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# Uneven global distribution of food web studies under climate change

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**Abstract.** Trophic interactions within food webs affect species distributions, coexistence, and provision of ecosystem services but can be strongly impacted by climatic changes. Understanding these impacts is therefore essential for managing ecosystems and sustaining human well-being. Here, we conducted a global synthesis of terrestrial, marine, and freshwater studies to identify key gaps in our knowledge of climate change impacts on food webs and determine whether the areas currently studied are those most likely to be impacted by climate change. We found research suffers from a strong geographic bias, with only 3.5% of studies occurring in the tropics. Importantly, the distribution of sites sampled under projected climate changes was biased—areas with decreases or large increases in precipitation and areas with low magnitudes of temperature change were under-represented. Our results suggest that understanding of climate change impacts on food webs could be broadened by considering more than two trophic levels, responses in addition to species abundance and biomass, impacts of a wider suite of climatic variables, and tropical ecosystems. Most importantly, to enable better forecasts of biodiversity responses to climate change, we identify critically under-represented geographic regions and climatic conditions which should be prioritized in future research.

**Key words:** aquatic; climate change; data gaps; extreme events; food webs; freshwater; global; marine; precipitation; species interactions; terrestrial; warming.

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## Introduction

Trophic interactions within food webs are important regulators of biodiversity and ecosystem function in marine, freshwater, and terrestrial ecosystems. Across ecosystems, food webs are structured by similar mechanisms that are driven by the availability of resources (bottom up) such as nutrients, energy, and water and/or by consumers (top down) such as herbivores and top predators (White 1978, McQueen et al. 1986). However, geographic variation in environmental conditions leads to trophic interactions and food webs that can differ fundamentally through space (Chamberlain et al. 2014) and evolutionary constraints have generated substantial differences in trophic interactions among biomes. For instance, in contrast to terrestrial habitats, in aquatic habitats the patterns in allocation in autotrophs and the community size structure lead to larger impacts of consumption on primary producers and larger indirect effects of predators (Shurin et al. 2006). Trophic interactions can also vary geographically (e.g., latitudinal gradients in the intensity of predation, Roslin et al. 2017). This variability in the nature and complexity of interactions within food webs, both among systems and through space, makes understanding how environmental changes such as climate change restructure communities and ecosystems challenging.

Climate change is not occurring evenly across the globe, and some regions such as the Arctic are experiencing, or are projected to experience, particularly large shifts in temperature and precipitation (IPCC 2014). Organisms also vary in their vulnerability to climate change. Species that have different ecological tolerances for abiotic factors, such as temperatures or pH, may shift their distributions or activities based on different cues under climate change (Tylianakis et al. 2008, Walther 2010). In turn, these impacts can affect food web structure. Trophic interactions are sensitive to the phenology, behavior, and physiology of multiple species, which will likely each simultaneously be impacted directly (and differentially) by climate change, in addition to being impacted by indirect effects that cascade through food webs. For example, lower trophic levels show greater phenological sensitivity to climate change (e.g., freshwater phytoplankton is especially sensitive) than secondary consumers, which may lead to mismatches between predators and prey (Thackeray et al. 2016). Climate change is not resulting in similar environmental changes across biomes, and communities that are adapted to different environmental conditions may respond differently even to the same climate change driver; for example, experimental warming appears to strengthen top-down control in food webs in colder regions, but weakens it in warmer regions (Marino et al. 2018). Therefore, it is essential that we understand how climate change effects vary geographically due to variation in underlying environmental and historical contexts (Chamberlain et al. 2014).

To improve predictions of community and ecosystem structure in the future, there is an urgent need for observations and experiments to be conducted that examine trophic interactions under climate change (Alexander et al. 2016). A balanced global picture of trophic interactions depends upon a reasonably spatially representative sampling of food webs across different regions, habitats, and climatic conditions. However, little information exists about the sampling representativeness of ecological studies in general, and studies on food webs in particular, across major geographic/climatic zones, though the few available studies indicate that sampling is generally extremely spatially patchy (Martin et al. 2012, Sotomayor and Lortie 2015, Bellard and Jeschke 2016). Here, we review where experimental and observational studies on climate change and food webs have already been conducted to highlight geographic regions and aspects that are most in need of attention. Specifically, we conducted a global synthesis of research on climate change effects on food webs in terrestrial, freshwater, and marine ecosystems to identify those which are under or overrepresented in current studies. To place this analysis in the context of ongoing climate change, we further examined spatial biases in the distribution of studies in relation to key aspects of current and projected future climate change.

