

Predator Diversity and Thermal Niche Complementarity Attenuate Indirect Effects of Warming on Prey Survival

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ABSTRACT: Climate warming has broad-reaching effects on communities. Although much research has focused on direct abiotic effects, indirect effects of warming mediated through biotic interactions can be of equal or greater magnitude. A body of theoretical and empirical work has developed examining the effects of climate warming on predator-prey interactions, but most studies have focused on single predator and prey species. We develop a model with multiple predator species using simulated and measured realized thermal niches from a community of ants to examine the influence of predator diversity and other community thermal traits on the indirect effects of climate warming on prey survival probability. We find that predator diversity attenuates the indirect effect of climate warming on prey survival probability and that sufficient variation of predator thermal optima, closer prey and mean predator thermal optima, and higher predator niche complementarity increases the attenuation effect of predator diversity. We therefore predict that more diverse and complementary communities are likely more affected by direct versus indirect effects of climate warming, and vice versa for less diverse and complementary communities. If general, these predictions could lessen the difficulty of predicting the effects of climate warming on a focal species of interest.

Keywords: climate warming, predator-prey interactions, biodiversity-ecosystem function, complementarity, Sagehen Reserve.

Introduction

Understanding the effects of climate drivers on population dynamics has become an important goal in ecological research, with the ultimate aim of predicting the effects of climate change on communities and ecosystems (Walther et al. 2002; Parmesan 2006). A main driver of climate effects on population dynamics is warming, which affects ectotherms primarily through increased metabolic rate (Uszko

et al. 2017). The direct effects of increased metabolic rates on ectotherms are complex and depend on details of life history, but some predictions are possible on the basis of sufficient life-history information (e.g., Bale et al. 2002; Deutsch et al. 2018). However, the effects of climate change on ecological communities are complicated by biotic interactions, and many effects of climate change on population and community dynamics are likely to be indirect and mediated through biotic interactions (Tylianakis et al. 2008; Post 2013), which cannot be predicted based solely on the life history of the focal species. This complexity makes predicting the impacts of climate warming on individual species—let alone whole communities—extremely difficult.

Recognizing the importance of biotic interactions as mediators of climate change effects, some research has investigated which factors influence climate effects on interactions. For example, mechanistic models and experimental work suggest that the equilibrium population size of predators and prey with warming can be predicted based on predator foraging mode and asymmetries in the relative response rates of predator and prey movement velocity to environmental temperature (Dell et al. 2014; Ohlund et al. 2014). Other work suggests that asymmetries in relative response rates of predator attack rate and development rates of prey with size- or stage-dependent refuges will also affect equilibrium population sizes (Culler et al. 2015; Pepi et al. 2018).

Thus far, most research has focused on single predator-prey pairs. However, most prey species likely interact with multiple predators, all of which will be affected by a warming climate in ways that vary with species' life histories (Barton and Schmitz 2009). Predator diversity is likely to have important impacts on how climate warming affects prey population size, owing to the compensatory effects on many trophic links. These compensatory effects might arise due to variation in predator thermal niches (i.e., range of environmental temperatures utilized within a habitat) that are complementary with respect to foraging activity

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or fitness in a given range of temperatures (i.e., low thermal niche overlap). In this situation, the change in maximum metabolic rate and thus potential attack rate (Vucic-Pestic et al. 2011; Karban et al. 2015) in response to environmental temperature by one predator might be concurrent with changes in another predator that may compensate for the change in attack rate by the first. Alternatively, variation in predator thermal niches may not result in compensation if thermal niches are similar (i.e., a large overlap): with very similar thermal niches, effects of warming on predation might be even more intense than expected for a single predator-prey pair, as attack rates for both predators increase or decrease together with temperature. Besides thermal optima and niche breadth, variation in thermal sensitivity of predators and skewness of thermal response curves may affect the likelihood of compensation across temperature to occur. In particular, significant variation in thermal sensitivity is likely to reduce this compensation effect because predators of significantly different thermal sensitivity will not create effective functional redundancy across temperature.

How warming will affect predator-prey interactions considering multiple predators likely depends on the commu-

nity distribution of thermal response curves, or the community thermal niche (Kühnel and Blüthgen 2015). However, there has been very limited empirical work in this area. Kühnel and Blüthgen (2015) examined flower visitation rates by pollinators in agricultural meadows and characterized the realized thermal niche of 511 species of arthropods based on activity rates across a range of temperatures, finding that higher thermal niche complementarity within communities resulted in greater predicted resilience of pollination function with warming. Systematic variation by insect order was observed, with a great degree of variability of realized thermal niches across species within each community (SD of activity thermal optimum from 3.1° to 5.9°C in different taxa). There was also variation between communities in thermal niche complementarity, which was defined as a weighted coefficient of variation of thermal optima within the community.

For a community with substantial thermal niche variation, if prey species are consumed by multiple predators, it is likely that there will be both positive and negative asymmetries in thermal response rates between the prey species and predators (fig. 1). From this perspective, we can predict that thermal trait responses (e.g., growth rate) of a given

