

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21

**Predator diversity and thermal niche complementarity attenuate indirect effects of  
warming on prey survival  
Adam Pepi and Marshall McMunn**

## 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 aspects of 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 predict therefore 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. In general, these predictions could lessen the difficulty of predicting the effects of climate warming on a focal species of interest.

## 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 based on 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 upon 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, due 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 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 community 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 (s.d. of activity thermal optimum from 3.1-5.9°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 (Figure 1). From this perspective, we can predict that thermal trait responses (e.g., growth rate) of a given 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

76 predator and prey will remain becomes lower, if the predator thermal niches are not all warmer or  
77 cooler than the prey. In this latter situation, we would expect that the indirect climate effects mediated  
78 by biotic interactors become less important, and thus the direct effects of warming should be more  
79 important.

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

## 96 **Methods**

### 97 *Simulation model*

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

101 growth of prey, prey size-dependent predation, and temperature-dependent attack of predators to  
 102 simulate predation risk  $P$  at environmental temperature  $T$  :

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

103 in which  $t_i$  is time in days,  $m$  is the length of the simulation in days,  $x_0$  is log initial caterpillar mass  
 104 (10 mg),  $T$  is environmental temperature in Celsius (from 10-30 °C),  $r$  is instantaneous daily growth  
 105 rate of the prey as a function of temperature,  $a_0$  and  $a$  represent the intercept and slope of size-  
 106 dependent daily predation,  $c$  is a constant to scale size-dependent predation at the starting size to 1,  $n$  is  
 107 the number of predators species in the community,  $r_j$  is the daily predation rate of the predator  $j$  on  
 108 prey as a function of temperature. To determine predation risk at each temperature, daily size-  
 109 dependent predation risk is calculated based on prey size (scaled relative to a maximum predation rate  
 110 of 1 at  $x_0$  ), which in turn is calculated based upon temperature-dependent exponential growth. Size-  
 111 dependent predation risk is multiplied by the combined (unweighted) average search and consumption  
 112 (attack) rate of all predators in the community. The temperature-dependent growth rate ( $r$ ) of prey and  
 113 attack rate of predators ( $r_j$ ) are modelled as unimodal Gaussian functions of environmental temperature  
 114 ( $T$ ) after Taylor (1981):

$$r(T) = r_{max} e^{-0.5 \left( \frac{T - T_{opt}}{\sigma_{opt}} \right)^2} \quad (2)$$

115  
 116 in which  $r_{max}$  is the maximum rate,  $T_{opt}$  is the thermal optimum, and  $\sigma_{opt}$  determines the spread of the  
 117 unimodal curve. For predators, the thermal optimum is drawn from normal distribution with mean  $\mu$   
 118 and s.d.  $\sigma^2$ .

119 Simulations were conducted of predator communities including 1, 2, 3, 10, and 30 predators to  
 120 assess the effects of predator diversity on prey under warming. Size-dependent predation risk was  
 121 parameterized based on field data from *Arctia virginalis* caterpillars preyed upon by *Formica lasioides*  
 122 (Pepi et al. 2018; Table 1). Temperature-dependent survival and growth of *A. virginalis* caterpillars  
 123 reared in incubators at constant temperatures from 10-25° C were estimated using equation 2 and used  
 124 to compare the direct vs. indirect effects of warming (Pepi et al. 2018). A mean thermal optimum of  
 125 23.5 °C (to match the thermal optimum of *A. virginalis*; Table 1) was used for the distribution of the  
 126 predator community, with an s.d. of 5, which is within the upper range of variation documented by  
 127 Kühnel and Blüthgen (2015) in natural arthropod communities.

128 For each simulation, the indirect effect of warming on survival ( $\Delta_{indirect}$ ) was calculated. We  
 129 define this as the net change (positive and negative) in the difference between rearing survival and  
 130 survival including rearing survival and predation risk with respect to environmental temperature  
 131  $T$  between minimum and maximum  $T$ . We calculate this value by integrating the absolute value of the  
 132 derivative with respect to  $T$ :

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

133  
 134 in which  $R(T)$  is rearing survival at temperature  $T$ , and  $P(T)$  is predation risk at temperature  $T$  as  
 135 defined in equation 1. We used the absolute value derivative because we are interested in how much  
 136 net change is due to the indirect action of warming, in a positive or negative direction.

