Climate Change Responses

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Interactive effects of multiple climate change variables on trophic interactions: a meta-analysis

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Abstract

Background: Climate change is expected to simultaneously alter many of the abiotic qualities of ecosystems as well as biotic interactions, especially trophic interactions. However, research to date has mostly focused on elucidating the effects of single climate change variables on individual species. Here, we use established meta-analysis techniques to synthesize the existing literature on the interactive effects of multiple climate change variables on trophic interactions.

Results: Most of the studies included in our meta-analysis examined plant-insect herbivore interactions. We found that the majority of trophic interaction response variables (55%) displayed multiplicative reactions to interacting climate change variables while 36% and 9% displayed antagonistic and synergistic reactions, respectively. We also found that only one of six climate change variable pairings had consistent positive or negative effects on trophic relationships, largely because interaction type and magnitude were both highly context dependent across the pairings. Most notably, males and females frequently responded differently to interacting climate change variables, and the response strength frequently varied with the underlying nutrient load of the system.

Conclusions: Our results suggest that trophic interactions commonly respond antagonistically to interacting climate change variables whereas synergistic and simple additive/multiplicative reactions are less common than previously thought. In addition, response type and magnitude are highly context dependent. These findings further suggest that in many cases, future ecosystem responses to climate change, whether positive or negative, may be dampened relative to predictions based on experiments that investigate the effects of single climate change variables on single species. However, there is a paucity of work that has focused on the effects of interacting climate change variables on dynamic biotic relationships, likely because such research requires complex experimentation. Increasing the complexity of climate change research is necessary for accurately predicting ecosystem responses.

Keywords: Carbon dioxide, Feeding, Food web, Global change, Log response ratio, Ozone, Photoperiod, Rainfall, Temperature, Ultraviolet radiation

Background

Climate change stands to alter ecosystem structure and function through numerous and diverse pathways. In addition to changing the fundamental abiotic qualities of ecosystems (e.g., temperature, water availability, CO_2 concentration), climate change is expected to alter the behavior and life history characteristics of organisms which could lead to dramatic changes in inter and intra-specific competition, predation, mutualisms, species distributions, biodiversity patterns, and the provisioning of ecosystem services [1-6]. Yet most studies have tended to examine climate effects on biotic components by focusing on single species while treating the larger community as background variation [7] and by typically focusing on a single climate change variable at a time [8-10]. Whether or not such approaches adequately capture how systems will respond to climate change remains uncertain.

We address this uncertainty by comparing the responses of interacting species subjected to the manipulation of a single climate change variable with their responses to simultaneous manipulations of multiple climate change variables. Specifically, we use a meta-analytic approach to

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synthesize existing literature, identify trends and patterns, and highlight areas that deserve immediate attention and other areas in which consensus may have already been reached [11]. Meta-analysis, as used in ecological research, is a statistical technique that combines data from independent studies to elucidate overall, net effect magnitudes of biotic or abiotic variables on a response of interest [12,13]. Meta-analysis has already been effective in providing synthetic insights into the interacting effects of multiple anthropogenic variables, or "stressors", like pollutants, invasive species, habitat fragmentation, and eutrophication on responses like species interactions within communities and ensuing ecosystem functioning [2,8,9,14-19]. But the effects of interacting climate change variables on these responses have yet to be the subject of synthesis. Meta-analysis is particularly suited for synthesizing results of climate change studies that cover many different species and habitat types because such studies frequently vary in sample size and statistical power, issues that are explicitly accounted for in meta-analysis. Furthermore, meta-analysis is useful in research on climate change as individual studies often produce conflicting results [13].

Our focus here is on the role of simultaneously (and rapidly) changing climate variables on trophic interactions, as these factors are among the major drivers of ecosystem structure and function [20]. Using established meta-analysis techniques, we determined the frequency of different interaction types (multiplicative, synergistic, antagonistic: see the "Effect size calculations" section) across different combinations of climate change variables and then elucidated the potential mechanisms underlying the interactions. We also investigated how the environmental context in which the variables were manipulated influenced the nature and strength of trophic interactions (i.e., examined context dependency) because many studies manipulated additional factors (e.g., nutrient levels, community composition) in addition to systematic manipulation of the common climate variables that are the focus of our analysis.

Our analysis was motivated by the broad, working hypothesis that non-linear (synergistic or antagonistic) interactions would largely result from combinations of climate change variables that operated through different pathways [10,14]. For example, in a plant-herbivorous insect trophic interaction, warmer temperatures may increase the insect's metabolism and an increase in atmospheric CO_2 may decrease the nutritional quality of the plant [21-23]. Thus, any simultaneous increases in levels of these two climate change variables stand to reinforce each other to increase the feeding rate of the insect, but through different pathways, and thereby result in a net synergistic trophic interaction.

Results

Database

Our literature search produced 2,122 candidate studies, of which 15.5% (n = 328) were experimental or modeling studies that examined the effects of at least one climate change variable on multi-trophic interactions. Only 2.2% (n = 47) of the studies examined the effects of multiple interacting climate change variables, with 1.9% (n = 41) using two interacting climate change variables and 0.3% (n = 6) using three interacting climate change variables. Of these 47 studies, 6 did not report all the necessary mean and variance data from the 4 required treatment groups and 7 did not report data for any response variables directly related to feeding interactions. Therefore, 34 of the studies from the original candidate pool met all of our criteria and were included in our analyses. In the terrestrial studies (n = 26), most of the feeding interactions examined were either between plants and herbivorous insects, or plants, herbivorous insects, and parasitoids, but two studies examined plant-microbial decomposer interactions. In the marine studies (n = 5), all the feeding interactions examined involved plants and herbivorous invertebrates. In the freshwater studies (n = 3), all of the feeding interactions examined were between phytoplankton and zooplankton. Additional details about each study, including study length and climate change variables manipulated, are provided in Table 1.