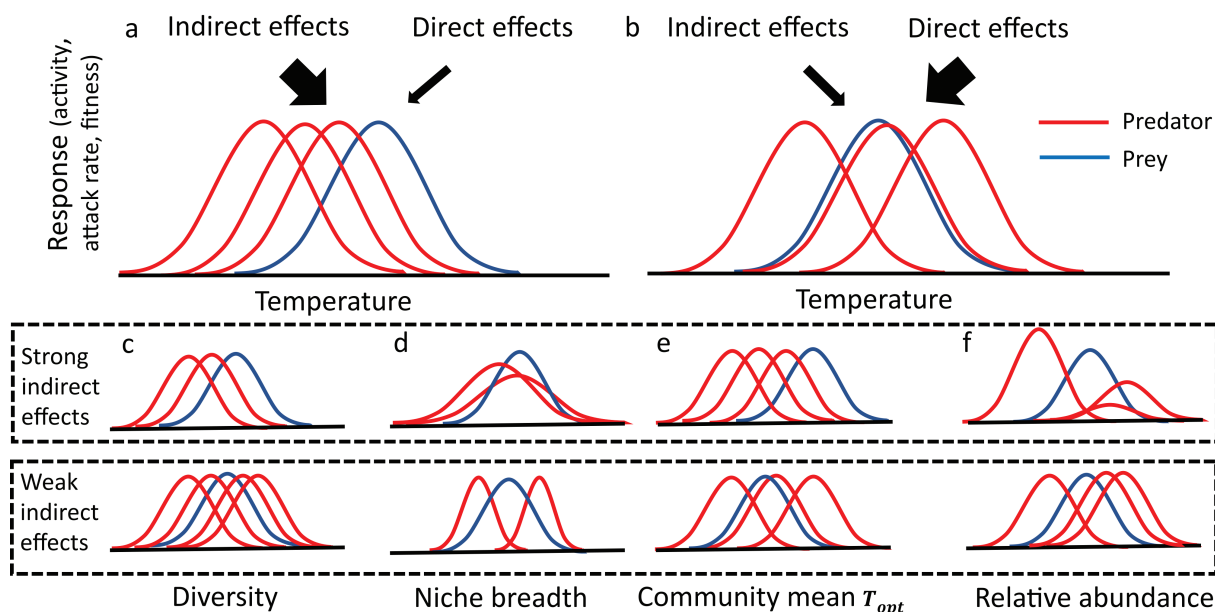


Figure 1: Schematic diagram of community traits that influence the relative importance of direct versus indirect effects of warming on interactions between a prey species (blue) and a community of predators (red). Large asymmetries in thermal niches between predators and prey will result in large indirect versus direct effects of warming (a), whereas symmetric thermal niches will result in larger direct versus indirect effects (b). Asymmetries in thermal responses between prey and the predator community and thus the relative magnitude of indirect versus direct effects depend on multiple aspects of the predator community thermal niche. Based on our simulation models, we hypothesize that greater diversity (c), narrower thermal niche breadth (d), correspondence between the community mean thermal optimum and prey thermal optimum (e), an even predator species abundance distribution (f), and greater community variation in species thermal optima (not shown) will result in weaker indirect effects versus direct effects of warming. The top row of c–f represents scenarios in which strong indirect effects are expected, while the bottom row of c–f represents scenarios in which weak indirect effects are expected.

prey species relative to all the thermal trait responses of the predators (e.g., attack rate) with which it interacts will determine whether climate effects mediated by predation lead to an increase or decline of the prey species. This means that for prey populations interacting with a single or few predator species, it is very likely that asymmetries will be an important mediator of climate effects of population levels. However, as the number of interacting predator species increases, the likelihood that a large net asymmetry in thermal trait responses between predator and prey will remain becomes lower if the predator thermal niches are not all warmer or cooler than the prey. In this latter situation, we would expect that the indirect climate effects mediated by biotic interactors become less important and thus the direct effects of warming should be more important.

To investigate the effects of predator diversity on prey abundance owing to thermal rate asymmetries in a warming environment, we developed a simulation model of predator-prey communities. For this study, we use the example of a univoltine invertebrate prey species with a temperature-dependent window of vulnerability, based on data from an Arctiine moth (*Arctia virginalis*; Pepi et al. 2018). This type of life history, in which a species is vulnerable to predators during a juvenile stage or below a certain size threshold that is approached at a temperature-dependent growth rate, is common across taxa (e.g., insects [Benrey and Denno 1997], amphibians [Werner 1986], and marine organisms [Paine 1976; Mittelbach 1981; Christensen 1996]). We used simulated communities of predators to test our prediction that increased predator diversity will weaken indirect effects of warming. We also characterized the realized thermal niches of a community of 23 species of ants in California as an empirical example of our simulated predator communities. We conducted sensitivity analyses to examine under which conditions we would expect predator diversity to attenuate the indirect effects of warming. We conducted sensitivity analyses on the range of variation (SD) of predator thermal optima, predator thermal niche breadth, the relative value of the predator community mean thermal optimum versus the prey species thermal optimum, and evenness of the predator species abundance distribution on changes to prey survival probability with warming.

Methods

Simulation Model

We developed a demographic model to simulate temperature-dependent survival probability across one generation of a single prey species, interacting with one or many predator species, extending a model previously developed in Pepi et al. (2018). This model combines temperature-dependent growth of prey, prey size-dependent predation, and tem-

perature-dependent attack of predators to simulate predation risk P at environmental temperature T :

$$P(T) = \prod_{i=1}^m \text{logit}^{-1} \{ c \{ a_0 + a(x_0^{r(T)t_i}) \} \sum_{j=1}^n \frac{r_j(T)}{n} \}, \quad (1)$$

in which t_i represents time in days, m represents the length of the simulation in days, x_0 represents log initial caterpillar mass (10 mg), T represents environmental temperature in degrees Celsius (from 10° to 30°C; chosen to correspond with empirical values below), r represents the instantaneous daily growth rate of the prey as a function of temperature, a_0 and a represent the intercept and slope of size-dependent daily predation, c represents a constant to scale size-dependent predation at the starting size of one, n represents the number of predator species in the community, and r_j represents the daily predation rate of the predator j on prey as a function of temperature. To determine predation risk at each temperature, daily size-dependent predation risk is calculated based on prey size (scaled relative to a maximum predation rate of one at x_0), which in turn is calculated based on temperature-dependent exponential growth. Size-dependent predation risk is multiplied by the combined (unweighted) average search and consumption (attack) rate of all predators in the community. The temperature-dependent growth rate (r) of prey and attack rate of predators (r_j) are modeled as unimodal Gaussian functions of environmental temperature (T) after Taylor (1981):

$$r(T) = r_{\max} e^{-0.5((T-T_{\text{opt}})/\sigma_{\text{opt}})^2}, \quad (2)$$

in which r_{\max} represents the maximum rate, T_{opt} represents the thermal optimum, and σ_{opt} determines the spread of the unimodal curve. For predators, the thermal optimum is drawn from normal distribution with mean μ and standard deviation σ^2 .