## Methods

We synthesized the current research on climate change and trophic interactions within food webs by conducting a review using the keywords "climate change AND food web*." We focused on the term "food web" in order to capture studies where the authors examined multiple trophic levels of interactions in particular. We searched ISI Web of Science for articles published prior to 1 January 2017, which returned 2375 records. We filtered these articles to include only those that met the following criteria: (1) examined at least two trophic levels, with one or more taxonomic/functional groups at each level; (2) investigated the effects of climate change on abundance, biomass, diversity, and/or food web structure (e.g., number of links, connectance, nestedness, modularity); (3) included empirical data (reviews and modeling papers without data were excluded); and (4) were in natural systems (i.e., not highly managed agricultural ecosystems). For example, these studies included interactions such as predator–prey, plant–herbivore, and plant–pollinator interactions. Because our search captured very few host–parasite studies, we excluded these studies from our review. Studies that either manipulated climate change stressors to simulate potential future climate change or examined climate changes that were already occurring were included in our synthesis. In addition to field research, laboratory studies that involved samples collected from a specific location or locations were included. If a single paper described multiple studies that were conducted at different locations or involved different manipulations, each study within the paper was included as a separate record. To identify additional suitable articles beyond our search, we also searched the reference lists of all 339 review papers published prior to 1 January 2017 that were identified in our Web of Science search for relevant papers.

From each study, we extracted: (1) the geographical location and ecosystem type of the study (for laboratory studies, the location where the samples were collected was recorded); (2) whether it was conducted in the field or laboratory; (3) whether the study was experimental vs. observational, and involved modeling; (4) the trophic levels examined; (5) the climate change variables tested; and (6) the response variable(s) examined (abundance, biomass, diversity, food web structure). We examined studies that looked at effects of temperature, precipitation, [$CO_2$], ocean acidification, and extreme events (e.g., droughts, storms) as climate change stressors.

To explore the global distribution of food web studies, study locations were mapped in relation to terrestrial and freshwater major habitat type data (Olson et al. 2001, TNC and WWF 2008). In marine systems, study locations were mapped in relation to ocean biomes created by grouping the Longhurst biogeochemical provinces (Flanders Marine Institute 2009). We examined current (average of 1970–2000) mean annual temperature and precipitation at each terrestrial and freshwater study site using data from Worldclim v2 (Fick and Hijmans 2017) at a resolution of 5 min. As well, we examined current (average of 2000 to 2014) mean sea surface temperature at each marine site using data from Bio-ORACLE (Tyberghein et al. 2012, Assis et al. 2018) at a resolution of 5 min. We also created a graph to further examine the distribution of sites by extracting the mean of the mean annual temperature (from 1960 to 1990) and precipitation (from 1979 to 2013) of $1° \times 1°$ pixels for all terrestrial/freshwater areas using data from the CLiMond dataset (Kriticos et al. 2012) and the GPCC Global Precipitation Climatology Centre (Schneider et al. 2011). These points were color-coded based on the climate boundaries of the major biomes of the world proposed by Whittaker (1975). Finally, to examine the distribution of sites with respect to future projected climate change, we extracted the projected change in temperature and precipitation for the year 2090 under the RCP 6.0 scenario (NCAR GIS Program 2012) for each study location. This scenario was selected because it is in the middle of the range of RCP scenarios; that is, it is neither the most or least extreme. Under this scenario, emissions peak around 2080 and then decline.