Collectively, the 34 studies reported 126 response variables related to feeding interactions, but 11 were excluded because they were redundant (see the "Methods" section). Of the remaining 115 response variables, 65% (n = 75) measured weights of individuals or the biomass of groups, 34% (n = 39) measured feeding rates or growth rates, and 1% (n = 1) measured the size of individuals. Across the 115 response variables, 6 unique combinations of climate change variables were tested: CO_2 × temperature (n = 38), CO_2 × O_3 (n = 33), temperature × rainfall (n = 18), temperature × photoperiod (n = 14), CO_2 × rainfall (n = 9), and temperature × ultraviolet radiation (UV; n = 3).

Effect sizes and interaction types

Only one of the summary effect sizes for the climate change variables tested in isolation (UV) and one of the climate variable interaction pairings (temperature × UV) were significantly positive or negative (Figure 1). The majority of response variables (55%; n = 63) displayed multiplicative reactions (the null hypothesis) to interacting climate change variables while 36% (n = 41) and 9% (n = 11) displayed antagonistic and synergistic reactions, respectively. For each of the six unique combinations of climate change variables, the proportions of multiplicative, synergistic, and antagonistic interactions varied

Table 1 Studies used in meta-analysis

Source	Habitat type	Length of study (days)	Number of trophic levels	Climate variables manipulated					
				Temp	CO_2	Rain	O_3	Photo	UV
[24]	Freshwater	50	Food web	X		X			
[25]	Freshwater	4	Food web	X					X
[26]	Freshwater	50	2	X					X
[27]	Marine	36	Food web	X	X				
[28]	Marine	35	2	X	X				
[29]	Marine	11	2	X	X				
[30]	Marine	14	2	X	X				
[31]	Marine	42	2	X		X			
[32]	Terrestrial	1461	3	X	X				
[33]	Terrestrial	120	3	X	X				
[34]	Terrestrial	70	2	X	X				
[35]	Terrestrial	42	2	X	X				
[36]	Terrestrial	56	2	X	X				
[37]	Terrestrial	63	2	X	X				
[38]	Terrestrial	100	2	X	X				
[39]	Terrestrial	100	2	X	X				
[40]	Terrestrial	6	2	X	X				
[41]	Terrestrial	15	Food web	X	X	X			
[42]	Terrestrial	692	Food web	X	X	X			
[43]	Terrestrial	35	2	X	X	X			
[44]	Terrestrial	1460	Food web		X	X			
[45]	Terrestrial	Unknown	2		X	X			
[46]	Terrestrial	46	2		X	X			
[47]	Terrestrial	60	3		X		X		
[48]	Terrestrial	78	3		X		X		
[49]	Terrestrial	62	2		X		X		
[50]	Terrestrial	45	2		X		X		
[51]	Terrestrial	55	2		X		X		
[52]	Terrestrial	45	2		X		X		
[53]	Terrestrial	21	2		X		X		
[54]	Terrestrial	7	2		X		X		
[55]	Terrestrial	1096	2		X		X		
[56]	Terrestrial	45	2		X		X		
[57]	Terrestrial	1	3	X				X	

"Food web" indicates that multiple species at each of two or more trophic levels were studied. "X" indicates that a climate variable was manipulated in the particular study. All studies are experimental except [33] which is a modeling study.
"Temp"= temperature, "Photo"= photoperiod, and "UV"= ultraviolet radiation.

widely (Figure 2). For example, for both the CO_2 × temperature and rain × temperature pairings, roughly 35% of the response variables showed antagonistic interactions, 60% showed multiplicative interactions, and 5% showed synergistic interactions. In contrast, for the CO_2 × O_3 pairing, 85% of the response variables were evenly divided between antagonistic and multiplicative interactions while synergistic interactions accounted for the remaining 15% (Figure 2).

Context dependence

We found that between 6% and 50% of interaction types changed across different contexts, with the lowest percentage of interaction type variation caused by community composition and the highest percentage of interaction type variation caused by sex (Table 2). Furthermore, we found that between 5% and 83% of interaction effect size magnitudes were significantly different across contexts,

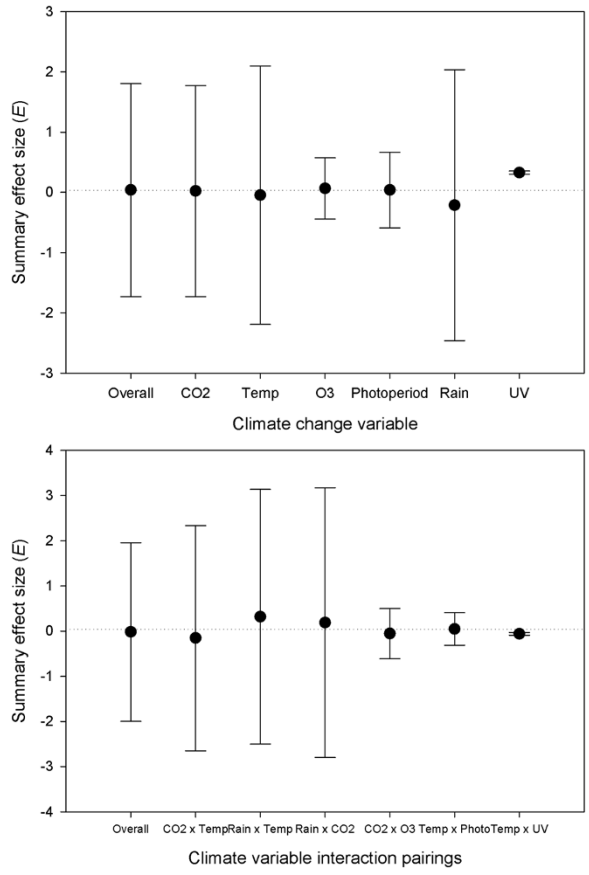

Figure 1 Summary effect sizes of individual climate change variables (top) and climate variable interaction pairings (bottom) on trophic relationships. Circles represent mean summary effect sizes, and lines represent 95% confidence intervals (CI). If 95% CIs overlap zero (dotted line), then the summary effect size is not significantly positive or negative. "Temp"= temperature, "Photo"= photoperiod, and "UV"= ultraviolet radiation.