Simulations of predator communities were conducted, including one, two, three, 10, and 30 predators to assess the effects of predator diversity on prey under warming. Size-dependent predation risk was parameterized based on field data from *Arctia virginalis* caterpillars preyed on by *Formica lasioides* (Pepi et al. 2018; table 1). Temperature-dependent survival and growth of *A. virginalis* caterpillars reared in incubators at constant temperatures from 10° to 25°C were estimated using equation (2) and used to compare the direct versus indirect effects of warming (Pepi et al. 2018). A mean thermal optimum of 23.5°C (to match the thermal optimum of *A. virginalis*; table 1) was used for the distribution of the predator community, with a standard deviation of 5, which is within the upper range of variation documented by Kühsel and Blüthgen (2015) in natural arthropod communities.

For each simulation, the indirect effect of warming on survival (Δ_{indirect}) was calculated. We define this as the net

Table 1: Values of parameters used for simulations, or values when parameters were held constant in sensitivity analyses

Parameter	Description	Value when constant
Size-dependent predation:		
a_0	Intercept	2.7576
a	Slope	-1.438
x_0	Starting size (mg)	10
c	Scaling constant	2.739361
Prey growth:		
r_{\max}	Maximum rate	5.9
T_{opt}	Thermal optimum (°C)	23.5
σ_{opt}	Niche breadth (°C)	6.7
Prey rearing survival:		
r_{\max}	Maximum rate	.75299
T_{opt}	Thermal optimum (°C)	17.661
σ_{opt}	Niche breadth (°C)	7.9
Predator attack rate:		
r_{\max}	Maximum rate	.8
μ of T_{opt}	Mean of thermal optimum (°C)	23.5
σ of T_{opt}	Standard deviation of thermal optimum (°C)	5
σ_{opt}	Niche breadth (°C)	4

Sources: Size-dependent predation: Pepi et al. (2018). Prey growth: fitted from rearing data in Pepi et al. (2018). Prey rearing survival: estimated from unpublished data and rearing method in Pepi et al. (2018). Predator attack rate: r_{\max} extrapolated from data in Karban et al. (2015), μ of T_{opt} set equal to T_{opt} of prey, and σ of T_{opt} and σ_{opt} chosen based on values in Kühsel and Blüthgen (2015).

change (positive and negative) in the difference between rearing survival and survival including rearing survival and predation risk with respect to environmental temperature T between minimum and maximum T . We calculate this value by integrating the absolute value of the derivative with respect to T :

$$\Delta_{\text{indirect}} = \int_{T_{\max}}^{T_{\min}} \left| \frac{d\{R(T) - R(T)P(T)\}}{dT} \right| dT, \quad (3)$$

in which $R(T)$ represents rearing survival at temperature T and $P(T)$ represents predation risk at temperature T as defined in equation (1). We used the absolute value of the derivative because we are interested in how much net change is due to the indirect action of warming, in a positive or negative direction. According to the net change theorem and the definition of an absolute value, equation (3) simplifies to

$$\int_a^b \left| \frac{d\{R(T) - R(T)P(T)\}}{dT} \right| dT = |(R(a) - R(a)P(a)) - (R(b) - R(b)P(b))| \quad (4)$$

for any monotonic interval $a \rightarrow b$.

To identify subintervals that are monotonic, we fit a third-order polynomial function fit in the following form:

$$R(T) - R(T)P(T) \sim \alpha_0 + \beta_1 T + \beta_2 T^2 + \beta_3 T^3. \quad (5)$$

We then calculated all real roots of the derivative of this polynomial (5) to define monotonic subintervals. We cal-

culated the absolute value of change within these subintervals as in equation (4) and summed all intervals for net change between minimum and maximum temperature. For each predator community size, 10,000 simulations were conducted and the distribution of Δ_{indirect} was summarized.

To test the broader applicability of the simulation model beyond the particular parameter values chosen for the initial constant parameter model, and to understand the broader ecological implications of the results, we conducted univariate sensitivity analyses. Model sensitivity to community thermal niche parameters was analyzed by individually varying the standard deviation and mean of the distribution of predator thermal optima, as well as the spread of predator thermal niches (σ_{opt} in eq. [2]). We conducted an additional sensitivity analysis of the main model assumption of a uniform predator species abundance distribution by using a lognormal species abundance distribution. For this sensitivity analysis, predator abundances were drawn from a distribution $N_j \sim \text{lognormal}(1, \sigma^2)$ and converted to relative abundances out of the total number of species. This was calculated as a weight by dividing by the sum of species abundances and multiplying by the number of species ($w_j = (nN_j / \sum_{j=1}^n N_j)$). This resulted in a modification of equation (1) with a weighted average of predator attack rates:

$$P(T) = \prod_{i=1}^m \text{logit}^{-1} \{c\{a_0 + a(x_0^{r(T)t_i})\} \frac{\sum_{j=1}^n r_j(T)w_j}{\sum_{j=1}^n w_j}\}. \quad (6)$$

Using this modification, σ^2 of the lognormal species abundance distribution was varied, starting at zero (which represents the base model assumption of even species abundances). All simulations were conducted in R (ver. 3.6.1; R Development Core Team 2020), and plots were created using ggplot2 (Wickham 2016).