To obtain a better understanding of which biomes, as well as which current and future climate conditions, were under-sampled vs. over-sampled, we performed chi-square tests that compared the observed number of studies with the number of studies expected if there was no spatial bias. Thus, to test for uneven sampling of biomes, we calculated the expected number of studies for each biome based on the proportion of the total area occupied by that biome. To examine bias with respect to current climate in terrestrial and freshwater systems, we calculated the expected number of studies for incremental categories of ~9°C and 400 mm by determining the proportion of the land area in a given category (e.g., $-19°$ to $-10°C$). We chose these cutoffs for categories because they produced 7–10 categories (i.e., were small enough that highly different amounts were not in the same category) and because they produced no categories with zero expected studies (as this would not allow a chi-square statistic to be calculated). For current sea surface temperatures, which had a smaller range, we calculated the expected number of studies for categories of ~4.5°C. To examine spatial bias of sites in relation to future climate conditions, we calculated the expected number of studies for ~1°C and 100 mm incremental categories by determining the area projected to change by a given amount (e.g., 1–2°C). We also used Hellinger's distance *d* to quantify the spatial bias of the study sites in our review in relation to the climate projection layers (Schmill et al. 2014, Gonzalez et al. 2016; code available at https://doi.org/10.5281/zenodo.2553122). Hellinger's distance compares similarities between the distribution of values captured by a set of points (e.g., the study sites in our review) with a uniform distribution. High values of *d* would indicate that the distribution of sites is strongly spatially biased. However, as the number of sites (N) increases and covers every pixel in a map, *d* becomes zero and the sample is no longer spatially biased. Because *N* will never be so large that it equals the total number of pixels, even a random sample of points will have some spatial bias and a non-zero value of *d*. To account for this, we compared our values of *d* to expected distributions that represent the amount of spatial bias that would be expected for an unbiased sample of the same number of studies as in our review (N = 308), by randomly sampling each climate projection map 1000 times. Analyses were performed in R version 3.3.1 (R Core Team 2016).

## Results

We obtained 2375 papers from our literature search and identified 264 studies that fit our criteria from the initial pool of papers (Data S1). In addition, 44 studies were added by examining the reference lists of 339 review papers. Thus, a total of 308 studies were included in our review. We did not place limits on publication year in our search, yet 55% of the studies were published within the last 5 yr and none were published before 1996. Most terrestrial, marine, and freshwater study sites were concentrated in the Northern Hemisphere, the United States and Europe specifically. Across all the studies, marine biomes were the most commonly examined (46%; $n = 141$), followed by terrestrial (31%; $n = 95$) and freshwater biomes (23%; $n = 72$). In terrestrial ecosystems, food webs were more extensively studied in temperate forests (59%; $n = 56$), which only cover approximately 9% of the Earth's land surface (Fig. 1a). Freshwater studies were concentrated in the temperate floodplain rivers and wetlands biome (39%; $n = 28$), which makes up 10% of the freshwater biomes (Fig. 1b). Marine food web studies were concentrated in the Atlantic Coastal biome (43%; $n = 61$), and in contrast, there was very little information available on the effects of climate change in deep water/fully pelagic biomes (Fig. 1c). Chi-squared tests for all systems indicated that studies were significantly unevenly distributed (Appendix S1: Table S1; terrestrial: $\chi^2 = 343.93$, df = 15, $P < 0.001$; freshwater: $\chi^2 = 151.77$, df = 12, $P < 0.001$; $\chi^2 = 975.07$, df = 13, $P < 0.001$). We acknowledge that additional appropriate studies have undoubtedly been published in languages other than English but do not expect that they would be numerous enough to eliminate this substantial geographic bias.

Study sites were unevenly distributed with respect to current climate. Very cold, hot, and dry climates were substantially under-represented, as most terrestrial and freshwater research occurred in areas with mean annual temperatures between −1° to 16°C and mean annual precipitation of <2000 mm (Appendix S1: Fig. S1, Table S1; temperature: $\chi^2 = 355.88$, df = 9, $P < 0.001$; precipitation: $\chi^2 = 121$, df = 11, $P < 0.001$). In marine habitats, most studies (65%) occurred in areas with mean annual temperatures of <12°C, leaving hot climates under-represented (Appendix S1: Table S2; $\chi^2 = 101.38$, df = 6, $P < 0.001$). Study sites in all ecosystem types were also unevenly distributed across the full range of magnitude of projected changes in climate (Fig. 2, 3; Appendix S1: Table S3; temperature: $\chi^2 = 230.18$, df = 6, $P < 0.001$; precipitation: $\chi^2 = 143.18$, df = 10, $P < 0.001$). Fewer studies were conducted in the areas with the least warming (<2°C). Areas projected to experience decreases in precipitation and areas with larger projected increases in precipitation (<113 mm) were also under-represented. Spatial bias was greater for temperature than precipitation (Hellinger's distances of 0.30 for temperature and 0.18 for precipitation).