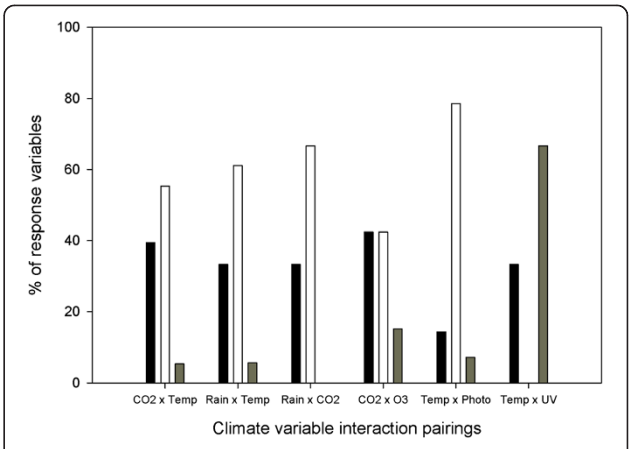

Figure 2 Percentage of different response variables across climate variable interaction pairings that fell into three interaction categories. Black bars= antagonistic, white bars= multiplicative, grey bars= synergistic. "Temp"= temperature, "Photo"= photoperiod, and "UV"= ultraviolet radiation.

with the lowest percentage of significant differences caused by species identity and the highest percentage of significant differences caused by nutrient levels (Table 2).

Publication bias

The possibility of publication bias in the literature we surveyed likely had no effect on our results. First, we found no significant correlation between effect size and study variance (τ = 0.099, Z = 1.57, p = 0.12). Second, Rosenthal's fail-safe number (1607.5) far exceeds the threshold value (585) produced by the equation $5n + 10$.

Discussion

This study reviewed the climate change literature to begin to offer synthetic understanding of the possible effects of multiple interacting climate change variables on trophic interactions. It is clear from the relatively small number of studies available (n = 47) and the even smaller number of studies that fit all of our meta-analytical criteria (n = 34) that further experimental research is needed on this topic. Despite the small number of studies, our analysis revealed a broad range of reactions to interacting climate change variables by trophic response variables that have thus far been widely overlooked.

Our analysis suggests that trophic relationships between organisms may frequently respond antagonistically to interacting climate change variables relative to single factor manipulations, whereas synergistic responses are rare. This result runs counter to assertions made in a modeling study that examined potential effects of interacting global change drivers on biodiversity patterns and hypothesized that the global change drivers would generally interact synergistically or not at all [15]. However, more recent meta-analytic studies that address the effects of multiple global change variables on species performances broadly agree with our results. For example, total aboveground plant biomass frequently responds antagonistically to CO_2 × temperature treatments relative to single factor manipulations [18], while animal mortality does not generally respond synergistically to interacting stressors [17]. A third study suggested that antagonisms and synergisms between global change drivers occur at roughly equal rates [9]. Importantly, all of these meta-analyses, including our own, examined different types of response variables yet came to roughly similar conclusions: antagonistic reactions to interacting global change drivers by organisms appear to be quite common while synergistic and simple additive/multiplicative reactions are less common than previously thought.

Another important conclusion of our meta-analysis is that reactions of trophic response variables to interacting climate change variables can be highly context dependent.

Table 2 Context dependence of trophic response variables examined across all 34 studies that manipulated multiple climate change variables

Context	Number of interaction pairs	Numbers that changed interaction type	% that changed interaction type	Numbers that changed interaction effect size magnitude	% that changed interaction effect size magnitude
Sex	14	7	50	5	36
Nutrient level	6	2	33	5	83
Genotype	15	5	33	8	53
Species identity	20	6	30	1	5
Climate variable combination	12	2	17	3	25
Community composition	17	1	6	3	18

For example, the interaction type (multiplicative, synergistic, antagonistic) was different between males and females 50% of the time and the interaction effect size magnitude was different between varying nutrient levels 83% of the time. Thus, increasing the number of global change drivers examined in a factorial study may alter the interaction outcome and/or the interaction effect size magnitude [58], and demographic and community composition factors, if not properly controlled for, could have additional effects. It has even been suggested that higher order interactions of global change drivers produce smaller magnitude responses which, if generally true, would mean that anticipated positive and negative impacts of global change might be dampened relative to current predictions based on single factor studies [58].

Some of the climate change variable pairings frequently produced unexpected emergent interaction types, suggesting that each climate variable exerts effects on trophic relationships through multiple pathways. As an example, consider the effects of the CO_2 × temperature interaction on a typical plant-herbivorous insect feeding relationship, which was the most commonly examined trophic relationship across the studies we analyzed. Plant quality from the perspective of herbivorous insects is generally determined by the nutrient profile of the plant (particularly the C:N ratio for nitrogen limited insects [59,60]), any defensive chemical compounds produced by the plant (e.g., phenolics and terpenes), and the physical traits of plant tissues (e.g., leaf toughness and thickness [22]). In general, plants raised in environments with high concentrations of CO_2 exhibit high C:N ratios, increased production of phenolics, and increased leaf toughness and thickness [21,22]. These relatively low-quality plants force insects to increase their feeding rates to compensate for the decreased food quality [61]. Increases in atmospheric CO_2 have few direct effects on insects [62], except in a few special cases such as hematophagous insects and phytophagous insect larvae that use CO_2 gradients to locate feeding opportunities [63]. In contrast, increased temperatures do not generally affect plant C:N ratios or physical traits but they can increase terpene production and can either cause increases or decreases in plant phenolics [22]. Insects exposed to increased temperatures generally exhibit increased metabolism and respiration [64], resulting in increased feeding, development, and reproduction rates [62].