137 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  $a \rightarrow b$*

138

139 To identify sub-intervals that are monotonic we fit a third order polynomial function fit in the following  
 140 form:

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

141

142 We then calculated all real roots of the derivative of this polynomial (5) to define monotonic sub-  
 143 intervals. We calculated the absolute value of change within these sub-intervals as in equation 4, and  
 144 summed all intervals for net change between minimum and maximum temperature. For each predator  
 145 community size, 10,000 simulations were conducted and the distribution of  $\Delta_{indirect}$  was summarized.

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

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

157 Using this modification,  $\sigma^2$  of the lognormal species abundance distribution was varied, starting  
 158 at zero (which represents the base model assumption of even species abundances).



All simulations were conducted in R version 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 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 hours 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 to species, and after confirmation of species identifications by Philip Ward (UC Davis), deposited vouchers at the Bohart Museum of Entomology (UC Davis).

The study area consisted of 4.2 hectares of mixed sagebrush shrubs and coniferous forest in the Sierra Nevada mountain range (2000 m, 39.435583°N, 120.264017° W). The range of *A. virginalis*, 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. virginalis* by only two species (*Formica lasioides* and *Tapinoma sessile*). We made collections between 19 June and 14 October 2015, concentrated in one- or two-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 3048 hour-long samples of ant abundance (24 hrs × 127

184 sites = 3048 hourly samples). The traps recorded temperature measurements every 5 minutes using a K-  
185 type thermocouple datalogger at a height of 1-3 mm above the surface of the leaf litter or above the  
186 surface of the soil if no litter was present (McMunn 2017). We took the mean of all temperature  
187 measurements within the 1-hour ant collection windows and used this hourly mean to estimate ant  
188 thermal niche. In general, ant body temperature rapidly equilibrates to environmental temperature due  
189 to small body size (Kaspari et al. 2015), so we assumed that ants captured at a given temperature likely  
190 experience a body temperature similar to temperature measured on our thermocouples.

191 Ant realized thermal niche was modelled by species with equation (2) fit using nls (package  
192 nlme, Pinheiro et al. 2017), using abundance data aggregated across all sampling locations and dates.  
193 We expected ant occurrence and abundance to be strongly affected by factors other than temperature  
194 (e.g., leaf litter depth, time of day) and suspect many of these factors contributed to the broad and  
195 overlapping realized thermal niches we observed. Realized thermal niche provides estimates of the  
196 effects of temperature on ant activity within a natural community and provide a conservative estimate  
197 of the attenuation effect of predator diversity on indirect effects of warming. Fitted parameter values  
198 for 23 ant species that were sufficiently abundant to successfully fit thermal response curves were used  
199 to generate simulated communities of varying diversity. Species were drawn randomly without  
200 replacement from this set of 23 for simulations, using the same procedure as described above, except  
201 that values of  $T_{opt}$  and  $\sigma_{opt}$  were fitted values from the ant community data. We did not account for  
202 predator body size in this updated model (or in the original), as nearly all ants were a similar magnitude  
203 smaller than prey species (roughly 1/10 the size of caterpillars or less). Since there were large  
204 differences in abundance between ant species in this community (which is dominated by 2-3 species),  
205 simulations were conducted both with estimated  $r_{max}$  values (maximum activity rate by species), and  
206 with all values of  $r_{max} = 0.8$ , to create an even distribution of species. Although this adjustment does  
207 not represent the likely effect of actual warming in this specific community, we set abundances to be  
208 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 due 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 (Figure 2), and the results of many simulations together showed a decrease in  $\Delta_{indirect}$  with higher predator diversity (Figure 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  $\Delta_{indirect}$  with fitted  $r_{max}$  values (Figure 3b), but with all values of  $r_{max} = 0.8$ , greater ant diversity did lead to a decrease in  $\Delta_{indirect}$  (Figure 3c).