In general, studies investigated from two ($n = 151$) to five ($n = 7$) trophic levels, but the majority of studies focused on only two levels (49%). Most studies examined the effects of

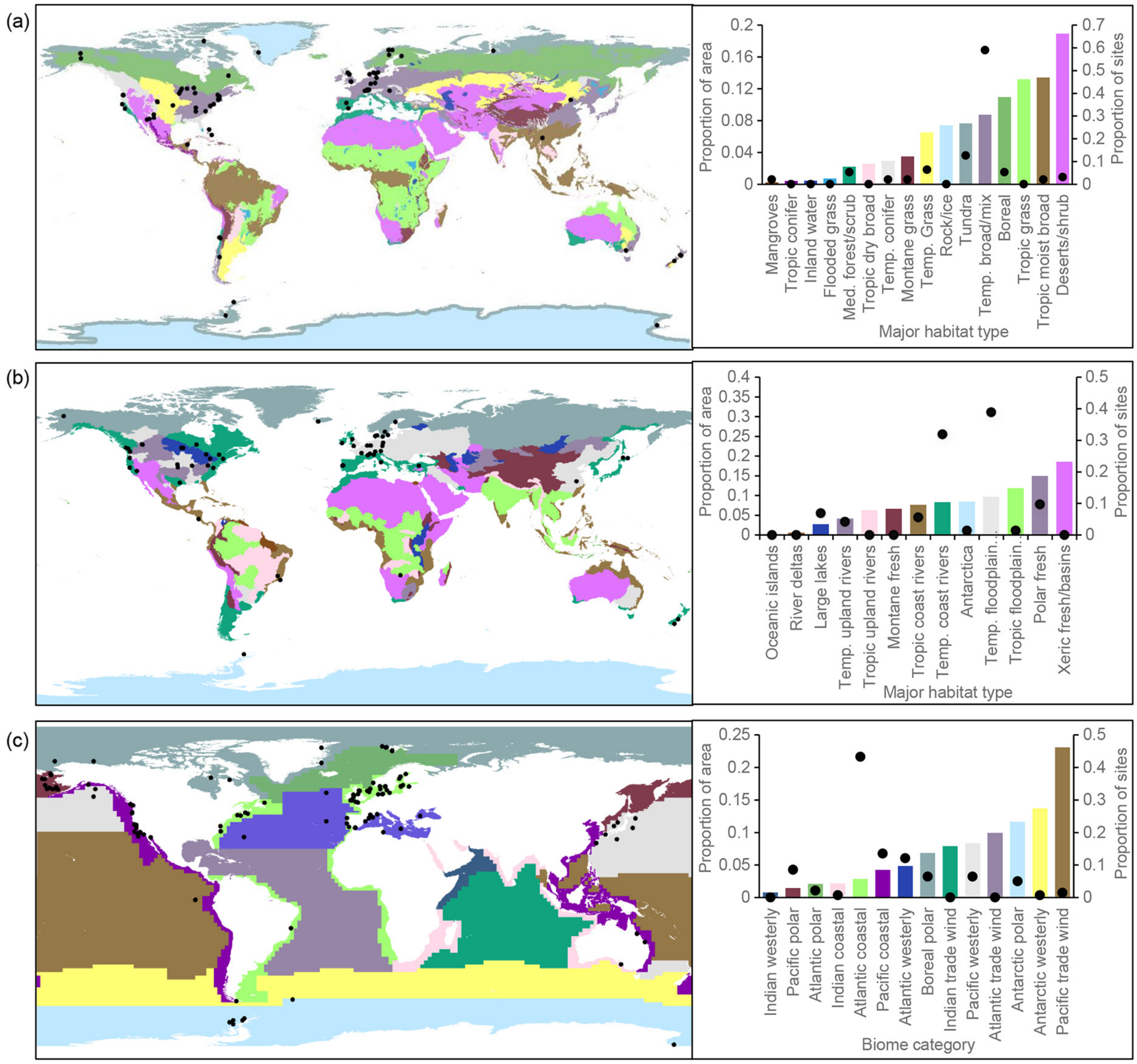


Fig. 1. Global maps of studies ($n$ = 308) conducted on climate change impacts on species interactions for (a) terrestrial systems; (b) freshwater systems; and (c) marine systems in relation to terrestrial/freshwater major habitat types (Olson et al. 2001, TNC and WWF 2008) and ocean biomes (Flanders Marine Institute 2009). Graphs accompanying each map show the proportion of the total area (colored bars; $y$-axis on left) and the proportion of study sites (black points; second $y$-axis on right) in relation to the major habitat types and biomes ($x$-axis).