On the basis of the individual effects of CO_2 and temperature on plant quality and insect metabolism discussed above, we would logically expect the interactive effects of CO_2 and temperature to promote synergistic and multiplicative responses in plant-herbivorous insect trophic interactions. However, our meta-analysis revealed more antagonistic reactions (n = 12) than synergistic and multiplicative reactions combined (n = 11). There are many potential explanations for this disparity. First, the inclusion of an additional trophic level, (i.e., a predator of the herbivorous insect) could alter the plant-herbivorous insect trophic relationship (e.g., [32]) by changing the timing and extent of feeding or the development rate of the herbivorous insect. Second, all the parts of a plant may not respond to climate change variables on the same time scales and mobile herbivorous insects could therefore seek out and continue to consume plant tissues with high nutrient value (e.g., [35]). Third, many plant and herbivorous insect species may physiologically respond differently to identical climate manipulations (e.g., [40,65]), and therefore, changes in trophic relationships may not be consistent across all scenarios. Lastly, if experiments testing the effects of interacting climate change variables on trophic relationships are not long enough, they may miss important interactions that only emerge over long time periods [40].

It is noteworthy that not all studies of the effects of climate change on ecological interactions may need to consider the interactive effects of all climate change variables. Though most climate change variables likely interact at least indirectly, the effects of some of these interactions on ecological relationships may be negligible. Indeed, one of the possible reasons for why we found so few studies that fit our meta-analysis criteria is that researchers may exclude some climate change variables from their experiments if they are fairly certain the variables will have little

impact on their results. However, given the frequent discoveries of "ecological surprises" in ecological climate change research (e.g., [24]), we encourage researchers to continue to test for the potential unexpected interactions between climate change variables rather than dismiss candidate variables under the presumption that they will not have an effect.

Our results lead us to agree with other recent meta-analyses and reviews: to understand and predict the effects of climate change and other anthropogenic forms of global change on ecosystem structure, function, and services, the complexity of experimental and modeling studies must increase to more closely reflect natural conditions [10,66]. The experimental challenge will be to account for a diverse array of factors [7], including the two we have highlighted in our meta-analysis: the interactions between climate change variables and the direct and indirect interactions that permeate food webs [1,2,67]. Also, future studies should 1) run longer to better understand the evolutionary and demographic stability of altered trophic interactions over multiple generations [23,68], 2) examine food webs in different kinds of ecosystems (the large majority to date have been terrestrial), 3) examine trophic relationships across more than simple two- and three-level linear interactions and beyond plant-insect feeding scenarios, 4) focus on more climate change variable pairings beyond CO_2 × temperature and CO_2 × O_3 (by far the most studied variable pairings to date), and 5) examine the role of body size and movement capabilities in determining the response of trophic relationships to interacting climate change variables. These recommended amendments to current experimental practices will help to increase realism by accounting for the inherent complexity of natural trophic interactions and thereby bring us closer to more accurate predictions of the consequences of climate change on ecosystem structure and function.

Conclusions

Despite the relatively small amount of research that has examined the effects of interacting climate change variables on trophic interactions, our meta-analysis of this literature revealed some striking patterns. First, trophic interactions frequently respond multiplicatively and antagonistically to interacting climate change variables, while synergistic responses are relatively rare. Second, both response type and magnitude are highly context dependent, indicating that unanticipated emergent effects of climate change on ecosystems are likely to occur. There is a paucity of work that has focused on the effects of interacting climate change variables on dynamic biotic relationships, likely because such research requires complex experimentation and in-depth understanding of many species' physiology, behavior, and life history. Nevertheless, increasing the complexity of climate change research is necessary for accurately predicting ecosystem responses and informing future conservation and management strategies.

Methods

Database development

We used Web of Science to search the literature for factorial experimental or modeling studies that investigated the individual and interactive effects of at least two climate change variables on the feeding interactions between species at different trophic levels. We chose to focus on six climate change variables that are most frequently included in experiments: temperature, precipitation, CO_2, O_3, photoperiod, and ultraviolet radiation. We used the search terms "food web", predator* or predation, prey or herbivore*, herbivore* and plant*, parasite* and host* in combination with "climate change", "climatic change", "global warming", "global change", and "global environmental change". We supplemented our database by searching through the literature-cited sections of key review papers and meta-analyses as well as publications from research sites that employ free-air carbon dioxide enrichment [21].

We chose to focus on response variables that are directly related to trophic interactions, such as feeding rate, weight gain, and population biomass at a specific trophic level. Some studies reported data from multiple response variables, and we excluded those that were redundant. For example, if a study reported both final herbivore weight and feeding rate from one experimental setup, then we only included feeding rate in our analyses because it is a more direct measure of trophic interactions. When studies reported response variables at multiple time points, we used the data from the final time point.

Studies were included in our analyses if they contained mean and variance data across all four treatment types: control, manipulation of variable A alone, manipulation of variable B alone, and manipulation of variables A and B together. Also, studies had to simultaneously expose species in the different trophic levels to both experimental climate manipulations (e.g., temperature and precipitation). Some of the studies we encountered exposed plants to one climate manipulation and then fed parts of those plants to herbivores exposed to a different climate manipulation. Such studies were excluded from our analyses. Lastly, a small number of studies manipulated three climate change variables within one experimental design. For these studies, we included the response variables from each unique climate variable pairing. Data were mined from graphs presented in each published study using the program Plot Digitizer (version 2.6.3; http://plotdigitizer.sourceforge.net) and, in some cases, data were provided by the authors of the studies.

Effect size calculations

We calculated main and interaction effect sizes for each study using methods for factorial meta-analysis [19,69,70]. We chose the log response ratio over other metrics, such as Hedge's *d* [71], because of 1) its ability to detect true effects [72], 2) its ability to remain more normally distributed even with small sample sizes [69], 3) its linear nature [69], and 4) its more explicit ties to ecological dynamics [73].