Empirical Data: Ant Community Thermal Niche

Realized thermal niches of ants were estimated by pairing passively collected foraging ants with detailed ground surface temperature measurements. This results in a combined activity-abundance measure as a function of temperature, which should be proportional to prey encounter rate. Collections were made using automated time-sorting pitfall traps, which simultaneously measure ground-surface temperature and separate active ants into 24 separate hour-long pitfall samples (McMunn 2017). To install traps, we carefully removed leaf litter and dug a small hole approximately 20 cm wide, 30 cm long, and 20 cm deep. We then buried the trap, replacing soil flush with the top of the trap entrance, a funnel coated with fluon (Insect-a-Slip; Bioquip, Rancho Cordova, CA). We replaced leaf litter, taking care to minimize the disturbance to the surrounding litter and soil. After installation, the traps remained closed to ants for 24 h to avoid ants being initially attracted to the soil disturbance following pitfall trap installation (Greenslade 1973). We separated ants from all other collected arthropods, identified each individual by species, and after confirmation of species identifications by Philip Ward (University of California, Davis) deposited vouchers at the Bohart Museum of Entomology (University of California, Davis).

The study area consisted of 4.2 hectares of mixed sagebrush shrubs and coniferous forest in the Sierra Nevada mountain range (2,000 m; 39.435583°N, 120.264017°W). The range of *A. virginialis*, which was used to parameterize the prey thermal response in the simulation model, extends to this geographic area. Of the ant species in this community with known diets, all are omnivorous and would consume lepidopteran larvae if encountered, though we have directly observed predation of *A. virginialis* by only two species (*Formica lasioides* and *Tapinoma sessile*). We made collections between June 19 and October 14, 2015, concentrated in 1- or 2-week sampling bouts each month. From a grid of 600 potential sites across the habitat, we randomly selected 127 sites for 24 hourly ant collections. Over the season, this resulted in 3,048 hour-long samples of ant abundance (24 h \times 127 sites = 3,048 hourly samples). The traps recorded temperature measurements every 5 min using a K-type thermocouple datalogger at a height of 1–3 mm above the surface of the leaf litter or above the surface of the soil if no litter was present (McMunn 2017). We took the mean of all temperature measurements within the

1-h ant collection windows and used this hourly mean to estimate ant thermal niche. In general, ant body temperature rapidly equilibrates to environmental temperature because of small body size (Kaspari et al. 2015), so we assumed that ants captured at a given temperature likely experience a body temperature similar to the temperature measured on our thermocouples.

Ant realized thermal niche was modeled by species with equation (2) fitted using nls (package nlme; Pinheiro et al. 2019), using abundance data aggregated across all sampling locations and dates. We expected ant occurrence and abundance to be strongly affected by factors other than temperature (e.g., leaf litter depth, time of day) and suspect that many of these factors contributed to the broad and overlapping realized thermal niches that we observed. Realized thermal niche provides estimates of the effects of temperature on ant activity within a natural community and provides a conservative estimate of the attenuation effect of predator diversity on indirect effects of warming. Fitted parameter values for 23 ant species that were sufficiently abundant to successfully fit thermal response curves were used to generate simulated communities of varying diversity. Species were drawn randomly without replacement from this set of 23 for simulations, using the same procedure as described above, except that values of T_{opt} and σ_{opt} were fitted values from the ant community data. We did not account for predator body size in this updated model (or in the original), as nearly all ants were a similar magnitude smaller than prey species (roughly one-tenth the size of caterpillars or less). Since there were large differences in abundance between ant species in this community (which is dominated by two or three species), simulations were conducted both with estimated r_{max} values (maximum activity rate by species) and with all values of $r_{\text{max}} = 0.8$, to create an even distribution of species. Although this adjustment does not represent the likely effect of actual warming in this specific community, we set abundances to be even to estimate the maximal effect of varying degrees of diversity using thermal traits of a real assemblage of species, since this community had a very low effective diversity owing to strong dominance and low evenness.

Results

Individual simulations generally showed more stability in overall predation rate over the environmental temperature range with higher predator diversity (fig. 2), and the results of many simulations together showed a decrease in Δ_{indirect} with higher predator diversity (fig. 3a) with the initial constant parameter values (table 1). In simulations using empirical ant community data, greater ant diversity did not generate a decrease in Δ_{indirect} with fitted r_{max} values

