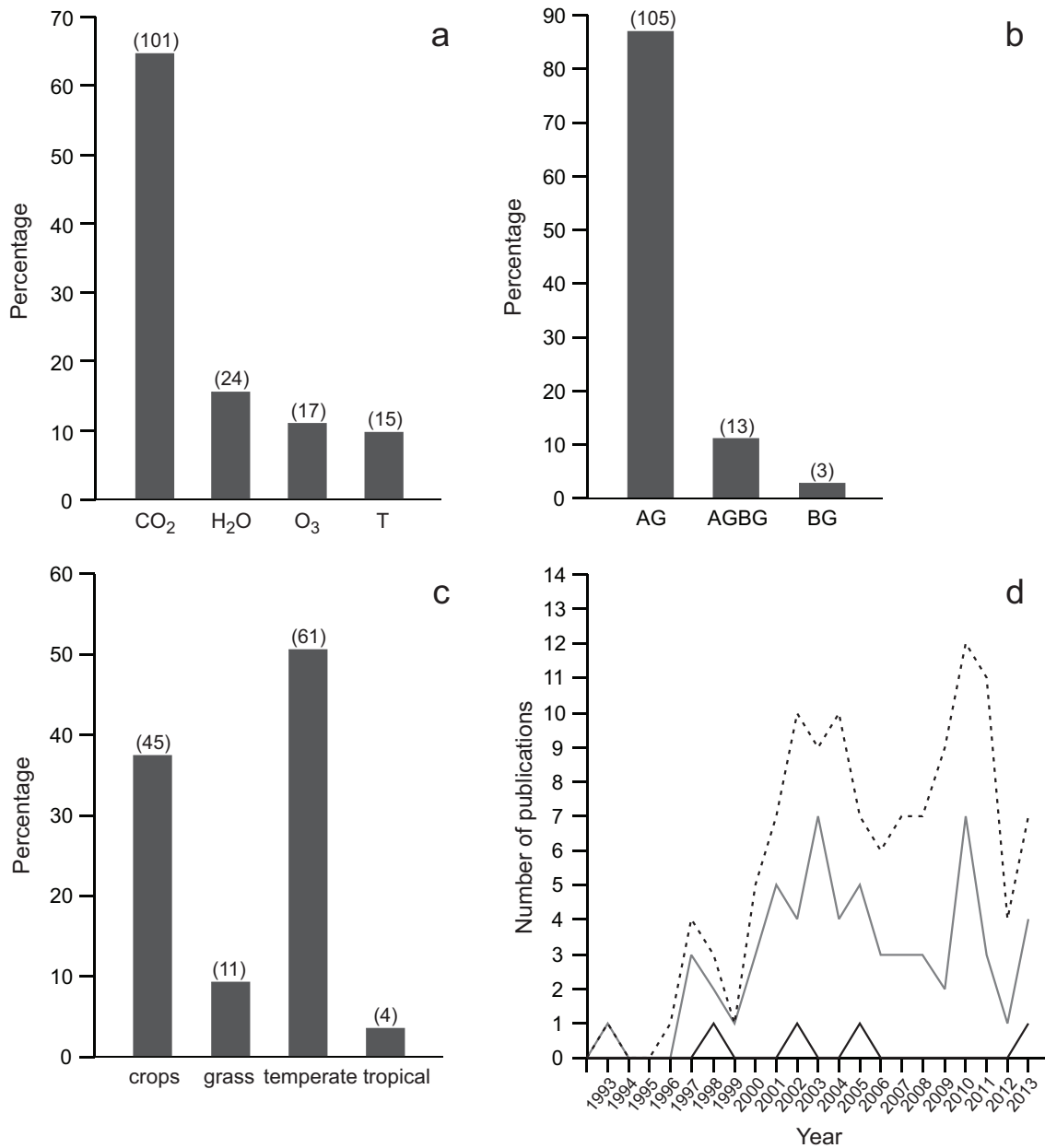


Figure 2: Climate change effects on plant and plant-herbivore interactions, general results. *a*, Percentage of experimental cases in each climate change factor. Precipitation includes increased and decreased levels. *T* = air temperature. *b*, Percentage of publications per subsystem. AG = aboveground herbivory and measurements; AGBG = herbivory and measurements in both subsystems or in opposite subsystems; BG = belowground herbivory and measurements. *c*, Percentage of publications in each group of species. Numbers inside parentheses represent the absolute number of cases considered. *d*, Number of publications per year. The dashed line represents the total number of publications (all four groups of species), the gray line represents the number of publications with temperate species, and the black line represents the number of publications with tropical species.

