

REVIEW AND SYNTHESIS

Geographical and experimental contexts modulate the effect of warming on top-down control: a meta-analysis

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Abstract

Ecologists have extensively investigated the effect of warming on consumer–resource interactions, with experiments revealing that warming can strengthen, weaken or have no net effect on top-down control of resources. These experiments have inspired a body of theoretical work to explain the variation in the effect of warming on top-down control. However, there has been no quantitative attempt to reconcile theory with outcomes from empirical studies. To address the gap between theory and experiment, we performed a meta-analysis to examine the combined effect of experimental warming and top-down control on resource biomass and determined potential sources of variation across experiments. We show that differences in experimental outcomes are related to systematic variation in the geographical distribution of studies. Specifically, warming strengthened top-down control when experiments were conducted in colder regions, but had the opposite effect in warmer regions. Furthermore, we found that differences in the thermoregulation strategy of the consumer and openness of experimental arenas to dispersal can contribute to some deviation from the overall geographical pattern. These results reconcile empirical findings and support the expectation of geographical variation in the response of consumer–resource interactions to warming.

Keywords

Climate change, consumer–resource interaction, ecological contingency, geographical gradient, meta-analysis, temperature, top-down control.

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INTRODUCTION

Consumers can exert strong top-down control on lower trophic levels through direct and indirect effects on the food web (Creel & Christianson 2008), with the direction and strength of these effects depending on biotic and abiotic contexts (Holland & DeAngelis 2009; Poisot *et al.* 2015). Because of this, responses to global change that lead to changes in environmental conditions and the establishment of communities with novel combinations of species could have major effects on trophic processes in food webs (Walther 2010; Lurgi *et al.* 2012). In fact, changes in the magnitude of top-down control have already been reported as a primary driver of population and food web responses to recent changes in climate (Winder & Schindler 2004; Ockendon *et al.* 2014). Therefore, a current challenge is to understand how drivers of global climate change affect consumer–resource interactions and, more specifically, top-down control of resources.

Temperature is an important abiotic condition related to global change that can affect consumer–resource interactions. Temperature has a strong effect on the biological rates that

control these ecological interactions (Brown *et al.* 2004; Burnside *et al.* 2014; Rosenblatt & Schmitz 2016), such as the attack rates of consumers on resources (Dell *et al.* 2011; Englund *et al.* 2011) and the rates of biomass production at different trophic levels (Allen *et al.* 2005; Yvon-Durocher *et al.* 2011). These warming-induced changes in *per capita* interaction strength and/or abundances of interacting species can lead to changes in the magnitude of top-down control on resources. However, it has so far been unclear how the strength of top-down control will be affected in a particular system. Experiments report that warming can cause increases (e.g. O'Connor 2009; Kratina *et al.* 2012), decreases (e.g. Barton 2010) or no net changes (e.g. Van De Velde *et al.* 2017) on the interactions between consumers and their resources. Therefore, it is challenging to predict *a priori* the response of consumer–resource interactions to warming and the conditions under which we can expect warming to modify the magnitude of top-down control.

One possible explanation for the reported contingency of the effect of warming on consumer–resource interactions is that the magnitude of top-down control itself varies naturally

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across experiments depending on the nature of the consumer–resource interaction analysed. For instance, early syntheses on the strength of trophic cascades (i.e. indirect effects that are initiated by consumers and propagate through the food web; Creel & Christianson 2008) suggest that top-down control of resources is stronger in aquatic than in terrestrial ecosystems (Shurin *et al.* 2002; but see Romero & Koricheva 2011) and also depends on the traits of consumers and resources, nutrient supply to lower trophic levels and the duration of the experiment (Hillebrand 2002; Borer *et al.* 2005; Gruner *et al.* 2008). The same set of predictors is also the focus of theoretical and conceptual models used to predict the effect of warming on top-down control (Vasseur & McCann 2005; Dell *et al.* 2011, 2014; O'Connor *et al.* 2011; Binzer *et al.* 2012, 2016; Gilbert *et al.* 2014; Amarasekare 2015; Osmond *et al.* 2017; Uszko *et al.* 2017). These models suggest that differences across habitats, taxa and their traits (e.g. body size, mobility and thermoregulation) determine the magnitude of change in top-down control in response to warming (Vasseur & McCann 2005; Dell *et al.* 2014). However, recent evidence also shows that the magnitude of top-down control can vary along latitudinal, altitudinal and climatic gradients (Rodríguez-Castañeda 2013; Romero *et al.* 2016; Reynolds *et al.* 2018; Roslin *et al.* 2017). This may occur due to geographical variations in local habitat conditions, species' abundances and their traits (Reynolds *et al.* 2017; Roslin *et al.* 2017). Thus, the effect of warming on top-down control may depend both on the consumer–resource interaction being tested and natural variation in the magnitude of this ecological interaction across locations.

Variation in the effect of warming could also occur if some consumer–resource pairs respond differently to warming than others. For example, the performance of consumers at higher trophic levels (e.g. carnivores) often peaks at lower temperatures compared to that of consumers at lower trophic levels (e.g. herbivores) (Dell *et al.* 2011, 2014; Englund *et al.* 2011; Rall *et al.* 2012; Iles 2014; Lang *et al.* 2017). Likewise, interactions between heterotrophs could be affected differently than those between a heterotroph and an autotroph, as heterotrophic metabolism is more sensitive to temperature changes than autotrophic metabolism (Yvon-Durocher *et al.* 2010). These examples suggest that a given increase in temperature may strengthen the interaction between a primary consumer and a producer while weakening the interaction between a primary and a secondary consumer.

Within a consumer–resource pair, geographical origin can also result in different responses to warming. De Block *et al.* (2013) conducted experiments using the same consumer–resource pair (a damselfly predator and a zooplankton prey) from three European countries and showed that warming had a stronger effect on the magnitude of top-down control when the interacting pair originated from the colder regions of northern Europe. Consequently, there may be a systematic difference in the sensitivity of food webs to a given temperature increase depending on their climatic origin, whereby the effect of warming on top-down control changes according to local climate. However, many experiments have focused on trophic interactions at a single location, hindering our capacity to test the possibility of a

dependency on geographical origin. This is a critical step if we are to provide objective information to develop a framework for predicting the sensitivity of trophic interactions to warming at a larger scale.