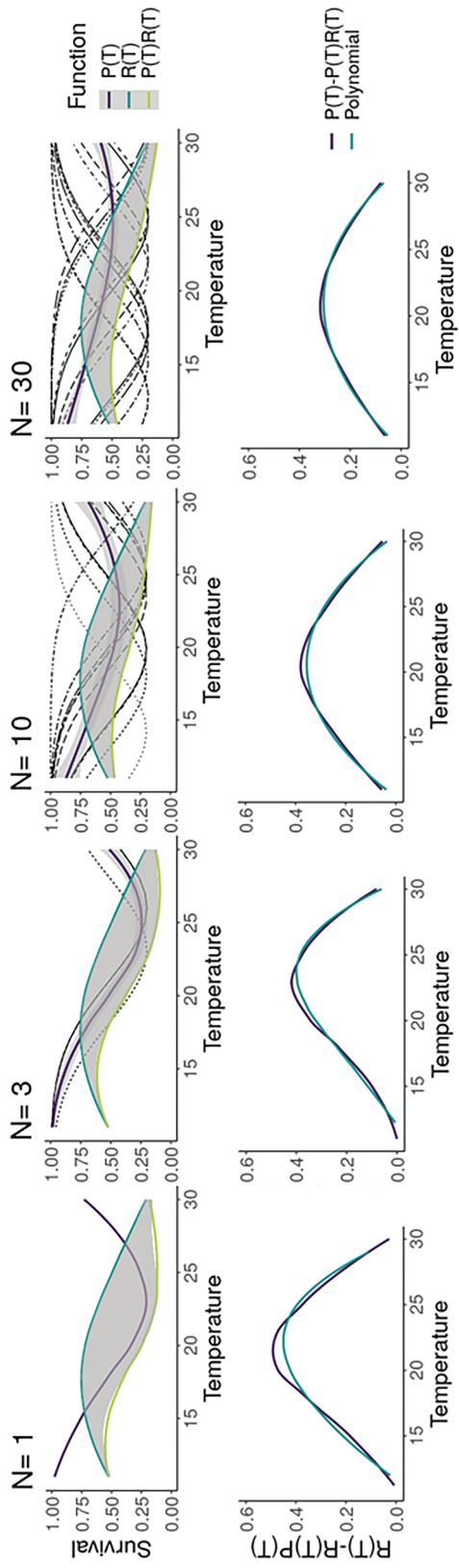


Figure 2: Representative simulation results of prey survival with increasing temperature preyed on by 1–30 predator species, from left to right, showing reduced indirect effects of warming with increasing diversity. In the first row, black lines show $(1 - \text{predation rate})$ of each predator (not visible for $N = 1$), with additional lines showing $P(T)$ ($1 - \text{mean predation rate}$; eq. [1]) of all predators with a 95% confidence interval, rearing survival of prey ($R(T)$; eq. [2]), and the combined effects of predation and rearing on survival ($R(T)P(T)$). The gray band in the first row shows the indirect effect of warming ($R(T) - R(T)P(T)$). In the second row, the indirect effect of warming ($R(T) - R(T)P(T)$) is shown along with the fitted cubic polynomial (eq. [5]).

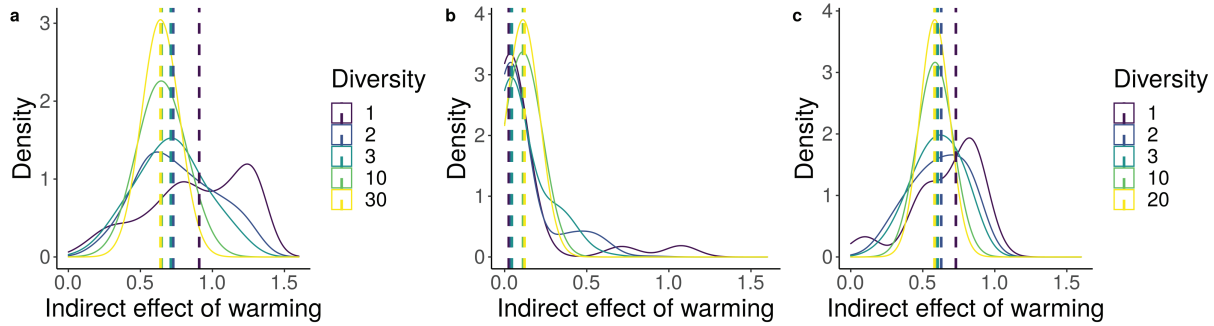


Figure 3: Distribution of indirect effects of warming from 10,000 simulations of a prey species preyed on by a community of 1–30 predators, with a simulated community of predators (a), a community of ants in California (b), and the same community of ants with $r_{\max} = 0.8$ for all species (c). The median of each distribution is displayed by a dashed vertical line.

(fig. 3b), but with all values of $r_{\max} = 0.8$, greater ant diversity did lead to a decrease in Δ_{indirect} (fig. 3c).

Increasing the standard deviation of predator thermal optima increased the effect of diversity on Δ_{indirect} up to a standard deviation of ~ 8 (fig. 4b), and changing the mean of predator thermal optima increased the effect of diversity of Δ_{indirect} when the mean was closer to the prey thermal optimum in terms of survival (17.66°C; fig. 4a). Increasing the breadth of predator thermal niches decreased the effect of diversity on Δ_{indirect} (fig. 4c). Increasing variation in relative species abundances increased the number of species required to reduce Δ_{indirect} (fig. 4d).

Discussion

We show in our simulations, using simulated and fitted parameter values from a predator-prey community of ants and a caterpillar, that increasing predator diversity may under some circumstances attenuate indirect effects of warming on prey species. The attenuation of the indirect effects of warming we define here as the change in survival probability owing to changing interactions with predators (Δ_{indirect}). The vast majority of the attenuation effect of diversity results from very small increases in diversity in most cases (figs. 3, 4), because having even two versus one species greatly reduces the likelihood of thermal asymmetries in simulated communities. We find that the attenuation effect of diversity is greater when there is sufficient variation in predator thermal optimum and when predators have narrower, nonoverlapping niches—that is, when predators have higher thermal niche complementarity. The effect of diversity on Δ_{indirect} is greater when the mean of the distribution of predator thermal optima is closer to the thermal optimum of prey survival. In addition, the effect of diversity on Δ_{indirect} is greater when relative predator species abundance is close to even. Overall, this suggests that higher effective predator diversity and thermal niche complemen-

tarity may buffer indirect effects of warming on a prey species. Our findings also predict that in general, climate warming effects on prey species that are preyed on by many thermally complementary predator species (i.e., with nonoverlapping niches) should primarily be direct as opposed to indirect effects. If generally applicable, this prediction could aid in distinguishing in which circumstances direct effects of warming—which have the potential to be predictable based on species life-history information—are likely to dominate versus those in which indirect effects of warming would be expected to dominate. This would have the potential for significant value in unraveling some of the complexity of the effects of climate on species when considering trophic interactions (e.g., Post 2013; Dell et al. 2014).

In addition to purely simulated communities of predators, we parameterized our simulation model using empirical data from a community of ants. In this case, rather than using measured attack rates, we use ant activity-abundance rates at a given temperature, which are likely to be proportional to attack rate on prey at a given temperature. In general, we expect attack rate to be proportional to search or discovery rate, which generally increases with temperature up to the thermal optimum of ants (Prather et al. 2018). Because of extreme variation in the rank abundances of ants (see table S1, available online), we found no effect of diversity on Δ_{indirect} with fitted r_{\max} values; however, there was an effect of diversity when all r_{\max} values were set to be the same. We set all r_{\max} values as equal because we were interested in examining the effect of varying levels of effective predator diversity using a real assemblage of species; using fitted r_{\max} values amounted to imposing a very low maximum diversity due to high dominance. The effect observed with equal r_{\max} values from the ant community was smaller than that of simulations using purely simulated parameter values, because this community of ants consists largely of thermal generalists that