Increasing the s.d of predator thermal optima increased the effect of diversity on  $\Delta_{indirect}$  up to an s.d. of ~8 (Figure 4b), and changing the mean of predator thermal optima increased the effect of diversity of  $\Delta_{indirect}$  when the mean was closer to the prey thermal optimum in terms of survival (17.66 °C ; Figure 4a). Increasing the breadth of predator thermal niches decreased the effect of diversity on  $\Delta_{indirect}$  (Figure 4c). Increasing variation in relative species abundances increased the number of species required to reduce  $\Delta_{indirect}$  (Figure 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 due to changing interactions with predators ( $\Delta_{indirect}$ ). The vast majority of the attenuation effect of diversity results from very small increases in diversity in most cases (Figures 3,4), because having even two vs. one species greatly reduces the likelihood of thermal asymmetries in simulated communities. We find the attenuation effect of diversity is greater when there is sufficient variation in predator thermal optimum and when predators have narrower, non-overlapping niches: that is, when predators have higher thermal niche

234 complementarity. The effect of diversity on  $\Delta_{indirect}$  is greater when the mean of the distribution of  
235 predator thermal optima is closer to the thermal optimum of prey survival. In addition, effect of  
236 diversity on  $\Delta_{indirect}$  is greater when relative predator species abundance is close to even. Overall, this  
237 suggests that higher effective predator diversity and thermal niche complementarity may buffer indirect  
238 effects of warming on a prey species. Our findings also predict that in general, climate warming effects  
239 on prey species that are preyed upon by many thermally complementary predator species (i.e., with  
240 non-overlapping niches) should primarily be direct as opposed to indirect effects. If generally  
241 applicable, this prediction could aid in distinguishing in which circumstances direct effects of warming,  
242 which have the potential to be predictable based on species life-history information, are likely to  
243 dominate vs. those in which indirect effects of warming would be expected to dominate. This would  
244 have the potential for significant value in unravelling some of the complexity of the effects of climate  
245 on species when considering trophic interactions (e.g., Post 2013; Dell et al. 2014).

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

ants consists largely of thermal generalists that have large niche breadths ( $\sigma_{opt}$ ) relative to the variation of thermal optima ( $T_{opt}$ ) and low complementarity (i.e., large niche overlap; Figure S1). The fact that we observed an effect of predator diversity on  $\Delta_{indirect}$  (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 Kühnel 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 datasets 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 work (e.g., Rall et al. 2010; Dell et al. 2014; Uszko et al. 2017) 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

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

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

302         From here, we can ask in which communities do we expect to see narrower thermal niches,  
303 greater variation in thermal optima, and greater diversity of predators, and therefore weaker indirect  
304 effects of warming? Generally, we expect to see narrower thermal niches (Janzen 1967; Deutsch et al.  
305 2008) and greater diversity (Mittelbach et al. 2007) of ectotherms in the tropics. All else being equal  
306 this would predict weaker indirect effects of warming in the tropics. However, if ectotherms in

307 temperate environments have higher variation in thermal optima than in the tropics, this might  
308 counteract broader niches in the temperate zone in terms of the attenuation effect of predator diversity  
309 on indirect effects of warming. In this scenario, whether temperate and tropical ectotherm predator  
310 communities have similar or different thermal niche complementarity might depend on if the relative  
311 magnitude in the increase of niche breadth and variation in thermal optima with latitude are similar or  
312 different enough to result positive, negative, or no change in complementarity with latitude.

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

326         Our modelling approach makes several simplifying assumptions. First, we examine only short-  
327 term dynamics, consider only prey survival and reproduction, and do not consider long-term outcomes.  
328 This is because coexistence of multiple predators in the long term is not simple, since generally  
329 whichever predator more efficiently utilizes a prey species will outcompete all the others (Tilman  
330 1982), and examining mechanisms of predator coexistence is beyond the scope of this study. In  
331 addition, we do not consider the effects of warming on predator-predator interactions, nor of functional

responses to prey density. The effect 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.

Based on our results, we see several further theoretical and empirical research directions that we believe would provide significant insight into the topic of predicting indirect vs. direct effects of climate warming on predator-prey communities. Further modelling 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 modelling 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 vs. 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 which would otherwise be logistically difficult. Lastly, 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 vs. 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 multi-species 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 upon 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).

## References

- Angilletta Jr, M. J., 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 antipredator 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

382 increased mortality from predators by growing faster. *Proceedings of the Royal Society B: Biological*  
383 *Sciences* 282:20151549.

384 Dell, A. I., S. Pawar, and V. M. Savage. 2011. Systematic variation in the temperature dependence of  
385 physiological and ecological traits. *Proceedings of the National Academy of Sciences* 108:10591–  
386 10596.

387 Dell, A. I., S. Pawar, and V. M. Savage. 2014. Temperature dependence of trophic interactions are  
388 driven by asymmetry of species responses and foraging strategy. *Journal of Animal Ecology* 83:70–84.

389 Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R.  
390 Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the*  
391 *National Academy of Sciences* 105:6668–6672.