Following [19], main and interaction effect sizes based on a multiplicative model were calculated as

$$L_{\mathrm{a}} = \ln\left(\frac{\bar{y}_{\mathrm{a}}}{\bar{y}_{\mathrm{con}}}\right)$$

$$L_{\mathrm{b}} = \ln\left(\frac{\bar{y}_{\mathrm{b}}}{\bar{y}_{\mathrm{con}}}\right)$$

$$L_{\mathrm{ab}} = \ln\left(\frac{\bar{y}_{\mathrm{ab}}}{\bar{y}_{\mathrm{b}}}\right) - \ln\left(\frac{\bar{y}_{\mathrm{a}}}{\bar{y}_{\mathrm{con}}}\right)$$

where L_x is the log response ratio for the indicated response variable (in subscript) and $\bar{y}_x$ is the mean value for the indicated response variable (in subscript). Individual estimates of variance were calculated as

$$v_{\mathrm{a}} = s_{\mathrm{a,pooled}}\left(\frac{1}{n_{\mathrm{con}}(\bar{y}_{\mathrm{con}})^2} + \frac{1}{n_{\mathrm{a}}(\bar{y}_{\mathrm{a}})^2}\right)$$

$$v_{\mathrm{b}} = s_{\mathrm{b,pooled}}\left(\frac{1}{n_{\mathrm{con}}(\bar{y}_{\mathrm{con}})^2} + \frac{1}{n_{\mathrm{b}}(\bar{y}_{\mathrm{b}})^2}\right)$$

$$v_{\mathrm{ab}} = s_{\mathrm{ab,pooled}}\left(\frac{1}{n_{\mathrm{con}}(\bar{y}_{\mathrm{con}})^2} + \frac{1}{n_{\mathrm{a}}(\bar{y}_{\mathrm{a}})^2} + \frac{1}{n_{\mathrm{b}}(\bar{y}_{\mathrm{b}})^2} + \frac{1}{n_{\mathrm{ab}}(\bar{y}_{\mathrm{ab}})^2}\right)$$

where $s_{x,\mathrm{pooled}}$ is the pooled standard deviation for the indicated response variable (in subscript) and n_x is the sample size for the indicated response variable (in subscript). The pooled standard deviation was calculated as

$$s_{\mathrm{a,pooled}} = \sqrt{\frac{(n_{\mathrm{con}}-1)(s_{\mathrm{con}})^2 + (n_{\mathrm{a}}-1)(s_{\mathrm{a}})^2}{n_{\mathrm{con}} + n_{\mathrm{a}} - 2}}$$

$$s_{\mathrm{b,pooled}} = \sqrt{\frac{(n_{\mathrm{con}}-1)(s_{\mathrm{con}})^2 + (n_{\mathrm{b}}-1)(s_{\mathrm{b}})^2}{n_{\mathrm{con}} + n_{\mathrm{b}} - 2}}$$

$$s_{\mathrm{ab,pooled}} = \sqrt{\frac{\begin{array}{l}(n_{\mathrm{con}}-1)(s_{\mathrm{con}})^2 + (n_{\mathrm{a}}-1)(s_{\mathrm{a}})^2 \\ +(n_{\mathrm{b}}-1)(s_{\mathrm{b}})^2 + (n_{\mathrm{ab}}-1)(s_{\mathrm{ab}})^2\end{array}}{n_{\mathrm{con}} + n_{\mathrm{a}} + n_{\mathrm{b}} + n_{\mathrm{ab}} - 4}}$$

where s_x is the standard deviation of the mean for the indicated response variable (in subscript). We then calculated 95% confidence intervals (CI) around each L_x value using the equation

$$L_x \pm 1.96 * \sqrt{v_x}$$

where v_x is the variance estimate for variable A, variable B, or variables A and B together. Following [11], weighted summary effect sizes (E) were calculated for k response variables as

$$E = \frac{\sum_{i=1}^{i=k}\left(\frac{1}{v_i}\right) * e_i}{\sum_{i=1}^{i=k}\left(\frac{1}{v_i}\right)}$$

where v_i is the variance estimate and e_i is the log response ratio for each response variable. Significant weighted summary effect sizes were those that had 95% CIs that did not contain zero, and E values were calculated for each climate change variable tested in isolation as well as all variables pooled together.

We based our analyses of multiple interacting climate change variables on an underlying multiplicative model, as opposed to a more conservative additive model [74], because multiplicative models are more ecologically realistic representations of interacting effects [75] and the log response ratio itself is based on a multiplicative model [76]. Interaction effects were classified as multiplicative (the null hypothesis) if the 95% CI around the interaction effect size (L_{ab}) contained zero. If both variable A and B effect sizes (L_{a} and L_{b}) were positive, the interaction effect was classified as synergistic when the L_{ab} 95% CI was greater than zero and antagonistic when less than zero. If both L_{a} and L_{b} were negative or one was negative and one positive, then the classifications were reversed [19]. Following [74], multiplicative interactions in the multiplicative model are defined as instances where the effect size of the interaction between variables A and B is equal to the product of the effect sizes of variables A and B alone. Synergistic interactions are those in which the effect size of the interaction between variables A and B is greater than the product of the effect sizes of variables A and B alone, and antagonistic interactions are those in which the effect size of the interaction between variables A and B is less than the product of the effect sizes of variables A and B alone.

Context dependence

Cumulatively, the studies included in our meta-analysis explicitly or implicitly tested six different kinds of context dependence: nutrient level, sex, species identity, community composition, genotype, and combinations of climate change variables. We examined each of the six independently to determine if interaction type or interaction effect size magnitude (L_{ab} ± 95% CI) were context dependent. For example, interaction type might be different for males and females (e.g., antagonistic for one and synergistic for the other) because of behavioral or physiological differences

between the sexes, and interaction effect size magnitude would be significantly different between sexes for a particular study if the L_{ab} ± 95% CI ranges for males and females did not overlap.

Publication bias

The strength of any given meta-analysis can be affected by publication bias, defined as the preferential publication of studies reporting certain kinds of results over those reporting other types of results [77]. This can lead to overestimation of the quantity of significant results reported from a given field of study. To investigate the likelihood of publication bias affecting the results of our own meta-analysis we employed two techniques: Kendall's tau and the fail-safe number. We used Kendall's tau to assess the correlation between effect sizes and variance from each study, with a significant correlation suggesting a high probability of publication bias [78]. We used Rosenthal's fail-safe number to estimate the number of hypothetical additional studies reporting non-significant results needed to reduce the effect size to non-significance [79]. If the fail-safe number exceeds $5n + 10$ (n = the number of studies used in the meta-analysis), then, we can assume that publication bias likely did not affect our results [79]. We used MetaWin 2.0 (www.metawinsoft.com) to carry out these analyses.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

AER conceived of the study, developed the literature database, performed the meta-analysis, and drafted the manuscript. OJS assisted with the design and execution of the meta-analysis and helped to draft the manuscript. Both authors read and approved the final manuscript.