bivore body mass generally decreased with increasing CO₂ and reduced precipitation (fig. 4*a*), while herbivore consumption rates significantly increased under elevated CO₂. There was no effect of increases in temperature on both body mass and consumption (fig. 4*a*, 4*b*).

Support for Predictions: Effects on Tropical versus Temperate Plant Species

Testing Coley's (1998) predictions for tropical plant-herbivore interactions was a challenge due to the small

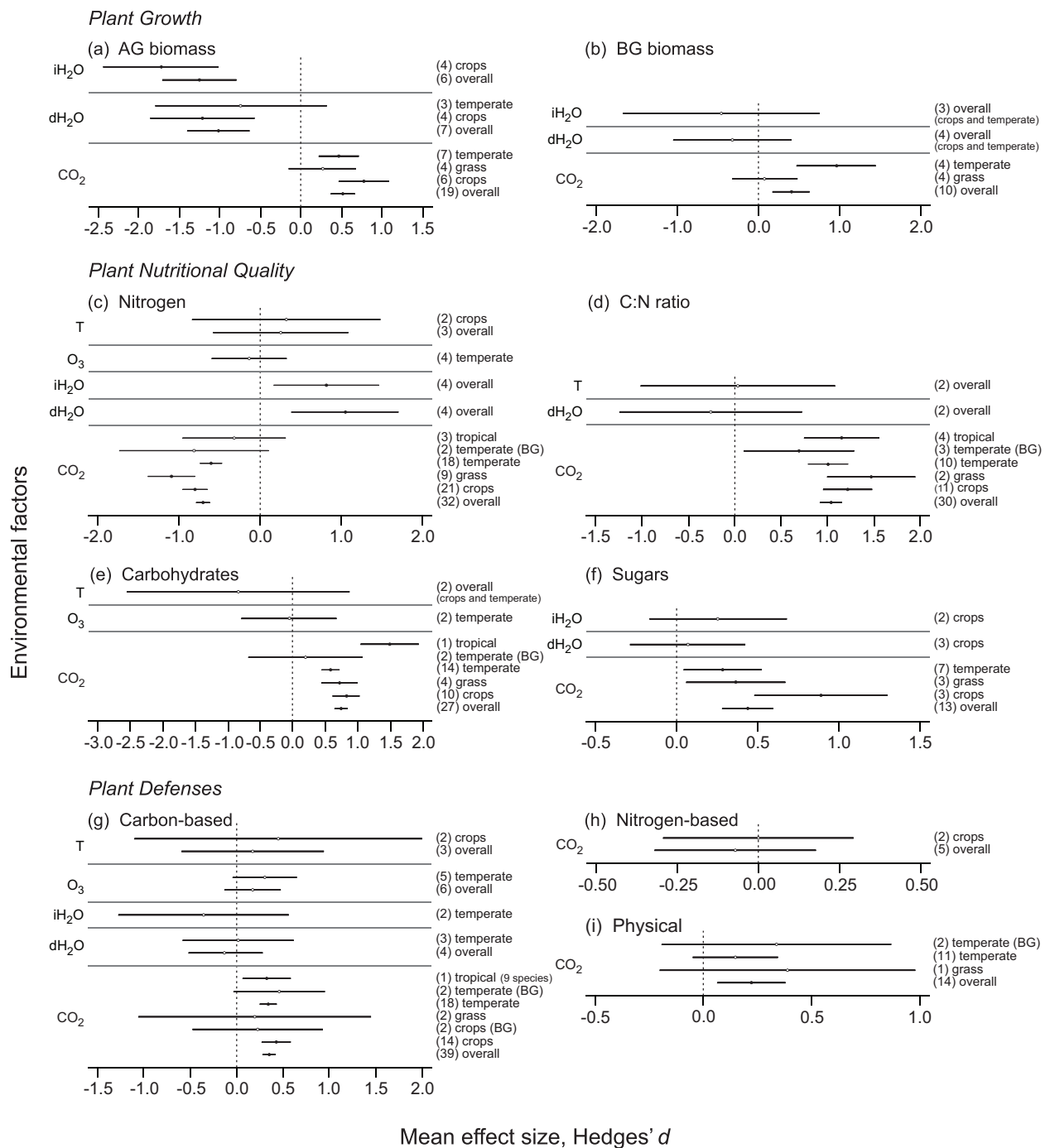


Figure 3: Influence of climate change on plant traits for different groups of plant species. Experimental manipulations include elevated carbon dioxide (CO₂) and ozone (O₃), increased air temperature (T), and precipitation decreases (dH₂O) or increases (iH₂O). Numbers in parentheses represent the number of studies considered. The analysis for all plant species combined is indicated by “overall.” Belowground measurements are denoted by BG; all others are aboveground measurements. Mean effect sizes are shown with 95% confidence intervals (CIs). Effects are considered significant if their associated CIs do not overlap 0 (i.e., the dashed line). Solid circles indicate statistically significant effects. Data underlying this figure are deposited in the Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.dn048> (Mundim and Bruna 2016).

Table 1: Heterogeneity (Q_b) for the overall plant species between CO_2 and the other climate change factors

	Q_b	df	P
Plant growth:			
Aboveground biomass	140.139	2	<.001
Belowground biomass	14.013	2	<.005
Plant nutritional quality:			
Nitrogen	130.937	4	<.001
Carbohydrates	25.095	2	<.001
Sugars	5.008	2	>.05
C:N ratio	19.165	1	<.001
Plant defenses:			
C based	14.842	4	<.01
Plant-herbivore interactions:			
Body mass	9.250	4	>.05
Consumption	3.914	4	>.1

Note: Boldface type indicates statistical significance.