Here, we explore the knowledge gap between theoretical predictions and empirical evidence of how warming affects consumer–resource interactions by synthesizing published experiments that tested the interactive effect of warming and top-down control on resource biomass – a common currency in theoretical models and empirical food web studies. We gathered data on the outcome and experimental design of each experiment and conducted a meta-analysis to address two questions: (1) What is the effect of warming on the magnitude of top-down control of resource biomass across experiments? and (2) How can differences in reported outcomes of these experiments be explained? We show that warming has no overall consistent effect on top-down control of resources. However, the lack of consistency in individual outcomes could largely be explained by two factors: (1) systematic variation in response to warming related to the geographical distribution of studies and (2) differences in some aspects of the experimental design. Therefore, we suggest that the underlying cause of differential responses in top-down control to warming may lie in how consumer–resource interactions from different climatic regions respond to warming, indicating a geographical pattern in the effect of warming on food web interactions.

MATERIAL AND METHODS

Study selection

We conducted an extensive literature search for primary research that experimentally tested the combined effects of warming and the presence of consumers at higher trophic levels, and measured the effects on biomass at lower trophic levels. We searched the ISI Web of Science for all studies published through 8 November 2017, using the following search term combinations: ('climat*' AND ('change' OR 'event' OR 'extreme' OR 'warming') OR 'global' AND ('change' OR 'warming') OR 'environmental' ('change' OR 'warming') OR 'warming' OR 'temperature') AND ('food' AND ('web' OR 'chain') OR 'top*down' OR 'bottom*up' OR 'trophic' AND ('cascade' OR 'interaction') OR 'multi-trophic' OR 'tritrophic' OR 'consumer' OR 'graz*' OR 'herbivor*' OR 'predat*' OR 'parasit*' OR 'detritivor*'). We expanded the literature search by examining the references cited in all relevant studies found, including some reviews on this research topic. We used the same set of search terms described above to locate additional studies on *Google Scholar*. We did not include data from books and grey literature (theses, annuals and meetings) in our search.

We used five criteria to determine whether to include a study in our meta-analysis. First, the study had to use a full-factorial experimental design, combining temperature and consumer manipulations. Second, consumers had to be experimentally manipulated through presence/absence or their abundance (e.g. low vs. high). We excluded studies that used artificial simulations of the effect of consumers, such as those where clipping was used to simulate herbivory. Third, we only included studies where

temperature was experimentally increased, not decreased; in doing so, we excluded studies that simulated environmental cooling. Fourth, the study had to quantify some measure of biomass at a lower trophic level (e.g. body mass, total biomass, aboveground biomass, belowground biomass, standing stock). Finally, the study had to provide measures of mean, error (standard error, standard deviation or confidence intervals) and sample size for the resource biomass response to each of four treatment combinations: ambient temperature and consumers absent (Amb, Ab); ambient temperature and consumers present (Amb, Pres); warming and consumers absent (Warm, Ab); warming and consumers present (Warm, Pres). Following these criteria, we retained 56 studies for use in our meta-analysis (see Table S1).

Data extraction and moderators

We considered each combination of consumer manipulation and resource biomass response within a study to be an independent observation. As such, for each observation, we recorded the information on biological, climatic and experimental moderators that are expected to explain the contingent effects of warming on top-down control (see Appendix S1 for a full description of the moderators extracted). We recorded the identity of the consumer–resource pair, the number of trophic levels analyzed (according to the information provided in each study; categorical moderator: two or three), the type of ecosystem studied (freshwater, marine or terrestrial), the consumer type (carnivore, herbivore, detritivore or parasite), the trophic level of the resource (heterotrophic or autotrophic), the resource generation time relative to the experimental duration (multiple or single generation), the mobility of the resource (mobile or sessile; following Dell *et al.* 2014), the consumer hunting mode as a proxy for foraging strategy (active, sit-and-wait or grazing; following the definition proposed by Dell *et al.* 2014) and the thermoregulation strategy of the consumer (ectotherm or endotherm). We had planned to also record the resource thermoregulation strategy for use in analysis, but all resources examined were ectotherms. Next, we compiled information on the experimental venue (field or laboratory), whether nutrients were added (yes or no), whether experimental arenas were left open to dispersal or colonization ('openness', open or closed), the duration of the experiment (in days, continuous moderator), the intensity of experimental warming (the average difference in temperature between the ambient and warming treatment in degrees centigrade; ΔT , continuous moderator) and the mean annual temperature at the study location (MAT, in degrees centigrade, continuous moderator). We used latitude and longitude data from each study to obtain MAT data from the BIO1 raster file downloaded from WorldClim (Hijmans *et al.* 2005) at 1-km² resolution maps. We used the WorldClim data as a standard measure for MAT because most studies did not report climate data for their site. In addition, in cases where populations of consumer–resource pairs from different geographical origins were tested, we extracted the MAT data using the coordinates of the population of origin provided in the study (De Block *et al.* 2013). We used the function *extract* from the *raster* package (Hijmans 2016) in R v3.4.0 (R Core Team 2017) to download and obtain MAT data for each observation.

We recorded the biomass data on the means, error and sample size from each observation for each of the four treatment combinations, by extracting data directly from the text, tables or digitized figures – or through direct requests to the corresponding author of the study. In the few cases where data were presented in a boxplot, we used the method proposed by Hozo *et al.* (2005) to determine the mean and variance for each treatment combination. We used DataThief III (Tummers *et al.* 2015) to extract data from figures.

We adopted four approaches to minimize problems related to non-independence of study outcomes during data extraction – a common issue in ecological meta-analyses (Mengersen *et al.* 2013). First, we considered only the temperature treatment that used the highest increase from the ambient condition when multiple temperature treatments were tested. Second, as 7 of the 56 studies presented data for multiple experimental durations, we maintained consistency across studies by only extracting the data for the endpoint. Third, some studies provided several correlated measures of biomass response for the same consumer–resource pair within a study (e.g. total biomass, aboveground biomass and belowground biomass). We removed these non-independent measures by preferentially retaining the data related to total biomass, followed by data on aboveground biomass and, if neither of these were available, data on belowground biomass. Fourth, when the results of the same experiment were presented in different papers, we considered only the results that had not been previously reported. Following this procedure, we extracted 177 observations of consumer–resource pairs from the 56 studies included in the meta-analysis (see Table S2 for a list of observations extracted from each study).

Effect size calculation

To address our main research questions, we used a factorial version of the Hedge's g effect size metric (Gurevitch *et al.* 2000; Yue *et al.* 2017). This version of Hedge's g measures the magnitude of the difference between the levels of a given factor, after considering the difference between the levels of the other factor. Therefore, it can be used to calculate both the main and interactive effects of two different factors on a given response (as in a two-way ANOVA design). In our case, it allowed us to determine and explore the variation in the effect of warming on top-down control of resource biomass across studies (g_I , the interaction term), as well as in the main effects of warming (g_W) and top-down control on resources (g_C). Note, however, that our main interest in analysing the main effects lies in understanding their individual contribution to the observed contingency across the studies included in our synthesis. Therefore, a synthesis of these main effects is only a by-product of our analyses.