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References

1. Schmitz O, Post E, Burns CE, Johnston KM: **Ecosystem responses to global climate change: moving beyond color mapping.** *Bioscience* 2003, **53:**1199–1205.
2. Tylianakis J, Didham RK, Bascompte J, Wardle DA: **Global change and species interactions in terrestrial ecosystems.** *Ecol Lett* 2008, **11:**1351–1363.
3. Gilman S, Urban MC, Tewksbury J, Gilchrist GW, Holt RD: **A framework for community interactions under climate change.** *Trends Ecol Evol* 2010, **25:**325–331.
4. Traill L, Lim MLM, Sodhi NS, Bradshaw CJA: **Mechanisms driving change: altered species interactions and ecosystem function through global warming.** *J Anim Ecol* 2010, **79:**937–947.
5. van der Putten W, Macel M, Visser ME: **Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels.** *Philos Trans Roy Soc B* 2010, **365:**2025–2034.
6. Post E: *Ecology of Climate Change: the Importance of Biotic Interactions.* Princeton: Princeton University Press; 2013.
7. Jamieson M, Trowbridge AM, Raffa KF, Lindroth RL: **Consequences of climate warming and altered precipitation patterns for plant-insect and multitrophic interactions.** *Plant Physiol* 2012, **160:**1719–1727.
8. Harrington R, Woiwod I, Sparks T: **Climate change and trophic interactions.** *Trends Ecol Evol* 1999, **14:**146–150.
9. Crain C, Kroeker K, Halpern BS: **Interactive and cumulative effects of multiple human stressors in marine systems.** *Ecol Lett* 2008, **11:**1304–1315.
10. Todgham AE, Stillman JH: **Physiological response to shifts in multiple environmental stressors: relevance in a changing world.** *Integr Comp Biol* 2013, **53:**539–544.
11. Hillebrand H: **Meta-analysis in ecology.** In *Encyclopedia of Life Sciences.* Chichester: John Wiley & Sons; 2008. doi:10.1002/9780470015902.a9780470003272.
12. Gurevitch J, Hedges LV: **Statistical issues in ecological meta-analyses.** *Ecology* 1999, **80:**1142–1149.
13. Arnqvist G, Wooster D: **Meta-analysis: synthesizing research findings in ecology and evolution.** *Trends Ecol Evol* 1995, **10:**236–240.
14. Breitburg D, Baxter JW, Hatfield CA, Howarth RW, Jones CG, Lovett GM, Wigand C: **Understanding effects of multiple stressors: ideas and challenges.** In *Successes, Limitations, and Frontiers in Ecosystem Science.* Edited by Pace M, Groffman PM. New York: Springer-Verlag; 1998:416–431.
15. Sala O, Chapin FS III, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH: **Global biodiversity scenarios for the year 2100.** *Science* 2000, **287:**1770–1774.
16. Norby R, Luo Y: **Evaluating ecosystem responses to rising atmospheric CO_2 and global warming in a multi-factor world.** *New Phytol* 2004, **162:**281–293.
17. Darling E, Cote IM: **Quantifying the evidence for ecological synergies.** *Ecol Lett* 2008, **11:**1278–1286.
18. Dieleman W, Vicca S, Dijkstra FA, Hagedorn F, Hovenden MJ, Larsen KS, Morgan JA, Volder A, Beier C, Dukes JS, King J, Leuzinger S, Linder S, Luo Y, Oren R, de Angelis P, Tingey D, Hoosbeek MR, Janssens IA: **Simple additive effects are rare: a quantitative review of plant biomass and soil process responses to combined manipulations of CO_2 and temperature.** *Global Change Biol* 2012, **18:**2681–2693.
19. Harvey B, Gwynn-Jones D, Moore PJ: **Meta-analysis reveals complex marine biological responses to the interactive effects of ocean acidification and warming.** *Ecol Evol* 2013, **3:**1016–1030.
20. Altieri A, Bertness MD, Coverdale TC, Herrmann NC, Angelini C: **A trophic cascade triggers collapse of a salt-marsh ecosystem with intensive recreational fishing.** *Ecology* 2012, **93:**1402–1410.
21. Ainsworth E, Long SP: **What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2.** *New Phytol* 2005, **165:**351–372.
22. Zvereva E, Kozlov MV: **Consequences of simultaneous elevation of carbon dioxide and temperature for plant–herbivore interactions: a metaanalysis.** *Global Change Biol* 2006, **12:**27–41.
23. DeLucia E, Nabity PD, Zavala JA, Berenbaum MR: **Climate change: resetting plant-insect interactions.** *Plant Physiol* 2012, **160:**1677–1685.
24. Christensen M, Graham MD, Vinebrooke RD, Findlay DL, Paterson MJ, Turner MA: **Multiple anthropogenic stressors cause ecological surprises in boreal lakes.** *Global Change Biol* 2006, **12:**2316–2322.
25. Bouvy M, Bettarel Y, Bouvier C, Domaizon I, Jacquet S, Le Floc'h E, Montanié H, Mostajir B, Sime-Ngando T, Torréton JP, Vidussi F, Bouvier T: **Trophic interactions between viruses, bacteria and nanoflagellates under various nutrient conditions and simulated climate change.** *Environ Microbiol* 2011, **13:**1842–1857.
26. Lewandowska A, Sommer U: **Climate change and the spring bloom: a mesocosm study on the influence of light and temperature on**