number of studies, the limited number of environmental factors manipulated in these studies, and the few response variables measured. In contrast, our predictions for the responses of temperate species were generally upheld (fig. 1). For example, temperate species had a significant decrease in N and an increase in the C:N ratio. In the few cases where comparison across biomes was possible, some responses were qualitatively similar; for example, there was a significant increase in the concentration of carbohydrates and C-based defenses under elevated CO_2 (fig. 3c, 3g). However, other responses differed notably among regions; for example, tropical species had a greater increase in leaf carbohydrates than temperate species ($Q_b = 40.31$, $df = 1$, $P < .001$). A lack of experiments or failure to measure plant responses and proxies for plant-herbivore interactions in the tropical experiments made other temperate-tropical comparisons impossible.

Effects of Experimental Climate Change BG

Most studies measured only AG responses and interactions (figs. 3, 4), and there are no predictions for how climate change will influence BG interactions and plant responses. The BG experiments that were conducted were all manipulations of CO_2 using temperate and crop species; few measured root nutritional quality or defense levels in roots. None of the effect sizes measured for BG studies differ significantly in magnitude from their AG counterparts ($Q_b = 0.58$, $df = 1$, $P > .05$; $Q_b = 0.74$, $df = 1$, $P > .05$; for temperate and crop species and C-based defenses, respectively). The CO_2 effect sizes for N or carbohydrate contents in roots were not significant, but it was positively significant for C:N ratio. Finally, the CO_2 effect size for carbon-based defenses in roots was not significant

for temperate species but was positively significant for crop species (fig. 3g).