According to the original formulation by Gurevitch *et al.* (2000), the interaction term (g_I) should be calculated as the difference in average resource biomass (\bar{x}) between the levels of the temperature treatment (*Warm* vs. *Amb*), after considering the difference in resource biomass between the levels of the consumer treatment (*Pres* vs. *Ab*). In our case, this could be mathematically described as: $g_I = (\bar{x}_{Warm,Pres} - \bar{x}_{Warm,Ab}) - (\bar{x}_{Amb,Pres} - \bar{x}_{Amb,Ab})$. However, if we used this

formulation, we would confound the interpretation of g_I with how top-down control primarily affects resources under each temperature treatment. For example, if a negative effect of top-down control on resources becomes stronger with warming, g_I would assume a negative value; if, instead, a positive effect of top-down control on resources also strengthens with warming, g_I would assume a positive value. Therefore, we modified the original calculation of g_I to make its interpretation straightforward. To this end, we calculated g_I as the magnitude of the difference between the two temperature treatments, after considering the *absolute* difference between the levels of the consumer treatment:

$$g_I = \frac{|\bar{x}_{Warm,Pres} - \bar{x}_{Warm,Ab}| - |\bar{x}_{Amb,Pres} - \bar{x}_{Amb,Ab}|}{s_{pooled}} J_m \quad (1)$$

In Eqn 1, \bar{x} represents the average biomass value for each of the four treatment combinations, s_{pooled} is the pooled standard deviation across the four treatments, and J_m is a correction term for small sample size. s_{pooled} is calculated using the sample size, n , and the standard deviation of the mean, s , from each treatment combination,

$$s_{pooled} = \sqrt{\frac{(n_{Warm,Pres} - 1)(s_{Warm,Pres})^2 + (n_{Warm,Ab} - 1)(s_{Warm,Ab})^2 + (n_{Amb,Pres} - 1)(s_{Amb,Pres})^2 + (n_{Amb,Ab} - 1)(s_{Amb,Ab})^2}{n_{Warm,Pres} + n_{Warm,Ab} + n_{Amb,Pres} + n_{Amb,Ab} - 4}} \quad (2)$$

whereas J_m is calculated as:

$$J_m = 1 - \frac{3}{4m - 1} \quad (3)$$

where m is the degrees of freedom ($m = (n_{Warm,Pres} + n_{Warm,Ab} + n_{Amb,Pres} + n_{Amb,Ab} - 4)$). Under this modified version of g_I , positive values indicate that warming strengthens top-down control of resource biomass, while negative values indicate that warming weakens this trophic process.

In a meta-analysis, the square root of the sampling variance is used to calculate the confidence intervals around the effect size for each observation, while the inverse of the sampling variance represents the precision of each observation in estimating the underlying effect and is used to down-weight observations with larger uncertainty in meta-analytic models (Mengersen *et al.* 2013). We calculated the sampling variance for g_I as:

$$s(g_I) = \frac{1}{n_{Warm,Pres}} + \frac{1}{n_{Warm,Ab}} + \frac{1}{n_{Amb,Pres}} + \frac{1}{n_{Amb,Ab}} + \frac{(g_I)^2}{2(n_{Warm,Pres} + n_{Warm,Ab} + n_{Amb,Pres} + n_{Amb,Ab})} \quad (4)$$

We then calculated the main effects of warming (g_W) and top-down control on resource biomass (g_C) as the difference between the levels of one treatment after pooling the average biomass responses across the levels of the other treatment. That is, for g_W :

$$g_W = \frac{(\bar{x}_{Warm,Pres} + \bar{x}_{Warm,Ab}) - (\bar{x}_{Amb,Pres} + \bar{x}_{Amb,Ab})}{2s_{pooled}} J_m \quad (5)$$

Similarly, for g_C :

$$g_C = \frac{(\bar{x}_{Warm,Pres} + \bar{x}_{Amb,Pres}) - (\bar{x}_{Warm,Ab} + \bar{x}_{Amb,Ab})}{2s_{pooled}} J_m \quad (6)$$

With s_{pooled} and J_m calculated as in Eqns 2 and 3, respectively. Positive values of g_W (or g_C) indicate that warming (or top-down control) increases resource biomass, while negative values indicate the opposite. The sampling variance for g_W and g_C are, respectively,

$$\hat{s}(g_W) = \left[\frac{1}{n_{Warm,Pres}} + \frac{1}{n_{Warm,Ab}} + \frac{1}{n_{Amb,Pres}} + \frac{1}{n_{Amb,Ab}} + \frac{(g_W)^2}{2(n_{Warm,Pres} + n_{Warm,Ab} + n_{Amb,Pres} + n_{Amb,Ab})} \right] \frac{1}{4} \quad (7)$$

$$\hat{s}(g_C) = \left[\frac{1}{n_{Warm,Pres}} + \frac{1}{n_{Warm,Ab}} + \frac{1}{n_{Amb,Pres}} + \frac{1}{n_{Amb,Ab}} + \frac{(g_C)^2}{2(n_{Warm,Pres} + n_{Warm,Ab} + n_{Amb,Pres} + n_{Amb,Ab})} \right] \frac{1}{4} \quad (8)$$

The R script used to calculate these effect sizes is available at: https://github.com/nacmarino/Scripts/blob/master/factorial_hedges_d.R. For further details on the rationale, calculation and discussion regarding Hedge's g metric and its factorial

version, please refer to Gurevitch *et al.* (2000), Rosenberg *et al.* (2013) and Yue *et al.* (2017).

Statistical analyses

What is the overall effect of warming on the magnitude of top-down control of resource biomass across studies?