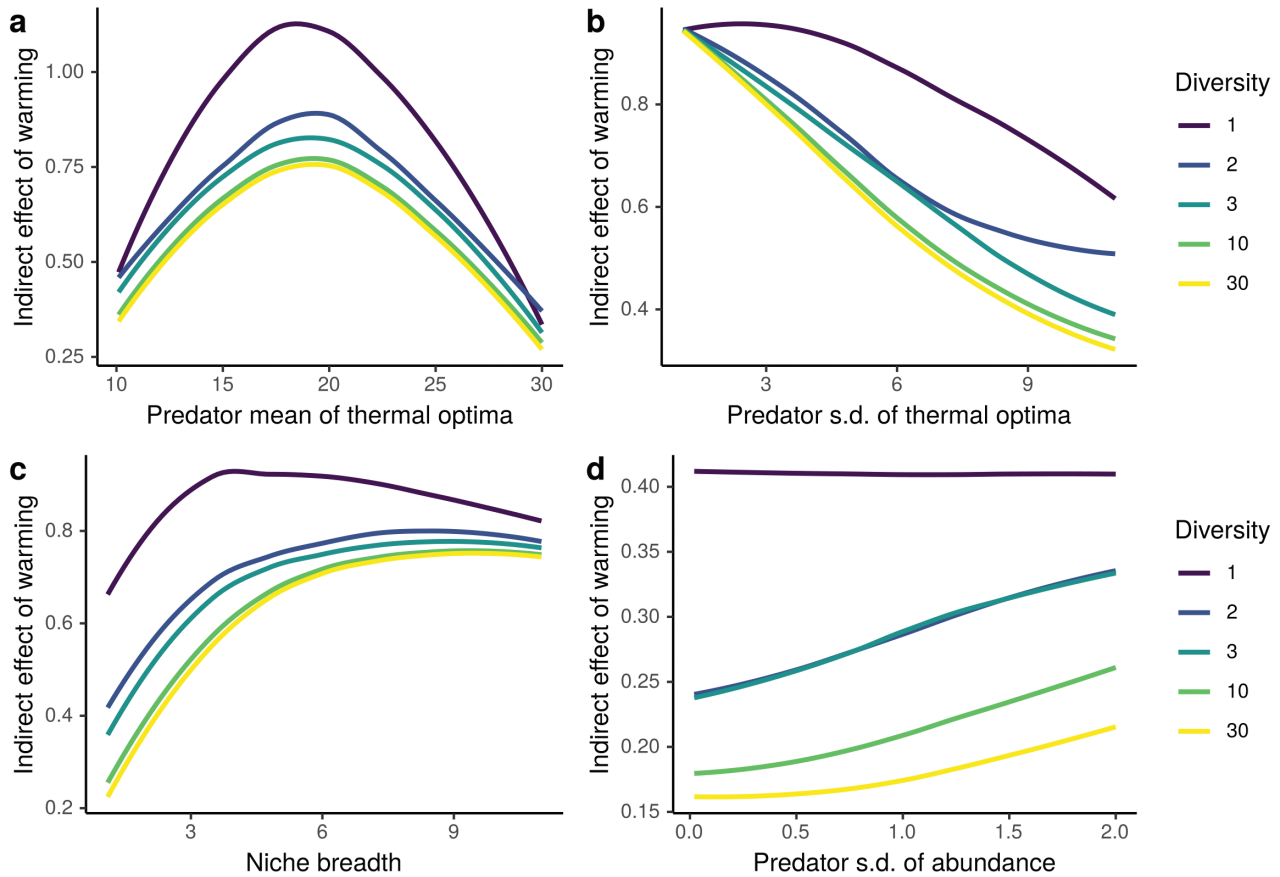


Figure 4: Sensitivity analysis of simulation model, showing the median indirect effect of warming (Δ_{indirect}) for communities of one, two, three, 10, and 30 predators. Sensitivity analyses are shown with respect to the mean of predator thermal optima (T_{opt} ; *a*), standard deviation (s.d.) of predator thermal optima (*b*), predator thermal niche breadth (σ_{opt} ; *c*), and standard deviation of the lognormal species abundance distribution (*d*).

have large niche breadths (σ_{opt}) relative to the variation of thermal optima (T_{opt}) and low complementarity (i.e., large niche overlap; fig. S1, available online). The fact that we observed an effect of predator diversity on Δ_{indirect} (albeit with adjusted r_{max} values) even in a predator community that our a priori expectation would be for little or no effect of diversity lends credence to the idea that this effect may be common in nature, in communities with similar or higher thermal niche complementarity. In addition, since our measured community includes only species from the same family (Formicidae), it is likely a significant underestimate of the thermal niche diversity in the full community of arthropods at this site, which includes taxa with generally very different thermal niches than ants (e.g., hemipterans, spiders, solifugids, etc.).

In this study, we emphasize the concept of the community thermal niche, first developed by Kühsel and Blüthgen (2015), which refers to the collection of the thermal niches of all the individual species in the community. In light of

what we have shown in our simulations, we believe that the community thermal niche is a valuable concept to help understand how communities are likely to respond to climate warming and that a collection of such community data sets would significantly advance our understanding of the ecological effects of warming. There has been a great deal of both empirical (e.g., Brown et al. 2004; Kingsolver and Huey 2008; Kingsolver 2009; Dell et al. 2011) and theoretical (e.g., Rall et al. 2010; Dell et al. 2014; Uszko et al. 2017) work on the effects of temperature on fitness, species interactions, and even simple food webs (Petchey et al. 1999, 2010; Barton and Schmitz 2009). However, the extension of thermal ecology to thermal community ecology should be a priority since individual species and species interactions exist within broader food webs and ecological communities. With the theoretical perspective developed here, some predictions can be made about which aspects of community thermal niche might be important for outcomes with a warming climate.