Discussion

Although scientists have been predicting and documenting the potential effects of climate change on ecosystems for decades, experimental evaluations of how climate change influences plant-herbivore interactions remain rare. Our meta-analysis uses quantitative data from experiments across the globe to evaluate the magnitude of responses by plants, herbivores, and their interactions to climate change under two predictive frameworks: Coley's framework for tropical species (Coley 1998) and our framework drawing together predictions for temperate ones. We found evidence to support most of the predictions for temperate species. However, despite 20 years having past since Coley published her comprehensive predictions, the lack of studies from the region makes it impossible to test them. Other gaps in knowledge revealed by our meta-analysis include how climate change factors influence BG processes and the links between AG and BG responses. Below we elaborate on these results and propose how to move forward to better understand the mechanisms by which climate change will influence plant-herbivore interactions.

In our study, predicted changes in factors such as precipitation, temperature, and ozone levels did not have significant effects on plant-herbivore interactions—although this may well be because there simply have been so few experiments considering the effects of these changes, the limited number of species in which they have been evaluated, and a failure to consider the impact of linked interactions AG and BG. However, the best-studied factor—increased atmospheric CO_2 —has clear and large effects. Under elevated CO_2 , plants had augmented leaf and root production, with outcomes consistent with the “fertilization effect” (LaMarche et al. 1984) predicted to occur under a combination of increased CO_2 , temperature, and water stress. Although it is thought to affect C_3 and C_4 plants in different ways (Lincoln et al. 1984), we detected similar effects across plant groups in studies manipulating CO_2 . Although we documented species-specific response intensity, the CO_2 fertilization effect begins with increased photosynthetic CO_2 fixation (Poorter et al. 1988). During plant acclimation to elevated CO_2 levels an increase in carbohydrates and sugars and a decrease in protein content ensues, ultimately leading to increased C:N ratio in leaves (Yelle et al. 1989; Kozłowski and Pallardy 2002). Plants then decrease their photosynthetic capacity, ultimately leading to lower nitrogen content (Poorter et al. 1988; Yelle et al. 1989). In addition, higher CO_2 levels indirectly deprive insect herbivores of necessary nutrients for development. Since insect feeding depends strongly on

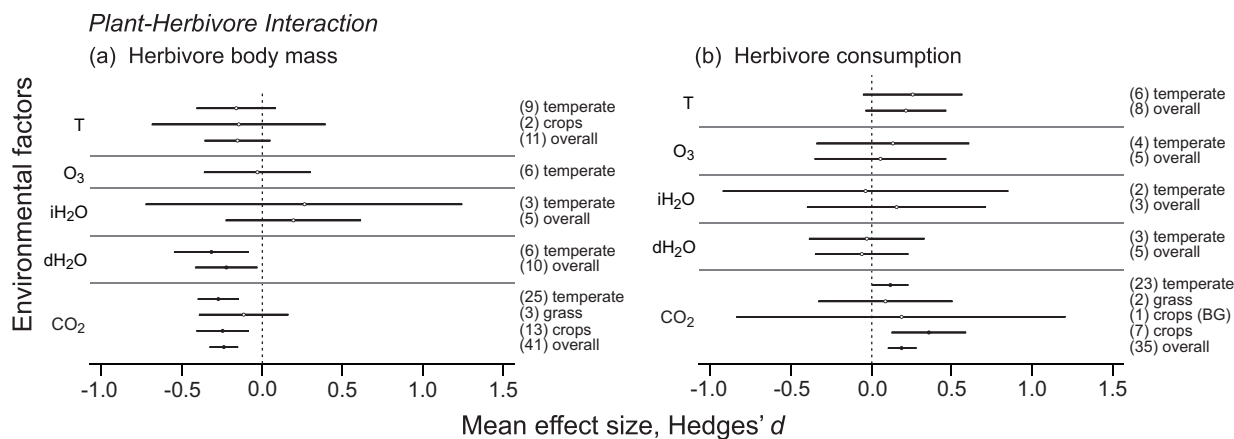


Figure 4: Influence of climate change on plant-herbivore interactions for different groups of plant species. Details are as described in figure 3.

nutrient availability and quality (Hunter 2001; Awmack and Leather 2002; Bale et al. 2002), the low nitrogen availability causes an increase in consumption despite the decrease in herbivore body mass (fig. 4). The CO_2 effects were evident for temperate, grass, and crop species (fig. 3) but may be more pronounced in agricultural systems due to the faster decrease of key nutrients (i.e., N, P, and K; Tan et al. 2005) and the potential for insect pest outbreaks to occur more frequently (see Logan et al. 2003).