climate change on species abundance (68%) and biomass (61%), while fewer measured climate change effects on diversity (25%) and food web structure (e.g., using genetic or stable isotope methods; 17%). Further, studies typically examined only one climate change mechanism (68%). Temperature was the most frequently investigated climate change variable (73%), followed by precipitation (18%). In addition, 9% of studies examined both extreme events and [$CO_2$], 3% studied acidification, and 1% ($n$ = 2) studied changes in snow or ice cover. Most studies were experimental (51%) or observational (40%), while the remainder involved more than one approach (a combination of experimental, observational, and/or modeling). Field studies were also more common (81%) than laboratory studies.

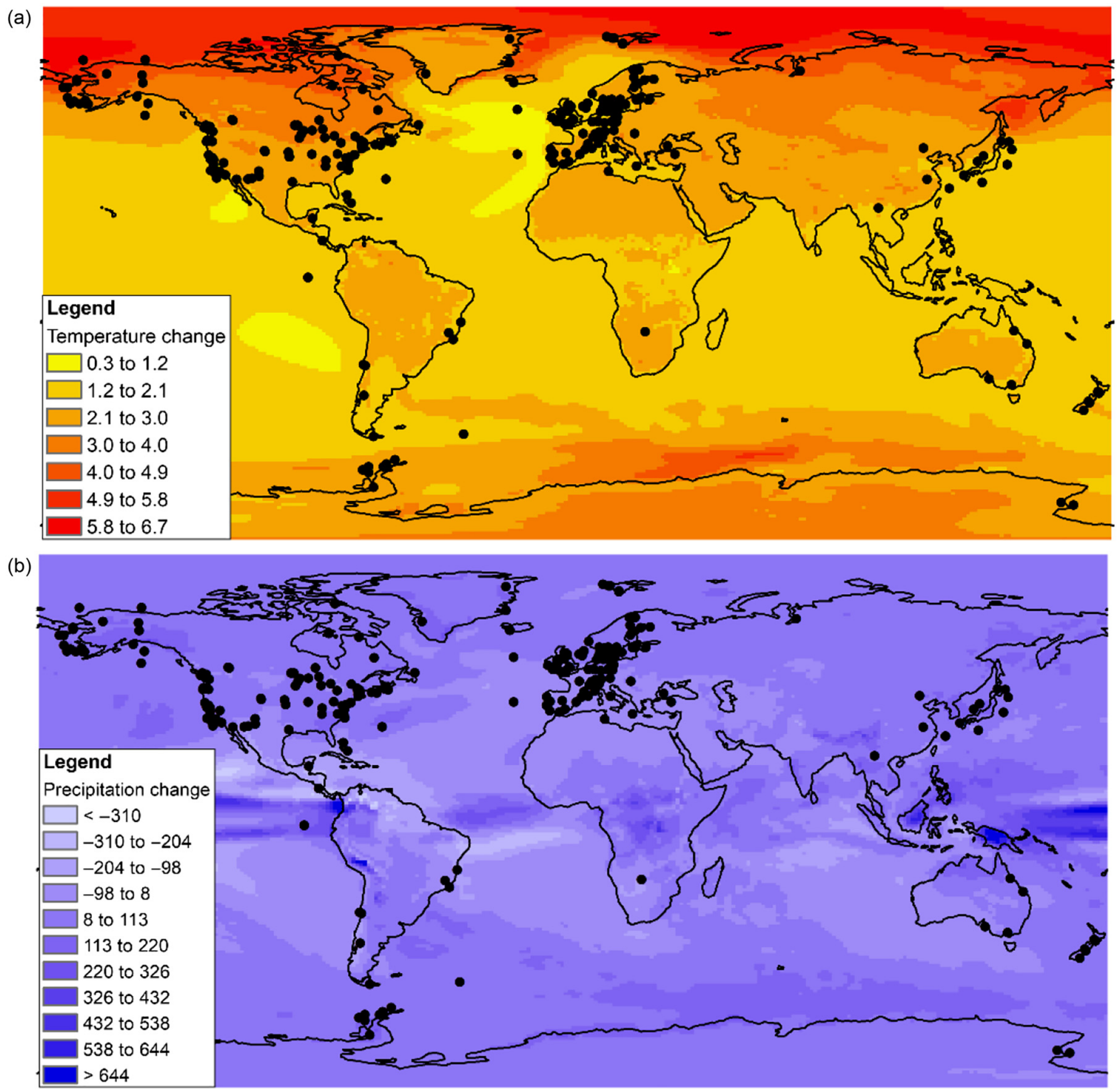


Fig. 2. Study sites (in black) in relation to projected changes by 2090 in median annual (a) temperature and (b) precipitation, under the RCP 6.0 scenario.

## Discussion

Our results highlight that research focusing on climate change effects on food webs suffers from a strong geographic bias, with most studies occurring in the USA and Europe (Fig. 1). Critically, the number of studies