392 Deutsch, C. A., J. J. Tewksbury, M. Tigchelaar, D. S. Battisti, S. C. Merrill, R. B. Huey, and R. L.  
393 Naylor. 2018. Increase in crop losses to insect pests in a warming climate. *Science* 361:916–919.

394 Greenslade, P. J. M. 1973. Sampling ants with pitfall traps: digging-in effects. *Insectes Sociaux*  
395 20:343–353.

396 Janzen, D. H. 1967. Why mountain passes are higher in the tropics. *The American Naturalist* 101:233–  
397 249.

398 Karban, R., P. Grof-Tisza, M. McMunn, H. Kharouba, and M. Huntzinger. 2015. Caterpillars escape  
399 predation in habitat and thermal refuges. *Ecological Entomology* 40:725–731.

400 Kaspari, M., N. A. Clay, J. Lucas, S. P. Yanoviak, and A. Kay. 2015. Thermal adaptation generates a  
401 diversity of thermal limits in a rainforest ant community. *Global Change Biology* 21:1092–1102.

402 Kingsolver, J. G. 2009. The well-temperated biologist. *The American Naturalist* 174:755–768.

403 Kingsolver, J. G., and R. B. Huey. 2008. Size, temperature, and fitness : three rules. *Evolutionary*  
404 *Ecology Research* 10:251–268.

405 Kühnel, S., and N. Blüthgen. 2015. High diversity stabilizes the thermal resilience of pollinator  
406 communities in intensively managed grasslands. *Nature Communications* 6:2–9.

407 McMunn, M. S. 2017. A time-sorting pitfall trap and temperature datalogger for the sampling of  
408 surface-active arthropods. *HardwareX* 1:38–45.

409 Mittelbach, G. G. . 1981. Foraging efficiency and body size : A study of optimal diet and habitat use by  
410 bluegills. *Ecology* 62:1370–1386.

411 Mittelbach, G. G., D. W. Schemske, H. V Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P. Harrison,  
412 et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography.  
413 *Ecology Letters* 10:315–331.

414 Ohlund, G., P. Hedstrom, S. Norman, C. L. Hein, and G. Englund. 2014. Temperature dependence of  
415 predation depends on the relative performance of predators and prey. *Proceedings of the Royal Society*  
416 *B: Biological Sciences* 282:20142254–20142254.

417 Paine, T. 1976. Size-limited predation : An observational and experimental approach with the *Mytilus-*  
418 *isaster* interaction. *Ecology* 57:858–873.

419 Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of*  
420 *Ecology Evolution and Systematics* 37:637–669.

421 Pepi, A., P. Grof-Tisza, M. Holyoak, and R. Karban. 2018. As temperature increases, predator attack  
422 rate is more important to survival than a smaller window of prey vulnerability. *Ecology* 99:1584–1590.

423 Petchey, O. L., U. Brose, and B. C. Rall. 2010. Predicting the effects of temperature on food web  
424 connectance. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2081–2091.

425 Petchey, O. L., P. T. McPhearson, T. M. Casey, and P. J. Morin. 1999. Environmental warming alters  
426 food-web structure and ecosystem function. *Nature* 402:69–72.

427 Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R. D. C. Team. 2019. nlme: Linear and nonlinear  
428 mixed effects models.

429 Post, E. 2013. *Ecology of climate change: the importance of biotic interactions*. Princeton University  
430 Press, Princeton.

431 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.

R Development Core Team. 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

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.

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., Prin.

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.

Uszko, 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.