We used the *lmer* function from the *lme4* package (Bates *et al.* 2015) to fit a weighted random-effects model using g_I as a response variable, with the study identity as a random intercept term, and the inverse of the sampling variance of g_I (i.e. $1/s_{g_I}$) in the weights argument (Mengersen *et al.* 2013). Prior to the analysis, we detected a single observation where warming altered the sign of the consumer–resource interaction (from a positive effect of consumers on resources in the ambient treatment to a negative effect in the warmed treatment). As such, while the interpretation of g_I for all other observations ($n = 176$) indicates how warming altered the *magnitude* of top-down control, the interpretation of g_I for this single observation describes how warming altered both the *direction* and the *magnitude* of top-down control. We were unable to run any separate analyses on this specific case, as $n = 1$. Thus, we removed this observation from all further steps of the data analysis. We verified parametric assumptions of the model by visual inspection of its residual plot and, after establishing the final model and obtaining the overall effect of g_I across studies, we extracted the 95% bootstrapped confidence interval for the estimated g_I based on the percentile interval (999 simulations). We considered the overall effect of warming on top-down control of resource biomass significant across experiments if the 95% confidence interval for g_I

did not contain zero. We performed the same procedures described above to determine the overall main effects of warming (g_W) and top-down control on resources (g_C) across the studies included in the meta-analysis. Finally, we assessed publication bias in effect sizes in all analyses through visual inspections of normal quantile plots (Wang & Bushman 1998).

How can differences in the effect of warming on top-down control across experiments be explained?

Several moderators may contribute to the variation in the effect of warming on top-down control (Appendix S1), and there is no reason to assume a single moderator should account for all the patterns reported across experiments. Therefore, we used an information-theoretic approach to determine the relative importance of each moderator in explaining the variation in experimental outcomes (Burnham *et al.* 2011; Grueber *et al.* 2011; Richards *et al.* 2011; Galipaud *et al.* 2017). We combined model selection and averaging based on Akaike's information criterion corrected for small sample sizes (AICc) to determine which models, accounting for different sets of moderators, were best supported by the data.

As a first step, we used a weighted mixed-effects model with g_I as a response variable and, as fixed predictors, additive terms for the type of ecosystem studied (categorical, 3 levels), the number of trophic levels (categorical, 2 levels); the consumer type (categorical, 3 levels; see below), hunting mode (categorical, 3 levels) and thermoregulation strategy (categorical, 2 levels); the resource mobility (categorical, 2 levels), trophy (categorical, 2 levels) and generation time (categorical, 2 levels); whether nutrients were added in the experiment (categorical, 2 levels), openness of the experimental arenas (categorical, 2 levels), experimental venue (categorical, 2 levels), duration of the experiment (continuous, ln-transformed), intensity of experimental warming (continuous, ln-transformed) and the mean annual temperature at the study location (continuous). We included a second-order polynomial term for the intensity of experimental warming and for the mean annual temperature, to account for possible nonlinear effects of temperature on biological rates (Brown *et al.* 2004) and in the magnitude of top-down control (Rodríguez-Castañeda 2013), respectively. We added an interaction term between the consumer type and the intensity of experimental warming (following the prediction that consumer types should differ in their response to a similar increase in temperature; Dell *et al.* 2011, 2014; Lang *et al.* 2017) and between the intensity of experimental warming and the mean annual temperature (to consider the prediction that consumer–resource pairs from different climatic origins should respond differently to the same temperature increase; De Block *et al.* 2013). There was a single observation from a consumer–resource interaction between a host and its parasite, which did not allow us to conduct robust statistical analyses if we considered the moderator consumer type in the models. Therefore, we removed this observation from our analyses (final number of observations in the mixed-effects model, n : 175; number of studies, k = 55). Finally, we included a random intercept term for the study identity and weighted each observation by the inverse of the sampling variance of g_I ($1/s_{g_I}$). Prior to the analysis, we followed Gelman (2008) and standardized by centring and scaling by two

standard deviations all the continuous and categorical inputs (including the response variable), using the *standardize* and *rescale* functions from the *arm* package (Gelman & Su 2016). We used the function *lmer* from the *lme4* package to fit the weighted mixed-effects model.

After fitting the full model, we performed model selection using the function *dredge* from the *MuMIn* package (Bartoń 2016) to contrast reduced models containing different combinations of moderators. We ranked models according to their AICc values and conducted model averaging using models within 2 Δ AICc units from the model with the lowest AICc, as models within this Δ AICc range are often similarly supported by the data (Burnham *et al.* 2011). We extracted the coefficients for each moderator from this confidence set as the weighted average of each coefficient across models containing that moderator, with the weights as the AICc weight (w_i) of each of these models (inclusion of models within 6 Δ AICc units from the model with the lowest AICc did not change the results we found; see Table S3). We then calculated the 95% confidence interval for each moderator included in the confidence set and the probability of each moderator appearing in the best model by summing the AICc weights (w_i) from each model containing that moderator (Galipaud *et al.* 2014). As we standardized inputs for the moderators and g_I prior to the analysis, the model-averaged coefficients are on comparable scales and represent a measure of the effect size of each moderator on g_I (Grueber *et al.* 2011; Galipaud *et al.* 2017). As such, we chose not to back-transform the moderators to their original scale.

Finally, we examined how the main effects of warming (g_W) and top-down control of resources (g_C) varied across experiments using the same steps described above. We used a similar model structure to the one described for g_I , but omitted all terms related to consumer traits and the consumer–resource pair when we used g_W as a response variable (i.e. number of trophic levels, consumer type, consumer hunting mode and the thermoregulation strategy of the consumer) as it would have been meaningless to test how these moderators contribute to variation in g_W . Similarly, the model exploring the natural variation in top-down control across experiments used g_C as the response variable, but the moderator for intensity of experimental warming was omitted.

In all cases, we present and interpret the model-averaged effect size for each moderator and classify a moderator as significantly contributing to the variation on a given response (g_I , g_W and g_C) if their 95% confidence intervals did not contain zero. In addition, we used the structure of the reduced models with the lowest AICc in the confidence set for graphical representation of the main trends and the description of the estimated coefficients for levels of categorical moderators, as parameter estimates across these models should be less biased and more precise (M. Galipaud, *personal communication*). In these models, we calculated coefficients and confidence intervals for each level of each categorical moderator using the function *lsmeans* from the *lsmeans* package (Lenth 2016) and used functions from the *visreg* package (Breheny & Burchett 2017) to create surface and regression plots according to the model predictions. We performed all analyses in R v3.4.0.

RESULTS

Overall effect of warming, top-down control and their interaction on resource biomass across studies

We found that warming had no consistent effect on top-down control of resource biomass (g_I : 0.061; 95% CI: -0.137 to 0.245; Fig. 1), following the contrasting results reported across studies. We also found no consistent effect of either warming (g_W : 0.260; 95% CI: -0.050 to 0.597; Fig. 1) or top-down control (g_C : -0.214; 95% CI: -0.679 to 0.204; Fig. 1) on resource biomass when all studies were combined. There was very little support for bias in g_I , g_W and g_C to affect these estimates (normal quantile plots, Appendix S2).