phytoplankton and mesozooplankton. *Mar Ecol Prog Ser* 2010, **405:**101–111.
27. Eklof J, Alsterberg C, Havenhand JN, Sundback K, Wood HL, Gamfeldt L: **Experimental climate change weakens the insurance effect of biodiversity.** *Ecol Lett* 2012, **15:**864–872.
28. Alsterberg C, Eklof JS, Gamfeldt L, Havenhand JN, Sundback K: **Consumers mediate the effects of experimental ocean acidification and warming on primary producers.** *Proc Natl Acad Sci* 2013, **110:**8603–8608.
29. Burnell O, Russell BD, Irving AD, Connell SD: **Eutrophication offsets increased sea urchin grazing on seagrass caused by ocean warming and acidification.** *Mar Ecol Prog Ser* 2013, **485:**37–46.
30. Poore A, Graba-Landry A, Favret M, Brennand HS, Byrne M, Dworjanyn SA: **Direct and indirect effects of ocean acidification and warming on a marine plant–herbivore interaction.** *Oecologia* 2013, **173:**1113–1124.
31. Blake R, Duffy JE: **Grazer diversity affects resistance to multiple stressors in an experimental seagrass ecosystem.** *Oikos* 2010, **119:**1625–1635.
32. Dyer L, Richards LA, Short SA, Dodson CD: **Effects of CO_2 and temperature on tritrophic interactions.** *PLoS One* 2013, **8:**e62528.
33. Hoover J, Newman JA: **Tritrophic interactions in the context of climate change: a model of grasses, cereal aphids and their parasitoids.** *Global Change Biol* 2004, **10:**1197–1208.
34. Johns C, Hughes L: **Interactive effects of elevated CO_2 and temperature on the leaf-miner *Dialectica scalariella* Zeller (Lepidoptera: Gracillariidae) in Paterson's curse, *Echium plantagineum* (Boraginaceae).** *Global Change Biol* 2002, **8:**142–152.
35. Johns C, Beaumont LJ, Hughes L: **Effects of elevated CO_2 and temperature on development and consumption rates of *Octotoma championi* and *O. scabripennis* feeding on *Lantana camara*.** *Entomol Exp Appl* 2003, **108:**169–178.
36. Williams R, Lincoln DE, Norby RJ: **Development of gypsy moth larvae feeding on red maple saplings at elevated CO_2 and temperature.** *Oecologia* 2003, **137:**114–122.
37. Flynn D, Sudderth EA, Bazzaz FA: **Effects of aphid herbivory on biomass and leaf-level physiology of *Solanum dulcamara* under elevated temperature and CO_2.** *Environ Exp Bot* 2006, **56:**10–18.
38. Murray T, Ellsworth DS, Tissue DT, Riegler M: **Interactive direct and plant-mediated effects of elevated atmospheric [CO_2] and temperature on a eucalypt-feeding insect herbivore.** *Global Change Biol* 2013, **19:**1407–1416.
39. Murray T, Tissue DT, Ellsworth DS, Riegler M: **Interactive effects of pre-industrial, current and future [CO_2] and temperature on an insect herbivore of *Eucalyptus*.** *Oecologia* 2013, **171:**1025–1035.
40. Williams R, Norby RJ, Lincoln DE: **Effects of elevated CO_2 and temperature-grown red and sugar maple on gypsy moth performance.** *Global Change Biol* 2000, **6:**685–695.
41. Stevnbak K, Scherber C, Gladbach DJ, Beier C, Mikkelsen TN, Christensen S: **Interactions between above- and belowground organisms modified in climate change experiments.** *Nat Clim Change* 2012, **2:**805–808.
42. Andresen L, Konestabo HS, Maraldo K, Holmstrup M, Ambus P, Beier C, Michelsen A: **Organic matter flow in the food web at a temperate heath under multifactorial climate change.** *Rapid Commun Mass Spectrom* 2011, **25:**1485–1496.
43. Scherber C, Gladbach DJ, Stevnbak K, Karsten RJ, Schmidt IK, Michelsen A, Albert KR, Larsen KS, Mikkelsen TN, Beier C, Christensen S: **Multi-factor climate change effects on insect herbivore performance.** *Ecol Evol* 2013, **3:**1449–1460.
44. Eisenhauer N, Cesarz S, Koller R, Worm K, Reich PB: **Global change belowground: impacts of elevated CO_2, nitrogen, and summer drought on soil food webs and biodiversity.** *Global Change Biol* 2012, **18:**435–447.
45. Roth S, McDonald EP, Lindroth RL: **Atmospheric CO_2 and soil water availability: consequences for tree-insect interactions.** *Can J Forest Res* 1997, **27:**1281–1290.
46. Zhang J, Xing G, Liao J, Hou Z, Wang G, Wang Y: **Effects of different atmospheric CO_2 concentrations and soil moistures on the populations of bird cherry-oat aphid (*Rhopalosiphum padi*) feeding on spring wheat.** *Eur J Entomol* 2003, **100:**521–530.
47. Holton M, Lindroth RL, Nordheim EV: **Foliar quality influences tree-herbivore-parasitoid interactions: effects of elevated CO_2, O_3, and plant genotype.** *Oecologia* 2003, **137:**233–244.
48. Awmack C, Harrington R, Lindroth RL: **Aphid individual performance may not predict population responses to elevated CO_2 or O_3.** *Global Change Biol* 2004, **10:**1414–1423.
49. Dermody O, O'Neill BF, Zangerl AR, Berenbaum MR, DeLucia EH: **Effects of elevated CO_2 and O_3 on leaf damage and insect abundance in a soybean agroecosystem.** *Arthropod-Plant Interact* 2008, **2:**125–135.
50. Kopper B, Lindroth RL: **Effects of elevated carbon dioxide and ozone on the phytochemistry of aspen and performance of an herbivore.** *Oecologia* 2003, **134:**95–103.
51. Kopper B, Lindroth RL: **Responses of trembling aspen (*Populus tremuloides*) phytochemistry and aspen blotch leafminer (*Phyllonorycter tremuloidiella*) performance to elevated levels of atmospheric CO_2 and O_3.** *Agric For Entomol* 2003, **5:**17–26.
52. Kopper B, Lindroth RL, Nordheim EV: **CO_2 and O_3 effects on paper birch (Betulaceae: *Betula papyrifera*) phytochemistry and whitemarked tussock moth (Lymantriidae: *Orgyia leucostigma*) performance.** *Environ Entomol* 2001, **30:**1119–1126.
53. Mondor E, Tremblay MN, Awmack CS, Lindroth RL: **Altered genotypic and phenotypic frequencies of aphid populations under enriched CO_2 and O_3 atmospheres.** *Global Change Biol* 2005, **11:**1990–1996.
54. Mondor E, Awmack CS, Lindroth RL: **Individual growth rates do not predict aphid population densities under altered atmospheric conditions.** *Agric For Entomol* 2010, **12:**293–299.
55. Percy K, Awmack CS, Lindroth RL, Kubiske ME, Kopper BJ, Isebrands JG, Pregitzer KS, Hendrey GR, Dickson RE, Zak DR, Oksanen E, Sober J, Harrington R, Karnosky DF: **Altered performance of forest pests under atmospheres enriched by CO_2 and O_3.** *Nature* 2002, **420:**403–407.
56. Vigue L, Lindroth RL: **Effects of genotype, elevated CO_2 and elevated O_3 on aspen phytochemistry and aspen leaf beetle *Chrysomela crotchi* performance.** *Agric For Entomol* 2010, **12:**267–276.
57. Perdikis D, Lykouressis DP, Economou LP: **The influence of temperature, photoperiod and plant type on the predation rate of *Macrolophus pygmaeus* on *Myzus persicae*.** *Bio Control* 1999, **44:**281–289.
58. Leuzinger S, Luo Y, Beier C, Dieleman W, Vicca S, Korner C: **Do global change experiments overestimate impacts on terrestrial ecosystems?** *Trends Ecol Evol* 2011, **26:**236–241.
59. Mattson W: **Herbivory in relation to plant nitrogen content.** *Annu Rev Ecol Syst* 1980, **11:**119–161.
60. Fajer E: **The effects of enriched CO_2 atmospheres on plant-insect herbivore interactions: growth responses of larvae of the specialist butterfly, *Junonia coenia* (Lepidoptera: Nymphalidae).** *Oecologia* 1989, **81:**514–520.
61. Lincoln D, Fajer ED, Johnson RH: **Plant-insect herbivore interactions in elevated CO_2 environments.** *Trends Ecol Evol* 1993, **8:**64–68.
62. Bale J, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, Brown VK, Butterfield J, Buse A, Coulson JC, Farrar J, Good JEG, Harrington R, Hartley S, Jones TH, Lindroth RL, Press MC, Symrnioudis I, Watt AD, Whittaker JB: **Herbivory in global climate change research: direct effects of rising temperature on insect herbivores.** *Global Change Biol* 2002, **8:**1–16.
63. Nicolas G, Sillans D: **Immediate and latent effects of carbon dioxide on insects.** *Annu Rev Entomol* 1989, **34:**97–116.
64. Neven L: **Physiological responses of insects to heat.** *Postharvest Biol Technol* 2000, **21:**103–111.
65. Lindroth R: **Impacts of elevated atmospheric CO_2 and O_3 on forests: phytochemistry, trophic interactions, and ecosystem dynamics.** *J Chem Ecol* 2010, **36:**2–21.
66. Robinson E, Ryan GD, Newman JA: **A meta-analytical review of the effects of elevated CO_2 on plant–arthropod interactions highlights the importance of interacting environmental and biological variables.** *New Phytologist* 2012, **194:**321–336.
67. Janssens L, Van KD, Debecker S, Bervoets L, Stoks R: **Local adaptation and the potential effects of contaminant on predator avoidance and antipredator responses under global warming: a space-for-time substitution approach.** *Evol Appl* 2014, doi:10.1111/eva.12141.
68. Suttle K, Thomsen MA, Power ME: **Species interactions reverse grassland responses to changing climate.** *Science* 2007, **315:**640–642.
69. Hedges L, Gurevitch J, Curtis PS: **The meta-analysis of response ratios in experimental ecology.** *Ecology* 1999, **80:**1150–1156.
70. Hawkes C, Sullivan JJ: **The impact of herbivory on plants in different resource conditions: a meta-analysis.** *Ecology* 2001, **82:**2045–2058.
71. Gurevitch J, Morrison JA, Hedges LV: **The interaction between competition and predation: a meta-analysis of field experiments.** *Am Nat* 2000, **155:**435–453.
72. Lajeunesse M, Forbes MR: **Variable reporting and quantitative reviews: a comparison of three meta-analytical techniques.** *Ecol Lett* 2003, **6:**448–454.