The increase in greenhouse gas emissions causes increases in temperature, ultraviolet radiation, and atmospheric ozone levels as well as changes in precipitation patterns (IPCC 2014). However, our results reveal that most studies have tested only for the effects of changes in CO_2 . Addressing single climate change variables in isolation is problematic—recent studies indicate that these factors can act in synergy to directly or indirectly induce changes in the responses of plants and insect herbivores. For example, several studies in which only CO_2 , T , or O_3 are increased or in which precipitation alone is decreased have shown a decrease in herbivore body mass (fig. 4a). However, decreases in body mass are greater in magnitude when CO_2 and T are manipulated in combination than when they are manipulated independently (Johns and Hughes 2002). Similarly, drought, combined with changes in CO_2 , T , or both, can also decrease body mass, with the magnitude of changes increasing the more factors are considered (Scherber et al. 2013). In contrast, CO_2 and O_3 can act synergistically to increase body mass (Kopper and Lindroth 2003). Although more work is needed to consider how interspecific differences in life history and food availability will alter the generality of these conclusions, the findings are consistent with those of other studies investigating how multiple anthropogenic disturbances alter

ecological systems (Cochrane and Laurance 2008; Brodie et al. 2012).

Our review also highlights important gaps in our understanding of how climate change might differentially influence tropical and temperate plant-herbivore interactions. Although few studies in the temperate zone investigated the effects of increasing temperature and the diversity of species studied was relatively low, the volume of work available provides robust quantitative support to many of our predictions for how these interactions will be altered. In contrast, data for the tropics were so sparse we were unable to test most of the predictions in Coley's framework. Interestingly, the limited work that was available suggests congruence in the results for these different regions. For example, most predictions regarding the increase in CO_2 levels show that although the magnitude of the effects differs across tropical and temperate species, the direction of the effects was similar. There is clearly a need for more comprehensive comparative studies considering the responses of a diverse array of species from multiple latitudes.

It is also important to remember that as our understanding of how climate change will impact different regions, it may be necessary to revise our predictions for how these changes influence interspecific interactions. For instance, we suggest that Coley's framework, which centered on the effects of changes in CO_2 , underestimates the effects on herbivory associated with the decreased precipitation at lower latitudes predicted by more recent models (IPCC 2014). Although many tropical species—including in lowland forests—are exposed to extended dry seasons, severe or prolonged decreases in rainfall can decrease plant growth and increase rates of mortality (Engelbrecht and Kursar 2003; Breshears et al. 2005). This could change the relative abundance of plant species and

hence the local pressure and impact of herbivores. In addition, the decrease in soil moisture could reduce decomposition rates and decrease the absorption of nutrients (Kozłowski and Pallardy 2002), resulting in lower concentrations of these limited nutrients in leaves and roots and favoring nitrogen-fixing species. With the decrease in water availability, plants would have to physiologically balance root/shoot growth, production of secondary metabolites, and reproduction. In the short term, the physiological stress and changes in the allocation of assimilated nutrients influenced by hormones (Kozłowski and Pallardy 2002) should favor growth and production of secondary metabolites. However, in the long-term defenses should decrease. BG herbivores would be less favored due to the low soil moisture, but leaf herbivory is expected to increase and be more severe because some herbivore populations may increase (Ayres and Lombardero 2000; Jactel et al. 2012), causing more frequent herbivore outbreaks. These predictions are based only on decreases in precipitation; if we consider the potential for additive or even synergistic effects of other factors, the effects could be even more severe. However, it is important to highlight that plants are known for their capacity to acclimate to changing conditions (see Valladares and Pearcy 1997; Morison and Lawlor 1999), so the speed at which the climate changes will play a critical role in mediating these responses.

Future Directions in a Changing World

Our meta-analysis has shown that climate change has significant effects on plants, herbivores, and their interactions. Here, we highlight five broad research priorities that we feel will greatly improve our ability to understand the potential effects of climate change on these critical interactions, whose effects ultimately cascade through communities and influence ecosystem services.