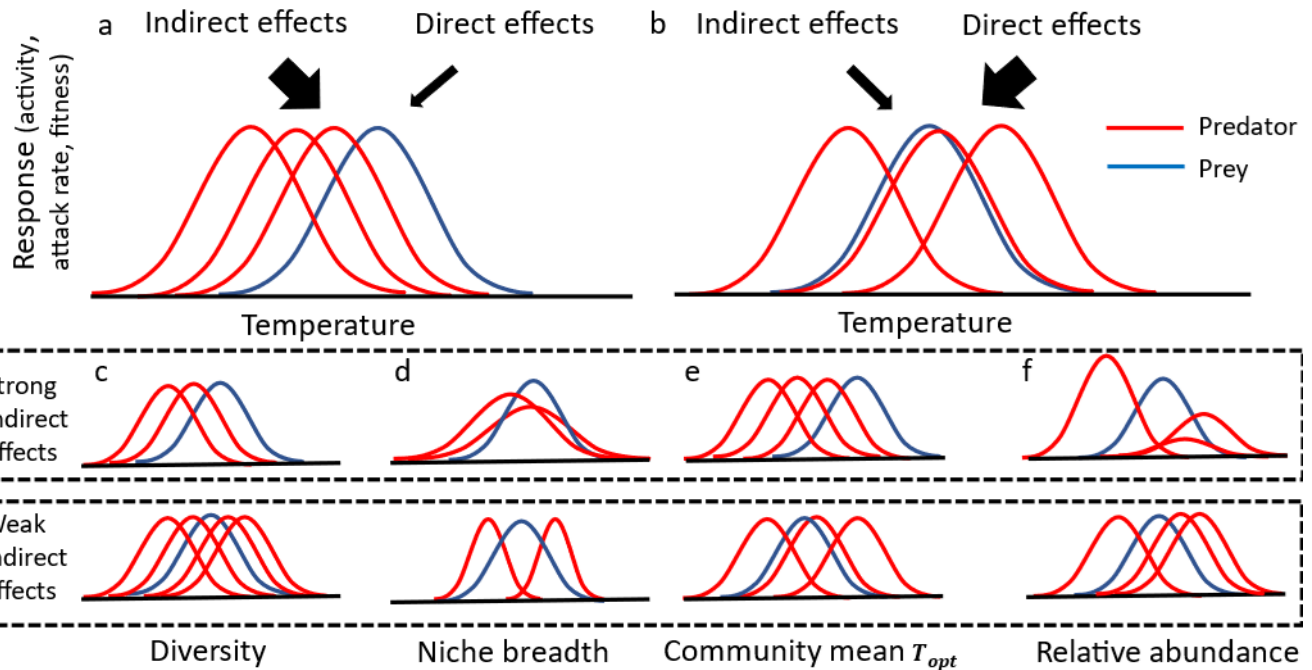
Walther, G., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. Fromentin, et al. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.

Werner, E. E. 1986. Amphibian metamorphosis: Growth rate, predation risk, and the optimal size at transformation. *American Naturalist* 128:765–770.

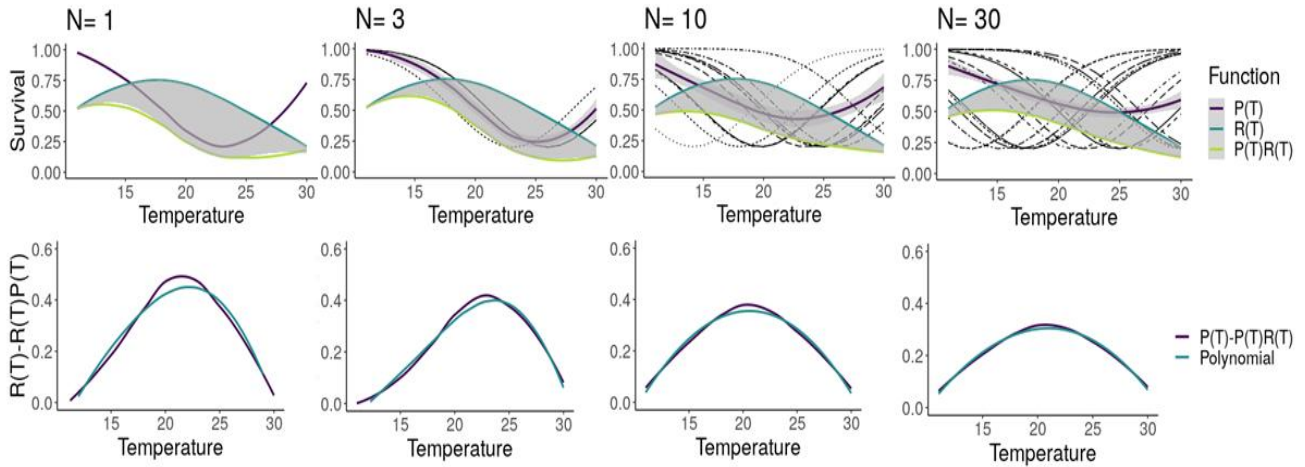
Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.