The range of variation of thermal optima in a community is the primary aspect of the community thermal niche that we expect to mediate effects of warming on a community. As identified by Kühsel and Blüthgen (2015), greater variation in thermal optima in a community represents higher functional diversity, which has been predicted by theory to create greater resilience to environmental change, which they found to be the case for the communities of pollinators that they studied. In the present study, we further show that large variation of thermal optima in a community increases the potential for predator diversity to attenuate indirect effects of warming on prey species. This has the potential to aid in predictions of the effects of warming on predator-prey dynamics: if a community has sufficient variation in predator thermal niches, then we can expect that climate will have a greater effect on prey species via direct effects than indirect effects.

The breadth of thermal niches within a community is another aspect of the community thermal niche that we expect to have important implications for the effects of warming on a community. For community resilience, greater thermal niche breadth has a positive effect, since greater breadth of function can only increase resilience (Kühsel and Blüthgen 2015). Kühsel and Blüthgen (2015) define thermal niche complementarity for their purposes as the weighted coefficient of variation of thermal optima. Since we are interested in the degree of change in predation risk with temperature, complementarity here results from a combination of sufficient variation in predator thermal optima as well as narrower predator niche breadth (fig. 4b, 4c). Narrower thermal niches with sufficiently different optima result in less change in predation risk with environmental temperature because as one predator becomes less active, there is another that is becoming more active, resulting in a consistent predation risk despite changing temperature. In this way, high complementarity combined with greater species diversity should lead to much weaker indirect effects of warming.

From here we can ask, in which communities do we expect to see narrower thermal niches, greater variation in thermal optima, and greater diversity of predators and therefore weaker indirect effects of warming? Generally, we expect to see narrower thermal niches (Janzen 1967; Deutsch et al. 2008) and greater diversity (Mittelbach et al. 2007) of ectotherms in the tropics. All else being equal, this would predict weaker indirect effects of warming in the tropics. However, if ectotherms in temperate environments have higher variation in thermal optima than in the tropics, this might counteract broader niches in the temperate zone in terms of the attenuation effect of predator diversity on indirect effects of warming. In this scenario, whether temperate and tropical ectotherm predator communities have similar or different thermal niche complementarity might

depend on whether the relative magnitude in the increase of niche breadth and variation in thermal optima with latitude are similar or different enough to result in positive, negative, or no change in complementarity with latitude.

We also found from sensitivity analyses that decreasing distance of the thermal optimum of prey survival (in our simulations, 17.66°C) from the mean of predator thermal optima leads to both greater overall indirect effects of warming and greater attenuation of indirect effects by predator diversity. This means that the thermal optimum of a prey species relative to the community of potential predators has important implications with respect to climate warming effects. If we assume that a species has an invariant thermal niche across its range (which may or may not be the case; Angilletta et al. 2002) and that most species are best adapted to thermal conditions at the climatic mean of their range, then on average a species near its range limit is likely to have a lower thermal optimum than most other species in the community at the warmer edge and a higher thermal optimum than most other species at the colder range edge. If this is the case, we can expect much stronger indirect effects of warming at range edges because of more consistent directional asymmetries and therefore weaker compensating effects of predator diversity. Such effects could contribute to range shifts owing to climate warming, through negative indirect effects at warmer range edges and positive indirect effects at the colder range edge.

Our modeling approach makes several simplifying assumptions. First, we examine only short-term dynamics, consider only prey survival and reproduction, and do not consider long-term outcomes. This is because coexistence of multiple predators in the long term is not simple, since generally whichever predator more efficiently utilizes a prey species will outcompete all the others (Tilman 1982) and examining mechanisms of predator coexistence is beyond the scope of this study. In addition, we do not consider the effects of warming on predator-predator interactions or of functional responses to prey density. The effects of predator-predator interactions are likely to result in dominance of some predators over others, which, based on our results, would be expected to reduce the attenuating effect of predator diversity on indirect effects of warming. Similarly, if predators differ in their functional responses to prey density as it decreases over time (e.g., prey switching or not), that would likely serve to reduce the attenuating effect of predator diversity. In both cases, greater predator diversity would likely be required for an equivalent attenuating effect.

Given our results, we see several further theoretical and empirical research directions that we believe would provide significant insight into the topic of predicting indirect versus direct effects of climate warming on predator-prey communities. Further modeling work could incorporate

short-term dynamics as explored here into dynamical models examining long-term behavior of predator-prey communities with varying traits that influence significant aspects of the community thermal niche. In addition, further modeling work could investigate the effects of multiple prey species and integrate effects of the community thermal niche and food web structure. The empirical characterization of the community thermal niche of more species assemblages is also an essential next step to further test ideas developed here. We believe that these data are essential for understanding how climate warming will affect communities through direct versus indirect pathways. Automated sampling methods as used here (McMunn 2017) offer the potential to relatively easily characterize the thermal activity distributions of other assemblages of invertebrates, a task that would otherwise be logistically difficult. Finally, manipulative experiments of warmed communities in mesocosms would offer the strongest test of hypotheses developed here with regard to how multiple aspects of the community thermal niche will influence the relative importance of direct versus indirect effects of warming on predator-prey communities.

Conclusions

Theoretical and empirical work investigating the effects of climate warming on species interactions has made significant progress in describing how climate warming is expected to affect ectotherm predator-prey pairs (e.g., Dell et al. 2014; Uszko et al. 2017). Little work has extended to examine the effects of warming on multispecies interactions (but see Barton and Schmitz 2009). We propose that the community thermal niche (Kühnel and Blüthgen 2015) is a useful concept and approach to investigate community dynamics under climate warming, based on predictions with regard to community thermal niche traits from our simulation models developed here. Specifically, we predict that species preyed on by many thermal complementary predators will experience weaker indirect effects of warming than those that are preyed on by fewer or less complementary predators. Predictions that can be derived from traits of species composing a community are essential if we are to decompose some of the complexity of climate warming effects on communities that are mediated through biotic interactions (cf. Tylianakis et al. 2008; Post 2013; Dell et al. 2014).