First, future studies must attempt to evaluate how multiple climate change factors interact to influence plants and their herbivores. Such experiments may be logistically challenging, but they more accurately reflect the reality of simultaneous changes in, for example, temperature, precipitation, and CO₂. Second, study length remains a critical weakness in studies of climate change and herbivory—most are of limited duration and conducted with plants from a single life-history stage. However, plant physiology and growth in response to environmental conditions vary ontogenetically (Bazzaz and Williams 1991; Kozłowski and Pallardy 2002); focusing on only a single life-history stage could mean failing to detect physiological acclimation to the changing climates. Finally, there is the potential for maternal and other multigenerational effects; all of these possibilities can be detected only with studies of much longer duration than most of those we reviewed.

Third, there is an urgent need for more studies of tropical species. Although there is a growing literature addressing how climate change will affect tropical species, some major questions regarding plant physiological responses, interaction networks across multiple trophic levels, and changes in biodiversity remain unanswered. In addition, it has been proposed that climate change and human land use interact synergistically (Brodie et al. 2012) and that biodiversity and trophic interactions are strongly affected by local as well as landscape-scale changes (Tschamntke et al. 2005). Thus, climate change associated with external perturbations could have a stronger impact on tropical species and their interactions. Further studies with tropical species would allow more robust predictions of these effects and also provide a more realistic approximation of future conditions and changes. A corollary to this is that while many plant and herbivore species have geographic ranges that transcend biomes, we know little about how climate change will influence their distribution or interactions with other species (but see Doak and Morris 2010). Studies manipulating climate change variables across latitudes therefore have the potential to greatly improve our existing predictive frameworks for studying these interactions.

Fourth, it is essential to consider BG subsystems when assessing responses of plant-herbivore interactions to changing climates. Studies with crops have shown that increased allocation of C to roots caused by increased levels of CO₂ enhance the proliferation and depth of roots (Prior et al. 1994; Suter et al. 2002; Madhu and Hatfield 2013), which may enhance nutrient acquisition in places where climate change will result in reduced precipitation (Madhu and Hatfield 2013). All of these climate change-driven shifts in plant physiology and growth, coupled with changes in rhizosphere dynamics, could have important consequences for plant and herbivore demography and the outcome of plant-herbivore interactions, but data on these BG changes are extremely limited. Experiments with a more holistic perspective are clearly necessary, not only because this subsystem has been ignored but because these BG plant-herbivore interactions are inextricably linked to those AG.

Fifth, comprehensively elucidating how plant-herbivore interactions will respond to climate change requires expanding experiments to include such groups as predators, competitors, and mutualists, all of which can influence the outcome of these interactions (Herrera et al. 2002; Trager and Bruna 2006; Poelman et al. 2011) and which may themselves be susceptible to climate change (e.g., Jevanandam et al. 2013). Moving beyond the “pairwise perspective” (sensu Stanton 2003) has been essential to advancing our understanding of other types of plant-animal interactions, and we anticipate that doing so in this context will provide exciting theoretical and empirical advances.

Conclusions

The majority of studies we analyzed found dramatic changes in plants, herbivores, and their interactions in response to experimentally simulated climate change. However, our meta-analysis also highlights profound gaps in our knowledge and a major bias toward research in the temperate zone. In light of the potential ecological and economic effects that changes in these interactions could bring, it is clear that there is an urgent need for more geographically, taxonomically, and ecologically diverse research on this fundamentally important topic.