Parameter	Description	Value when constant	Source
Size-dependent predation:			
$a_0$	Intercept	2.7576	Pepi et al, 2018
$a$	Slope	-1.438	
$x_0$	Starting size	10 mg	
$c$	Scaling constant	2.739361	
Prey growth:			
$r_{max}$	Maximum rate	5.9	Fitted from rearing data in Pepi et al. 2018.
$T_{opt}$	Thermal optimum	23.5°C	
$\sigma_{opt}$	Niche breadth	6.7°C	
Prey rearing survival:			
$r_{max}$	Maximum rate	0.75299	Estimated from unpublished data: rearing method in Pepi et al. 2018.
$T_{opt}$	Thermal optimum	17.661°C	
$\sigma_{opt}$	Niche breadth	7.9°C	
Predator attack rate:			
$r_{max}$	Maximum rate	0.8	$r_{max}$ extrapolated from data in Karban et al. 2015, $\mu$ of $T_{opt}$ set equal to $T_{opt}$ of prey, $\sigma$ of $T_{opt}$ and $\sigma_{opt}$ chosen based on values in Kühsel and Blüthgen 2015.
$\mu$ of $T_{opt}$	Mean of thermal optimum	23.5°C	
$\sigma$ of $T_{opt}$	Standard deviation of thermal optimum	5°C	
$\sigma_{opt}$	Niche breadth	4°C	

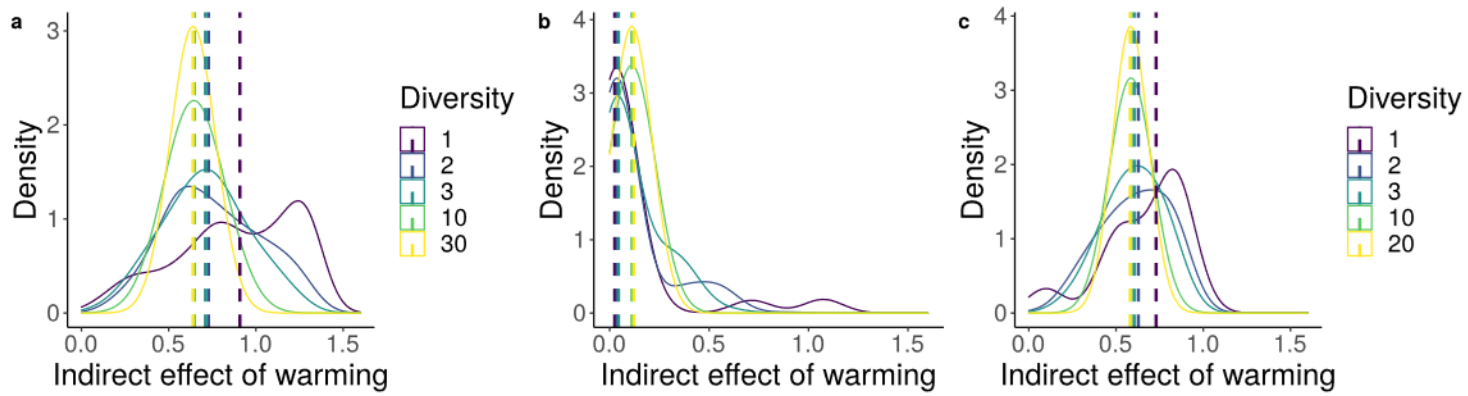
Table 1. Values of parameters used for simulations, or values when parameters were held constant in sensitivity analyses.