Explaining the contingency in the interactive effect of warming and top-down control on resource biomass

We found that some moderators were related to the differing effect of warming on top-down control reported across studies (Table 1, Fig. 2). Model-averaged parameter estimates indicated that the interaction between mean annual temperature and intensity of experimental warming (MAT: ΔT ; -0.497 [-0.843 to -0.151]), the thermoregulation strategy used by the consumer (standardized effect size and 95% CI: 0.696 [0.233 to 1.159]) and the openness of experimental arenas (openness: -0.204 [-0.376 to -0.033]) had stronger effects on g_I than any other moderator included in the confidence set (Fig. 2; see Table S3). These three moderators also had higher probabilities of being in the best model (given their importance values; point sizes in Fig. 2; Table S3) and were all included in the model with the lowest AICc value for g_I according to the model selection analysis (Table 1).

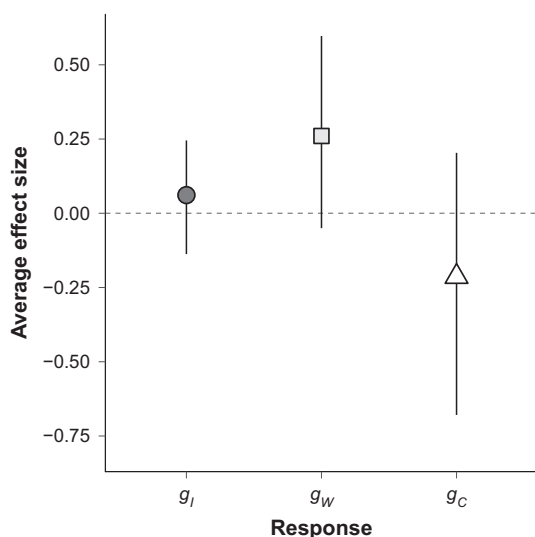


Figure 1 The overall main and interactive effects of warming on top-down control of resource biomass across experiments. Average effect sizes and 95% bootstrapped confidence intervals are presented for the impact of warming on top-down control of resource biomass (g_I , dark grey circle), as well as for the main effect of warming (g_W , light grey square) and top-down control on resource biomass (g_C , white triangle).

More specifically, the analysis of the reduced model containing all three moderators for g_I (Table S4) showed that warming had contrasting effects along a geographical temperature gradient, with a higher intensity of experimental warming resulting in stronger top-down control when experiments were conducted in colder regions, and weaker top-down control when experiments were conducted in warmer regions (Fig. 3; Table S5). We also found a stronger effect of warming on the magnitude of top-down control when consumers were endotherms (estimate: 1.457; 95% CI: 0.721 to 2.193) rather than ectotherms (estimate: 0.029; 95% CI: -0.10 to 0.158). Similarly, changes in the magnitude of top-down control in response to warming were slightly greater when experimental arenas were closed to dispersal (estimate: 0.927; 95% CI: 0.461 to 1.393) than when dispersal was allowed (estimate: 0.559; 95% CI: 0.230 to 0.888; although their 95% CIs overlap).

Evaluating the variation in the main effects of warming and top-down control on resource biomass across studies

Differences in the main effects of warming (g_W) and top-down control (g_C) on resource biomass were not related to the same moderators as those observed for their interactive effect (g_I ; Tables 1 and 2). For example, the model-averaged estimates for g_W showed that although resource biomass increased with the intensity of experimental warming across studies (ΔT and ΔT^2 , Table 2), there was little support for this relationship to vary along the geographical temperature gradient (MAT, Table 2; Table S5). Likewise, the main effect of top-down control on resources (g_C) was unlikely to vary along the geographical temperature gradient across studies (MAT, Table 2; Table S5). In fact, variation in both g_W and g_C was most related to the type of ecosystem studied, the intensity of experimental warming and the resource generation time for g_W , and the number of trophic levels for g_C (Tables 1 and 2; Tables S4 and S5).

DISCUSSION

The first study included in our synthesis dates back to 1996 (Beisner *et al.* 1996). Since then, an increasing number of experiments have investigated the effects of warming on top-down control of resources (Table S1). Because these experiments have yielded contrasting outcomes, understanding the factors moderating the effects of warming has become an important topic of theoretical and empirical research (Gilbert *et al.* 2014). Our synthesis shows that the effects of warming on top-down control of resource biomass can be explained by a common set of moderators across studies. From a long list of factors hypothesized to explain the differing effects of warming (Appendix S1), we were able to identify three that contributed most to the observed variation across experiments. First, variation in experimental outcomes followed a geographical gradient. Second, experiments with endothermic consumers displayed stronger top-down control of resources under experimental warming. Finally, warming led to slightly stronger top-down control when dispersal into and out of the experimental arenas was prevented. These results reconcile

Table 1 Models that were better supported by the data according to the Akaike information criteria for (a) g_I , (b) g_W and (c) g_C