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APPENDIX

Publication Bias Results

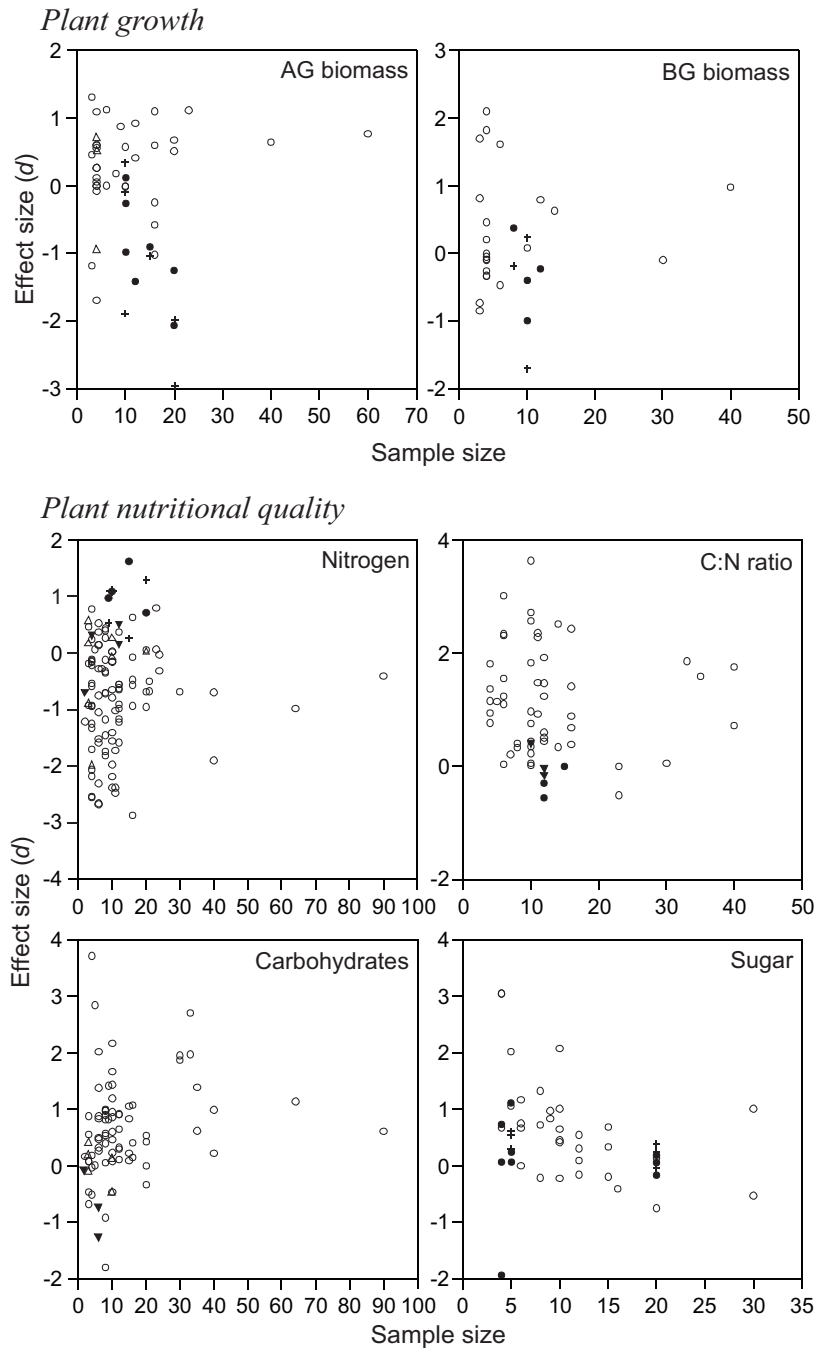


Figure A1: Funnel plots of effect sizes (d) and sample sizes. Each point represents the mean effect size for a single experimental case. The climate change factors comprise increased levels of carbon dioxide (CO_2) and ozone (O_3), increased air temperature (T), and decreased (dH_2O) and increased (iH_2O) precipitation levels. Data underlying this figure are deposited in the Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.dn048> (Mundim and Bruna 2016). AG = aboveground; BG = belowground.