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

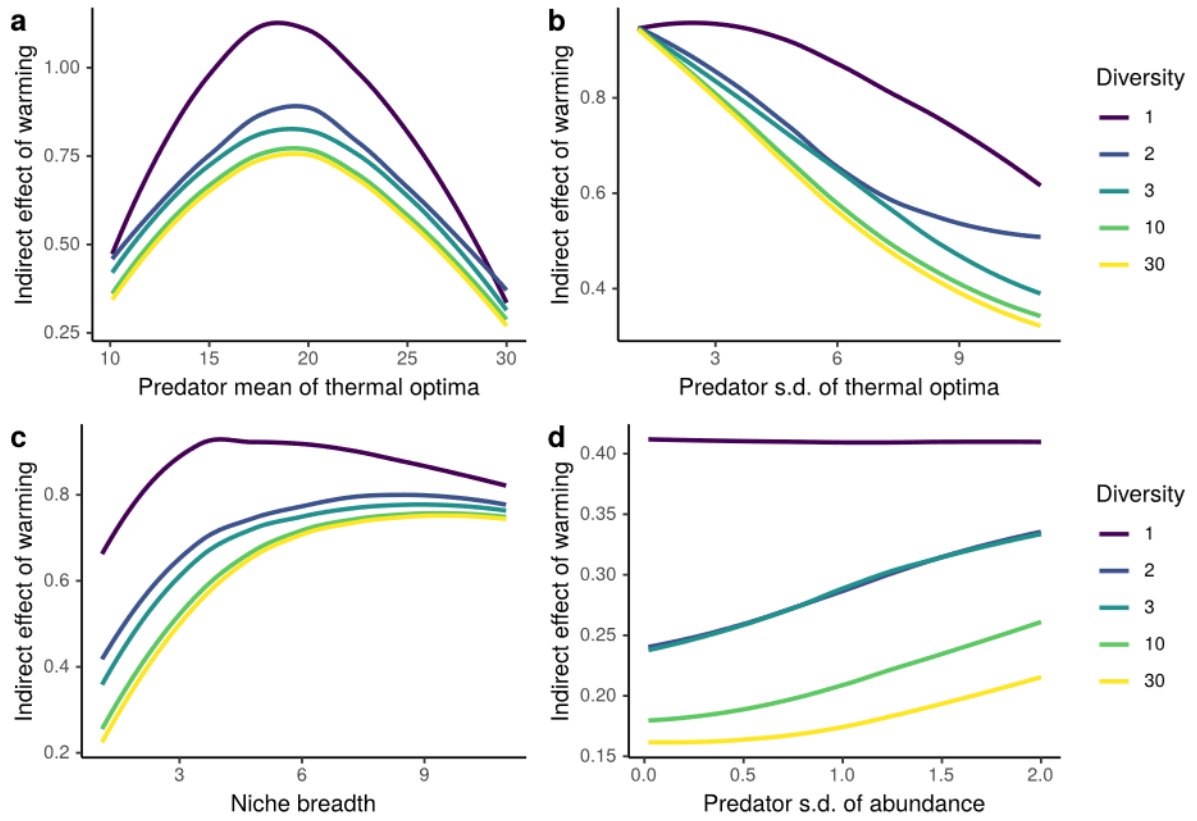


**Figure 2.** Representative simulation results of prey survival with increasing temperature preyed upon by 1-30 predator species, from left to right, showing reduced indirect effects of warming with increasing diversity. In the first row, black lines show  $(1 - \text{predation rate})$  of each predator (not visible for  $N=1$ ), with additional lines showing  $P(T)$  ( $1 - \text{mean predation rate}$ , eq. 1) of all predators with a 95% CI, rearing survival of prey  $[R(T)$ , eq. 2], and the combined effects of predation and rearing on survival  $[R(T)P(T)]$ . The grey band in the first row shows the indirect effect of warming on survival  $[R(T)-R(T)P(T)]$ . 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 upon by a community of 1-30 predators, with (a) a simulated community of predators (b) a community of ants in California and (c) the same community of ants with  $r_{max} = 0.8$  for all species. The median of each distribution is displayed by a dashed vertical line.