Model	Model structure	d.f.	logLik	AICc	$\Delta AICc$	w_i
(a) Effect of warming on top-down control of resource biomass (g_I)						
#1	$g_I \sim$ Consumer thermoregulation + Openness + MAT + ΔT + MAT: ΔT	8	-105.48	227.83	0	0.17
#2	$g_I \sim$ Consumer thermoregulation + Openness + MAT + MAT ² + ΔT + MAT: ΔT	9	-104.65	228.4	0.57	0.128
#3	$g_I \sim$ Consumer thermoregulation + Openness + MAT + ΔT + ΔT^2 + MAT: ΔT	9	-104.86	228.82	0.99	0.104
#4	$g_I \sim$ Consumer thermoregulation + Openness + MAT + MAT ² + ΔT + MAT: ΔT + MAT ² : ΔT	10	-103.91	229.17	1.34	0.087
#5	$g_I \sim$ Resource trophy + Consumer thermoregulation + Openness + MAT + ΔT + MAT: ΔT	9	-105.07	229.23	1.41	0.084
#6	$g_I \sim$ Consumer thermoregulation + Number of trophic levels + Openness + MAT + ΔT + MAT: ΔT	9	-105.1	229.29	1.46	0.082
#7	$g_I \sim$ Consumer thermoregulation + Openness + MAT + Study duration + ΔT + MAT: ΔT	9	-105.17	229.44	1.61	0.076
#8	$g_I \sim$ Consumer thermoregulation + Openness + MAT + MAT ² + ΔT + ΔT^2 + MAT: ΔT	10	-104.12	229.57	1.74	0.071
#9	$g_I \sim$ Consumer thermoregulation + Openness + MAT + MAT ² + Study duration + ΔT + MAT: ΔT	10	-104.16	229.66	1.83	0.068
#10	$g_I \sim$ Resource trophy + Consumer thermoregulation + Openness + MAT + MAT ² + ΔT + MAT: ΔT	10	-104.2	229.75	1.92	0.065
#11	$g_I \sim$ Consumer thermoregulation + Openness + Resource mobility + MAT + ΔT + MAT: ΔT	9	-105.34	229.77	1.95	0.064
(b) Effect of warming on resource biomass (g_W)						
#1	$g_W \sim$ Ecosystem type + Resource trophy + Resource generation time + ΔT + ΔT^2	8	-94.9	206.67	0	0.265
#2	$g_W \sim$ Ecosystem type + Resource generation time + ΔT + ΔT^2	7	-96.15	206.97	0.3	0.228
#3	$g_W \sim$ Ecosystem type + Resource trophy + Resource generation time + MAT + ΔT + ΔT^2	9	-94.4	207.89	1.22	0.144
#4	$g_W \sim$ Ecosystem type + Resource generation time + MAT + ΔT + ΔT^2	8	-95.59	208.05	1.38	0.133
#5	$g_W \sim$ Ecosystem type + Resource trophy + Resource generation time + ΔT + ΔT^2 + Experimental venue	9	-94.56	208.22	1.55	0.122
#6	$g_W \sim$ Ecosystem type + Resource generation time + ΔT + ΔT^2 + Experimental venue	8	-95.78	208.43	1.76	0.11
(c) Effect of top-down control on resource biomass (g_C)						
#1	$g_C \sim$ Ecosystem type + MAT + Number of trophic levels	6	-94.75	202.01	0	0.246
#2	$g_C \sim$ Ecosystem type + Number of trophic levels	5	-96.14	202.63	0.62	0.181
#3	$g_C \sim$ Ecosystem type + MAT + Number of trophic levels + Experimental venue	7	-94.14	202.95	0.94	0.154
#4	$g_C \sim$ Ecosystem type + Number of trophic levels + Experimental venue	6	-95.49	203.49	1.48	0.117
#5	$g_C \sim$ Consumer foraging + Ecosystem type + MAT + Number of trophic levels	7	-94.52	203.72	1.71	0.105
#6	$g_C \sim$ Ecosystem type + MAT + Number of trophic levels + Resource mobility	7	-94.52	203.72	1.71	0.105
#7	$g_C \sim$ Ecosystem type + Resource generation time + Number of trophic levels	6	-95.73	203.96	1.95	0.093

We fitted a weighted mixed-effects model for each response variable and conducted a model selection, whereby we ranked models according to their AICc values and selected the models within $\Delta AICc \leq 2$ of the model with the lowest AICc value for inference. The Akaike weight for a given model, w_i , represents the probability that a given model is the best model in the set. We used this confidence set in the model averaging. MAT: mean annual temperature (in degrees centigrade). ΔT : intensity of the experimental warming (ln-transformed, in degrees centigrade). Study duration: ln-transformed, in days.

empirical findings and will improve our ability to make predictions on the sensitivity of consumer–resource interactions to changes in temperature across spatial scales.

Geographical variation in the effects of warming on top-down control

Warming affected the magnitude of top-down control differentially across a geographical temperature gradient, strengthening top-down control when experiments were conducted in colder regions and weakening it in warmer regions. These opposing effects are not surprising given that latitude-specific responses in consumer–resource interactions to warming have previously been demonstrated within a consumer–resource species pair (Barton 2011; De Block *et al.* 2013). However, it is surprising that the same patterns were observed even when different consumer–resource combinations were tested in distinct locations. It is still unclear whether the geographical pattern in outcomes across experiments is linked to geographical variation in the temperature regime itself, or to other related factors.

The strength of consumer–resource interactions is expected to vary along large-scale latitudinal and climatic gradients (Schemske *et al.* 2009), with recent evidence suggesting that these interactions are stronger towards lower latitudes and in warmer regions (Rodríguez-Castañeda 2013; Romero *et al.*

2016; Reynolds *et al.* 2017; Roslin *et al.* 2017). However, here we found no evidence that the magnitude of top-down control (g_C) varied along a temperature gradient. Therefore, natural variation in the magnitude of top-down control over biogeographical gradients cannot be used to explain the differential effects of warming on consumer–resource interactions from colder to warmer regions.

Several lines of evidence show that species from different climatic regions may respond differently to warming. For example, in colder regions, warming often increases plant growth and biomass (Rustad *et al.* 2001; Lin *et al.* 2010) and advances plant and animal phenology, while having the opposite or no effect in warmer regions (Parmesan & Hanley 2015; Prevéy *et al.* 2017). This occurs because taxa from colder regions have broad thermal tolerances to cope with larger seasonal changes in temperature than taxa from warmer and less seasonal regions (Janzen 1967; Zuloaga & Kerr 2017). As a consequence, small increments in temperature should increase performance in the former taxa while pushing the latter beyond their physiological and metabolic limits (Deutsch *et al.* 2008; Tewksbury *et al.* 2008; but see Vasseur *et al.* 2014). If warming has different effects in the ecological performance of taxa across temperature gradients, then there should be a positive relationship between the effect of warming on resource and/or consumer performance and the temperature regime across study locations. We failed to find any evidence