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Statement of Authorship

A.P. conceived the project, conducted the analyses, and wrote the manuscript. M.M. collected the data and contributed to conceptual development, analyses, and writing. Both authors critically contributed to final drafts.

Data and Code Availability

The data and code associated with this paper are available on Knowledge Network for Biocomplexity: <https://doi.org/10.5063/MP51P6>.

Literature Cited

- Angilletta, M. J., Jr., P. H. Niewiarowski, and C. A. Navas. 2002. The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology* 27:249–268.
- Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, et al. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* 8:1–16.
- Barton, B. T., and O. J. Schmitz. 2009. Experimental warming transforms multiple predator effects in a grassland food web. *Ecology Letters* 12:1317–1325.
- Benrey, B., and R. F. Denno. 1997. The slow-growth-high-mortality hypothesis: a test using the cabbage butterfly. *Ecology* 78:987–999.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* 85:1771–1789.
- Christensen, B. 1996. Predator foraging capabilities and prey anti-predator behaviours: pre- versus postcapture constraints on size-dependent predator-prey interactions. *Oikos* 76:368–380.
- Culler, L. E., M. P. Ayres, R. A. Virginia, and L. E. Culler. 2015. In a warmer Arctic, mosquitoes avoid increased mortality from predators by growing faster. *Proceedings of the Royal Society B* 282:20151549.
- Dell, A. I., S. Pawar, and V. M. Savage. 2011. Systematic variation in the temperature dependence of physiological and ecological traits. *Proceedings of the National Academy of Sciences of the USA* 108:10591–10596.
- . 2014. Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. *Journal of Animal Ecology* 83:70–84.
- Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the USA* 105:6668–6672.
- Deutsch, C. A., J. J. Tewksbury, M. Tigchelaar, D. S. Battisti, S. C. Merrill, R. B. Huey, and R. L. Naylor. 2018. Increase in crop losses to insect pests in a warming climate. *Science* 361:916–919.
- Greenslade, P. J. M. 1973. Sampling ants with pitfall traps: digging-in effects. *Insectes Sociaux* 20:343–353.
- Janzen, D. H. 1967. Why mountain passes are higher in the tropics. *American Naturalist* 101:233–249.

- Karban, R., P. Grof-Tisza, M. McMunn, H. Kharouba, and M. Huntzinger. 2015. Caterpillars escape predation in habitat and thermal refuges. *Ecological Entomology* 40:725–731.
- Kaspari, M., N. A. Clay, J. Lucas, S. P. Yanoviak, and A. Kay. 2015. Thermal adaptation generates a diversity of thermal limits in a rainforest ant community. *Global Change Biology* 21:1092–1102.
- Kingsolver, J. G. 2009. The well-temperated biologist. *American Naturalist* 174:755–768.
- Kingsolver, J. G., and R. B. Huey. 2008. Size, temperature, and fitness: three rules. *Evolutionary Ecology Research* 10:251–268.
- Kühnel, S., and N. Blüthgen. 2015. High diversity stabilizes the thermal resilience of pollinator communities in intensively managed grasslands. *Nature Communications* 6:2–9.
- McMunn, M. S. 2017. A time-sorting pitfall trap and temperature datalogger for the sampling of surface-active arthropods. *HardwareX* 1:38–45.
- Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* 62:1370–1386.
- Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P. Harrison, et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters* 10:315–331.
- Ohlund, G., P. Hedstrom, S. Norman, C. L. Hein, and G. Englund. 2014. Temperature dependence of predation depends on the relative performance of predators and prey. *Proceedings of the Royal Society B* 282:20142254.
- Paine, T. 1976. Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology* 57:858–873.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37:637–669.
- Pepi, A., P. Grof-Tisza, M. Holyoak, and R. Karban. 2018. As temperature increases, predator attack rate is more important to survival than a smaller window of prey vulnerability. *Ecology* 99:1584–1590.
- Petchey, O. L., U. Brose, and B. C. Rall. 2010. Predicting the effects of temperature on food web connectance. *Philosophical Transactions of the Royal Society B* 365:2081–2091.
- Petchey, O. L., P. T. McPhearson, T. M. Casey, and P. J. Morin. 1999. Environmental warming alters food-web structure and ecosystem function. *Nature* 402:69–72.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Development Core Team. 2019. nlme: linear and nonlinear mixed effects models. <https://cran.r-project.org/web/packages/nlme/index.html>.
- Post, E. 2013. Ecology of climate change: the importance of biotic interactions. Princeton University Press, Princeton, NJ.
- Prather, R. M., K. A. Roeder, N. J. Sanders, and M. Kaspari. 2018. Using metabolic and thermal ecology to predict temperature dependent ecosystem activity: a test with prairie ants. *Ecology* 99:2113–2121.
- Rall, B. C., O. Vucic-Pestic, R. B. Ehnes, M. Emmerson, and U. Brose. 2010. Temperature, predator-prey interaction strength and population stability. *Global Change Biology* 16:2145–2157.
- R Development Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Version 3.6.1. <http://www.R-project.org>.
- Taylor, F. 1981. Ecology and evolution of physiological time in insects. *American Naturalist* 117:1–23.
- Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, NJ.
- Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11:1351–1363.
- Uzsko, W., S. Diehl, G. Englund, and P. Amarasekare. 2017. Effects of warming on predator-prey interactions—a resource-based approach and a theoretical synthesis. *Ecology Letters* 20:513–523.
- Vucic-Pestic, O., R. B. Ehnes, B. C. Rall, and U. Brose. 2011. Warming up the system: higher predator feeding rates but lower energetic efficiencies. *Global Change Biology* 17:1301–1310.
- Walther, G., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. Fromentin, et al. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.
- Werner, E. E. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. *American Naturalist* 128:765–770.
- Wickham, H. 2016. ggplot2: elegant graphics for data analysis. Springer, New York. <https://cran.r-project.org/web/packages/ggplot2/index.html>.

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