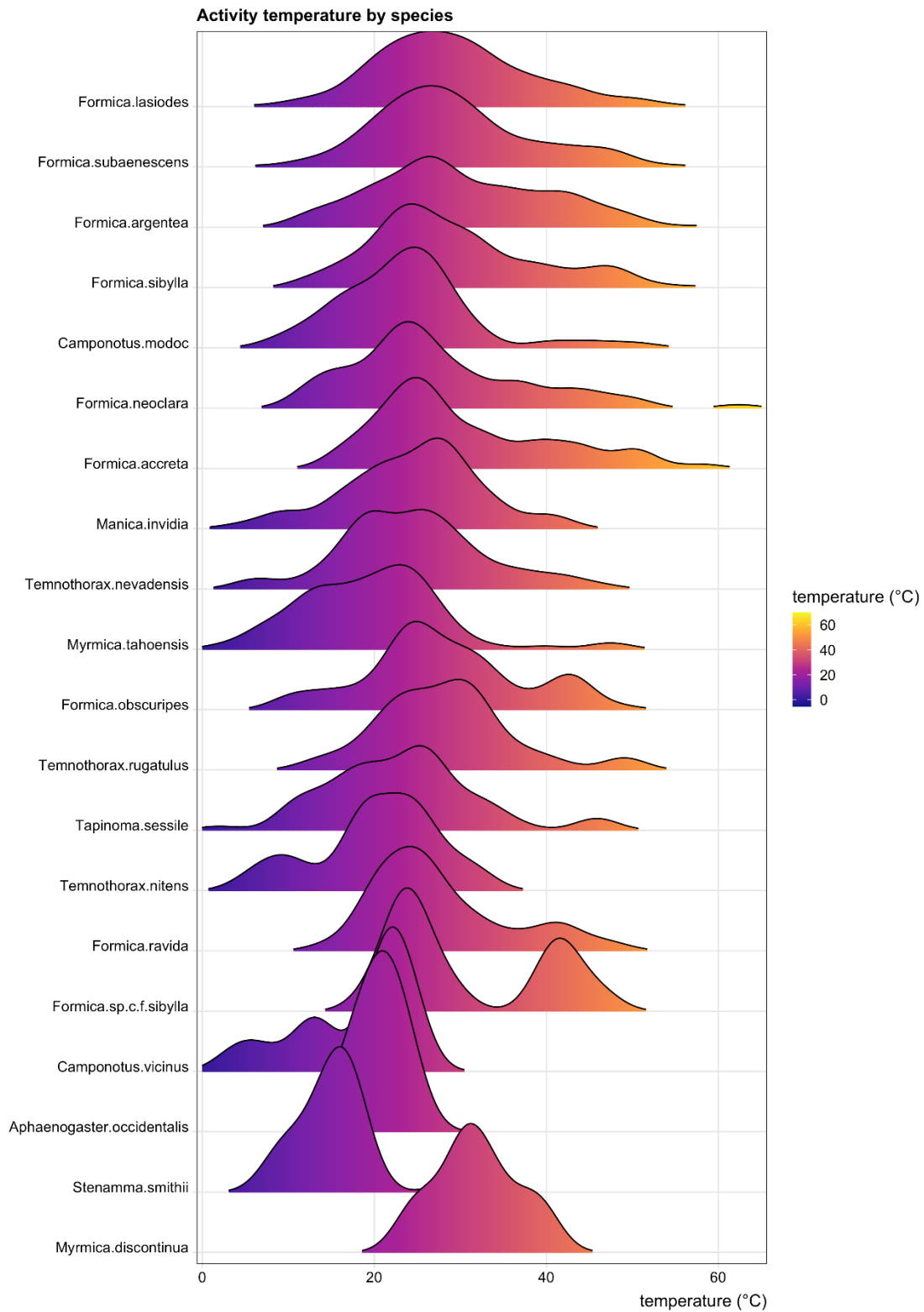


**Figure 4.** Sensitivity analysis of simulation model, showing the median indirect effect of warming ( $\Delta_{indirect}$ ) for communities of 1, 2, 3, 10 and 30 predators. Sensitivity analyses are shown with respect to (a) mean of predator thermal optima ( $T_{opt}$ ), (b) standard deviation (s.d.) of predator thermal optima, (c) predator thermal niche breadth ( $\sigma_{opt}$ ), and (d) s.d. of the lognormal species abundance distribution.

Species	Frequency
<i>Formica lasiodes</i>	1639
<i>Formica fusca</i>	1182
<i>Formica argentea</i>	334
<i>Formica sibylla</i>	220
<i>Camponotus modoc</i>	197
<i>Formica neoclara</i>	150
<i>Formica accrete</i>	123
<i>Manica invidia</i>	122
<i>Temnothorax nevadensis</i>	115
<i>Myrmica tahoensis</i>	82
<i>Temnothorax rugatulus</i>	70
<i>Formica obscuripes</i>	68
<i>Tapinoma sessile</i>	68
<i>Temnothorax nitens</i>	48
<i>Formica ravida</i>	44
<i>Formica sp. c.f. sibylla</i>	28
<i>Camponotus vicinus</i>	14
<i>Stenamma smithii</i>	13
<i>Aphaenogaster occidentalis</i>	6
<i>Myrmica discontinua</i>	5
<i>Camponotus laevissimus</i>	4
<i>Leptothorax muscorum complex</i>	3
<i>Camponotus essigi</i>	1

522

523    **Table S1.** Ranked frequency of ant species in collections, across all times and sampling locations.



524

525

526 **Figure S1.** Density plot of ant activity by temperature and species. Species are ordered by rank  
 527 abundance, from most abundant at the top to least abundant at the bottom.