conducted within each biome is not proportional to the overall size of the biome. For example, tropical regions account for ~40% of the Earth's surface and support the majority of the world's species, yet only 3.5% of the studies were conducted in the tropics (Fig. 1a). Desert and xeric shrublands make up 19% of the terrestrial biome, yet only 3% of the studies were conducted in this biome. Similarly, xeric fresh water and closed basin ecosystems comprise 19% of the global freshwater biomes, yet none of the studies we sampled were

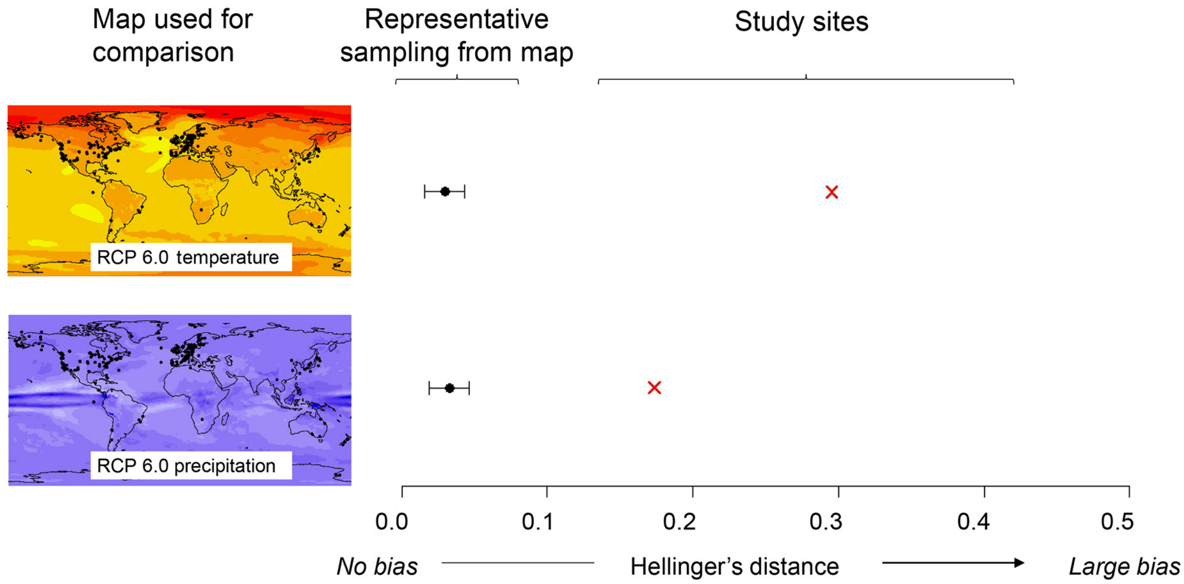


Fig. 3. Spatial bias of the study sites in relation to projected climate change layers. Climate change projection maps for the RCP 6.0 scenario (temperature and precipitation) are shown on the left. Hellinger's distance *d*, on the *x*-axis, quantifies the amount of spatial bias in study sites relative to each global map. The black circles with error bars (standard deviation) show the distribution of *d* values for 1000 random collections of samples where the number of samples is equal to the number of studies in our review ($n$ = 308). The red X symbols show the *d* values of our studies for each of the two climate change projection maps.