73. Osenberg C, Sarnelle O, Cooper SD: **Effect size in ecological experiments: the application of biological models in meta-analysis.** *Am Nat* 1997, **150:**798–812.
74. Folt C, Chen CY, Moore MV, Burnaford J: **Synergism and antagonism among multiple stressors.** *Limnol Oceanogr* 1999, **44:**864–877.
75. Sih A, Englund G, Wooster D: **Emergent impacts of multiple predators on prey.** *Trends Ecol Evol* 1998, **13:**350–355.
76. Morris W, Hufbauer RA, Agrawal AA, Bever JD, Borowicz VA, Gilbert GS, Maron JL, Mitchell CE, Parker IM, Power AG, Torchin ME, Vazquez DP: **Direct and interactive effects of enemies and mutualists on plant performance: a meta-analysis.** *Ecology* 2007, **88:**1021–1029.
77. Begg C: **Publication bias.** In *The Handbook of Research Synthesis.* Edited by Cooper H, Hedges LV. New York: Russell Sage Foundation; 1994:399–409.
78. Begg C, Mazumdar M: **Operating characteristics of a rank correlation test for publication bias.** *Biometrics* 1994, **50:**1088–1101.
79. Rosenthal R: **The "file drawer problem" and tolerance for null results.** *Psychol Bull* 1979, **86:**638–641.

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