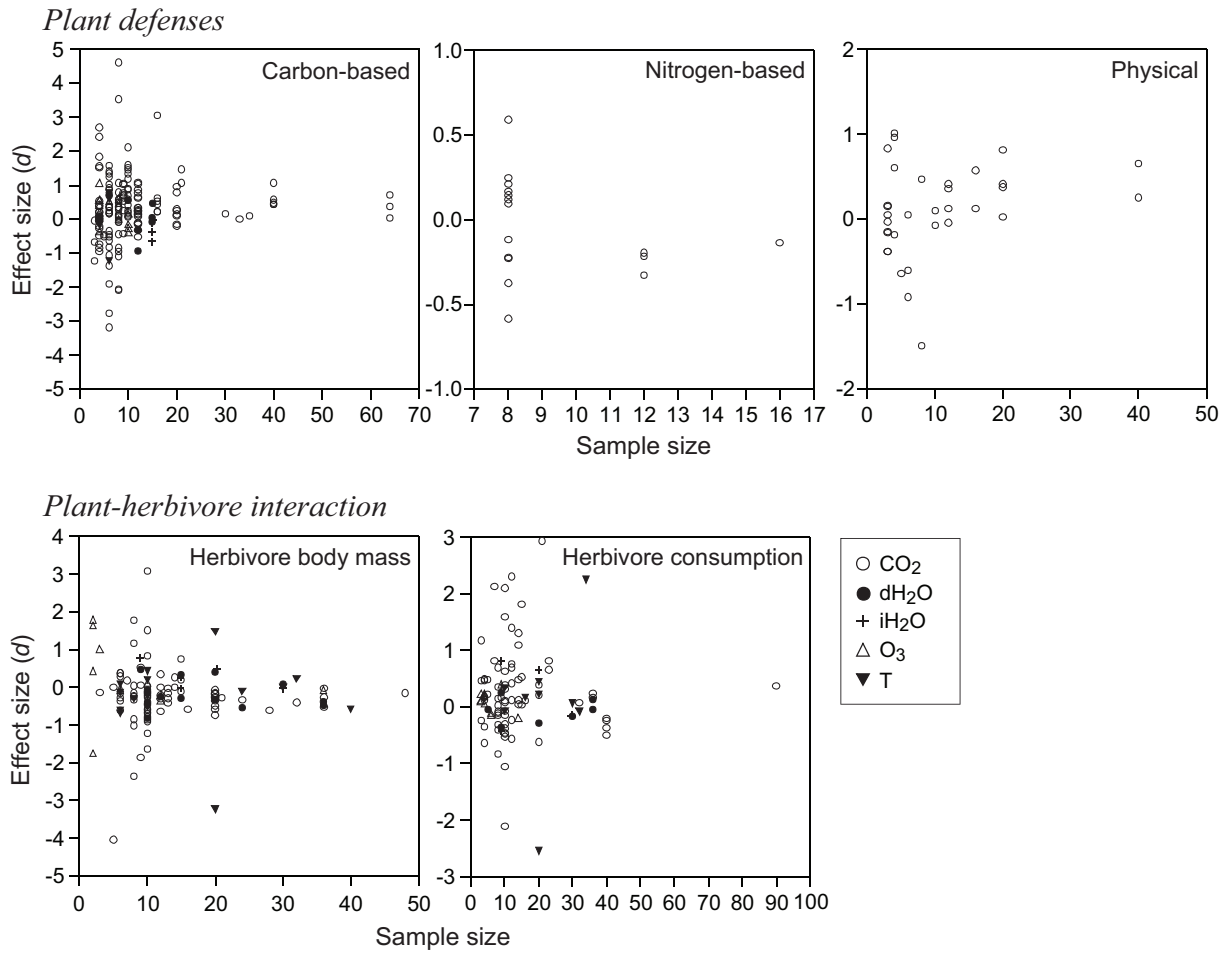


Figure A1 (Continued)

Table A1: Spearman's rank correlations between effect sizes (d) and sample sizes

	r	P
Plant growth:		
AG biomass	-.068	.633
BG biomass	-.014	.940
Plant nutritional quality:		
Nitrogen	.089	.338
C:N ratio	-.126	.326
Carbohydrates	.314	.004
Sugar	-.316	.028
Plant defenses:		
Carbon based	.136	.074
Nitrogen based	-.386	.113
Physical	.264	.095
Plant-herbivore interaction:		
Herbivore body mass	-.099	.278
Herbivore consumption	.004	.964

Note: Boldface type indicates statistical significance.

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