conducted in this biome (Fig. 1b). In addition, the Pacific Trade wind biome covers 23% of the ocean surface, yet only 1% of studies identified were conducted there (Fig. 1c). In contrast, temperate broadleaf and mixed forests, temperate coastal rivers, temperate floodplains, and the Atlantic coastal region are substantially over-sampled relative to their spatial extent.

If regions that are under-sampled are experiencing rates of climate change not represented by the locations that have been sampled more extensively, the uneven sampling of many of the globe's biomes may be especially problematic. The distribution of study sites in our synthesis was biased with respect to current climate conditions (Appendix S1: Fig. S1, Tables S1, S2), but importantly the distribution of sites sampled under projected future changes in climate was also biased (Figs. 2, 3; Appendix S1: Table S3). Coverage was uneven across the range of projected climate conditions, and areas with low projected temperature changes (<2°C change by 2090 in the RCP 6.0 scenario) were poorly studied (Fig. 3). Similarly, regions with projected decreases in precipitation (−522 to 0 mm change by 2090) were understudied, as well as regions with large projected increases (>113 mm change). This lack of research in areas with high predicted precipitation change is particularly concerning, due to the current trajectory of climate change and the potential for large effects on food webs in these regions. Future research should focus on understudied regions, regions where sites are poorly distributed (i.e., clustered), as well as sampling across the full range of projected climatic changes (from small to large changes).

Our findings are consistent with several articles examining geographical biases in other ecological subfields, including species invasions (Bellard and Jeschke 2016), range shifts (Lenoir and Svenning 2015), and species distributional data (Meyer et al. 2015) and likely reflect science funding patterns, locations near Universities, and papers that are published in English. In addition, an analysis of reviews synthesizing "global" climate change impacts found a severe geographic bias and noted that generalizing results from temperate areas to the globe is problematic because tropical species may be expected to respond differently to climate change than temperate species (Feeley et al. 2017). While some biomes are proportionally well sampled, even within those biomes, the study sites are sometimes clustered around single locations, calling into question how generalizable those results are for an entire region, especially in regions where the climate is changing rapidly (Metcalfe et al. 2018).

Across terrestrial and aquatic ecosystems, trophic interactions are important in determining how ecosystems function, the services they provide (e.g., fish stocks, biomass production, community stability) as well as their resistance and resilience to rapid climate change. Despite the importance of multi-trophic interactions, our data indicate that studies on multiple trophic levels (>2 levels) are not well represented in climate change research on food webs. Almost half of the studies in our review included only two trophic levels; however, this varied depending on the ecosystem studied. Studies in terrestrial systems examined more than two trophic levels (58%) slightly more often than studies in marine (49%) or freshwater (45%) systems. This is likely because assessing changes in biotic interactions are more challenging than examining the response of a single species or general biodiversity changes (McCann 2007, Tylianakis et al. 2008).

Recent advances in molecular (next generation sequencing, stable isotope probing) and analytical (e.g., network and latent variable modeling; Warton et al. 2015) techniques are improving our ability to examine these complex interactions within food webs. For example, one recent simulation study showed that higher-order interactions (where an interaction between two species is affected by a third species) influence the relationship between diversity and stability in ecosystems and impose a lower bound on the number of species in a community (Bairey et al. 2016). Yet in spite of these advances, the number of studies exploring multiple species and trophic levels remains low which limits our ability to extrapolate results using models.

Obtaining a synthetic understanding of the effects of climate change on food webs will not be possible without a greater understanding of the global variation in impacts across different ecosystems and climatic zones. Our review highlights a strong bias in the distribution of studies on food web responses to climate change at the global scale and identifies key areas where data are lacking, such as in deserts and the Indian Ocean as well as regions facing extreme shifts in temperature and rainfall due to climate change. Future work should be targeted to these understudied regions in order to improve our understanding of climate change impacts across a range of biomes, current climate conditions, and projected future climate conditions.

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## Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2645/full