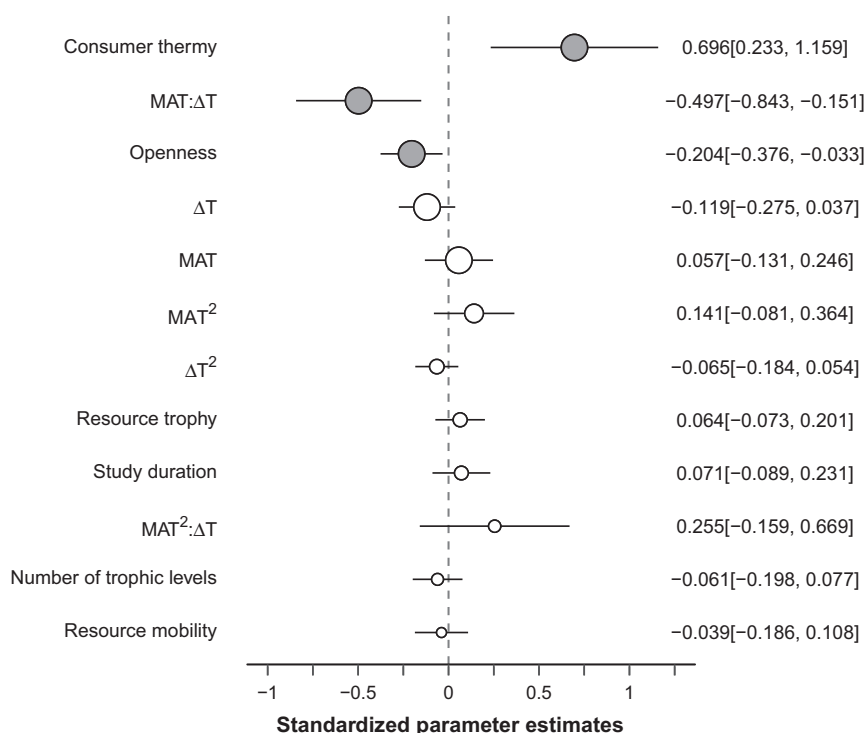


Figure 2 Moderators with a larger likelihood of explaining the contingent effects of warming on top-down control (g_T) across studies according to the model selection and model averaging approach. Moderators were ordered according to their importance (the size of each circle; probability of that moderator appearing in the best model), as well as with estimates of their standardized effect size and 95% confidence intervals according to the averaged model; empty circles represent moderators with 95% CIs that overlap zero (i.e. $P > 0.05$), while grey circles are moderators with 95% CIs that do not overlap zero (i.e. $P < 0.05$). MAT: mean annual temperature (in degrees centigrade). ΔT: intensity of the experimental warming (ln-transformed, in degrees centigrade). The tabular data used to create this figure are found on Table S3.

that warming (g_W) affected resource biomass (i.e. a measure of performance) differently across a gradient of mean annual temperature, but did find evidence that this effect varied along a gradient of temperature seasonality (*post hoc* analysis, Appendix S3). Therefore, we are unable to discard the possibility that geographical differences in the thermal sensitivity of the consumers and/or resources drive the systematic variation in the effects of warming on top-down control across experiments.

Other mechanisms related to the temperature gradient may also be operating and may explain the geographical pattern we found. For example, latitudinal differences in background nutrient levels and primary productivity are often related to temperature and precipitation gradients (Taylor *et al.* 2017). These differences in nutrient supply could buffer consumer–resource interactions from the effect of warming by boosting productivity and reducing the risk of consumer starvation (Binzer *et al.* 2012; Gilbert *et al.* 2014). Similarly, latitudinal gradients in body size within and among species could also contribute to the patterns we found, given that the size structure of food webs may determine their sensitivity to warming (Binzer *et al.* 2016). However, we are unable to determine whether these or other mechanisms contributed to the patterns we found, as data on them are often not reported. These possibilities remain open and should be addressed by future empirical studies.

Finally, geographical variation in the effect of warming on top-down control may also have occurred if there were a

geographical bias in the distribution of experiments along the gradient. We examined this possibility and observed that top-down control driven by endothermic consumers was generally tested towards colder regions (MAT range: -8°C to 0.7°C), while experiments using ectothermic consumers covered a larger climatic range (MAT: -2.2°C to 22.6°C). Given that warming had a stronger effect on top-down control by endotherms than ectotherms, we initially suspected that this geographical bias could explain why warming strengthened top-down control in colder regions. To discard this idea, we removed the observations from interactions driven by endothermic consumers and reran all analyses. We found no differences in the results between the reduced and the full data set (see Table S6). Therefore, it is unlikely that a geographical bias in experimental design alone can explain geographical variation in the effect of warming on top-down control.

Regardless of the underlying mechanisms, our synthesis provides evidence that warming affects the magnitude of top-down control along a large-scale geographical gradient. Given these results, we suggest that experiments replicated across broad climatic gradients are a much-needed step in determining the geographical sensitivity of trophic interactions to warming and should be the focus of future collaborative efforts. Furthermore, improving the reporting standards and quantifying the variation in important species' traits in relation to temperature across spatial scales (e.g. the performance

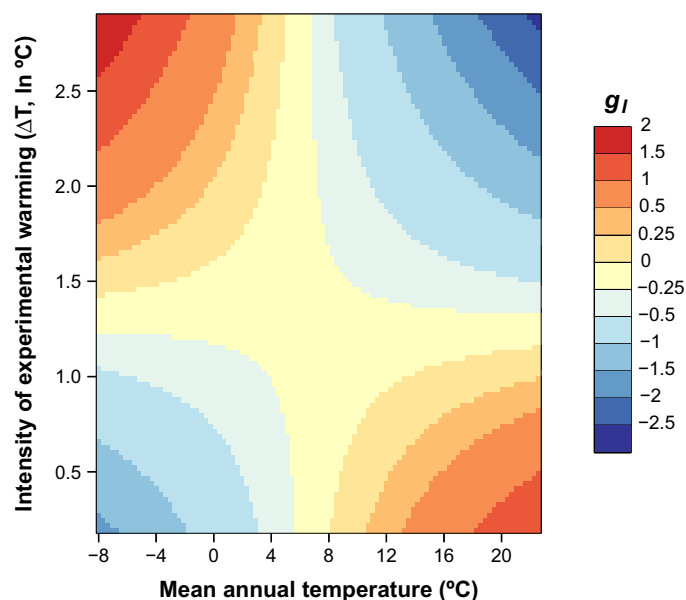


Figure 3 Systematic variation in the effect of warming on top-down control of resources (g_I) according to a gradient of mean annual temperature and intensity of experimental warming across study locations. Values of g_I are colour-coded, with positive values g_I indicating that warming strengthens top-down control (in red) and negative values indicating the opposite (in blue). Parameter estimates used to create this figure were obtained according to the model with the lowest AICc value in the confidence set for g_I and are available on Table S4, under the heading a.

of consumers and resources) would also help uncover the underlying mechanisms driving the geographical pattern we found (e.g. Mertens *et al.* 2015; Rosenblatt *et al.* 2016).

Experimental context as another source of variation for the effect of warming on top-down control

Differences in consumer thermoregulation (endotherm vs. ectotherm) and the openness of experimental arenas (open vs. closed to dispersal) also explained variation in experimental outcomes. For instance, at a given location, experiments using endothermic consumers were more likely to find stronger top-down control in response to warming than if the same experiment used ectothermic consumers. Similarly, in line with recent theory (Thompson & Gonzalez 2017), reducing connectivity among experimental arenas, and between them and the metacommunity, resulted in greater changes in the magnitude of top-down control than if connectivity was allowed. Under natural conditions, both dispersal rates and the presence of certain consumer traits depend on the biotic and abiotic contexts where each food web is embedded (Holland & DeAngelis 2009; Poisot *et al.* 2015). Therefore, we expect that local variation in species composition, dispersal and habitat structure among locations may result in deviations from the overall geographical pattern we found (Reynolds *et al.* 2017). This suggests that frameworks on the sensitivity of trophic interactions to warming should consider differences among habitats, taxa and their traits – not only within – but also across geographical scales (e.g. Lemoine 2017).

Caveats and research gaps

In addition to some limitations from our synthesis that have already been outlined, a few other caveats should be considered. First, we used measurements of mean annual air temperature available from WorldClim (Hijmans *et al.* 2005) as a proxy for background climate, because several studies did not report ambient climatic conditions during experiments. We used this approach to standardize the measure of background climate across studies conducted in terrestrial and aquatic ecosystems (*i.e.* marine and freshwater), as there is usually a correspondence between air and water temperature (O'Reilly *et al.* 2015). Also, several studies did not report important species traits, such as generation time, and we had to code some of these traits into categorical information. These are well-known limitations in ecological meta-analysis, which mostly relies on reporting standards across studies (Gerstner *et al.* 2017).

We were also unable to consider some moderators (or levels of them) in our statistical analysis due to the lack of sufficient observations. This was the case for the resource thermoregulation strategy, because all resource taxa examined were ectothermic. Similarly, very few studies were conducted on the effect of warming on non-trophic interactions (e.g. fear effects; $n = 3$), only a single study included a host–parasite interaction, and only one study was conducted in the Southern Hemisphere (Antiqueira *et al.* 2018). As such, the extent to which the patterns we found might differ in these scenarios remains unknown.

We encountered two important inconsistencies in the treatment of time across studies. First, only 10 studies of the 56 in our database lasted more than 1 year (range: 7 days to 5 years). Although experiment duration was not related to the patterns we found, other ecological responses to warming and related stressors have already been shown to change over even longer time scales (Mueller *et al.* 2016). Therefore, we are currently unable to determine whether warming over long time scales can have similar effects on consumer–resource interactions. Likewise, from the 10 studies that lasted more than 1 year, only 7 of them analysed the effect of warming on top-down control across seasons, while only 4 of them reported those data. Given this lack of consistency in data reporting across studies, we could not test for seasonal differences in experimental outcomes – although reports suggest that consumer–resource interactions may respond differently to warming depending on season (P. Kratina, *personal communication*).

As with several ecological meta-analyses, we found a strong hemispheric bias in our knowledge of the effects of warming on consumer–resource interactions (Zuk 2016; Feeley *et al.* 2017). With the exception of one study (22.35°S, Antiqueira *et al.* 2018), all empirical evidence came from experiments performed on latitudes $> 30.5^\circ$ in the Northern Hemisphere. Consequently, the extent to which the geographical pattern we found represents a global trend is still unknown (e.g. top-down control may vary with a climatic gradient in one hemisphere but not the other; Zhang *et al.* 2016). Given that the effect of warming on top-down control of resource biomass should be weaker in warmer regions or may even differ from theoretical expectations (*i.e.* weaker, rather than stronger, trophic interactions in response to warming), it would not be

Table 2 Standardized effect size estimates, standard errors, 95% confidence intervals, *z* and *p* values for the moderators included in the averaged models for (a) *gW* and (c) *gC*

Moderator	Estimate	SE	Lower 95% CI	Upper 95% CI	<i>z</i>	<i>P</i>	Importance across models
(a) Effect of warming on resource biomass (<i>gW</i>)							
Ecosystem type	0.33	0.126	0.082	0.578	2.608	0.0091	1
Resource generation time	−0.205	0.096	−0.393	−0.017	2.136	0.0327	1
ΔT	0.271	0.118	0.04	0.502	2.298	0.0216	1
ΔT^2	−0.17	0.065	−0.298	−0.042	2.611	0.009	1
Resource trophic	0.115	0.073	−0.029	0.258	1.565	0.1175	0.53
MAT	−0.123	0.121	−0.36	0.113	1.022	0.3066	0.28
Experimental venue	0.11	0.132	−0.149	0.368	0.833	0.4049	0.23
(b) Effect of top-down control on resource biomass (<i>gC</i>)							
Ecosystem type	−0.245	0.085	−0.411	−0.079	2.899	0.0037	1
Number of trophic levels	0.292	0.069	0.157	0.428	4.243	< 0.001	1
MAT	−0.132	0.078	−0.284	0.021	1.696	0.09	0.61
Experimental venue	0.083	0.072	−0.058	0.224	1.157	0.2474	0.27
Consumer foraging	0.052	0.076	−0.098	0.202	0.68	0.4964	0.1
Resource mobility	0.064	0.092	−0.116	0.244	0.696	0.4866	0.1
Resource generation time	−0.077	0.085	−0.244	0.09	0.902	0.3668	0.09

These coefficients were standardized by centring and scaling the inputs by two times their standard deviation, including the response variables. Therefore, the model-averaged coefficients are in comparable scales and represent a measure of the effect size of each predictor on the response. The importance of a moderator across models is given by the sum of Akaike weights (w_i) over all models that included that moderator and represents the probability of that moderator appearing in the best model. MAT: mean annual temperature (in degrees centigrade). ΔT : intensity of the experimental warming (ln-transformed, in degrees centigrade). Study duration: ln-transformed, in days.

surprising if studies from these regions suffer from the file-drawer effect. However, we are hopeful that the results of our meta-analysis will motivate publication of such studies, or generate new research in unrepresented regions, so that the trends revealed here can be further tested.

CONCLUSIONS

We showed systematic variation in the effect of warming on top-down control of resource biomass, linked to a geographical temperature gradient across locations, or to factors related to the gradient. Our synthesis suggests that some differences in experimental design across studies may have resulted in deviations from the overall geographical patterns. Nevertheless, There is still much to be learned about the variation in experimental outcomes, including whether consumer–resource interactions respond consistently to warming over larger temporal and global scales.

How does our meta-analysis contribute to a broader understanding of the effects of climate warming on trophic processes in food webs? Given the expected increase in global mean surface temperature towards the end of the century (2.5 °C–7.8 °C [in the log scale are, respectively, 0.916 °C and 2.054 °C]; IPCC 2014), the parameter space depicted in Fig. 3 shows that the magnitude of top-down control should increase in colder regions and decrease towards warmer regions. This indicates a geographical pattern in the response of consumer–resource interactions to climate warming, with cascading consequences for ecosystem functioning. This possibility highlights the urgent need to understand the response of ecological interactions to a changing world.

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AUTHOR CONTRIBUTIONS

NACM designed the study, performed the literature search and data analysis and wrote the first draft of the manuscript. All authors contributed substantially to revisions and the final format of the manuscript.

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