

1 **Title:** Temperature variability alters the stability and thresholds for collapse of interacting  
2 species

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17 climate change, climate variability, climate extremes, stability.

18 **Abstract**

19 Temperature variability and extremes can have profound impacts on populations and ecological  
20 communities. Predicting impacts of thermal variability poses a challenge because it has both  
21 direct physiological effects and indirect effects through species interactions. In addition,  
22 differences in thermal performance between predators and prey and non-linear averaging of  
23 temperature-dependent performance can result in complex and counterintuitive population

24 dynamics in response to climate change. Yet the combined consequences of these effects remain  
25 underexplored. Here, modeling temperature-dependent predator-prey dynamics, we study how  
26 changes in temperature variability affect population size, collapse, and stable coexistence of both  
27 predator and prey, relative to under constant environments or warming alone. We find that the  
28 effects of temperature variation on interacting species can lead to a diversity of outcomes, from  
29 predator collapse to stable coexistence, depending on interaction strengths and differences in  
30 species' thermal performance. Temperature variability also alters predictions about population  
31 collapse – in some cases allowing predators to persist for longer than predicted when considering  
32 warming alone, and in others accelerating collapse. To inform management responses that are  
33 robust to future climates with increasing temperature variability and extremes, we need to  
34 incorporate the consequences of temperature variation in complex ecosystems.

35

## 36 **Introduction**

37 Climate change is altering climate extremes and variability of environmental conditions  
38 [1], yet much of the focus on the impacts of climate change on wild populations remains on how  
39 shifts in average conditions will affect dynamics and distributions [2,3]. Yet as average  
40 temperatures shift, both temperature variability and the frequency of extreme events, such as  
41 marine heat waves, are changing [1,4–6]. Changes in temperature variation and extremes can  
42 have profound impacts on individuals and populations, as temperature affects their rates of  
43 metabolism, consumption, somatic growth, reproduction, and survival [7,8]. These processes  
44 underpin the productivity and resilience of populations and ecosystems [9], on which ecosystem  
45 services, such as fisheries yields [10], and population resilience depend. While the potential  
46 impacts of temperature variability and extremes have been demonstrated, and in some cases pose

47 a greater risk to species than increases in mean temperature [7,8,11], predicting the importance  
48 of temperature variability and extremes for populations, communities, and the ecosystem  
49 functions and services they support remains challenging. First, temperature can have both direct  
50 and indirect effects that create complex feedbacks and dynamics [12]. Directly, temperature  
51 affects species through physiological performance. But temperature can also impact species  
52 indirectly, as shown for warming [13,14], by increasing or decreasing important resources or  
53 prey species (in turn affecting consumers and predators), changing competitive abilities (altering  
54 prey abundance distributions), and altering feeding rates and top-down control (affecting prey)  
55 [15–18]. Second, even without shifts in mean temperatures, temperature variability can alter  
56 mean vital rates because of non-linear relationships between temperature and processes including  
57 growth, reproduction, and mortality (Fig 1; [19]). As a result, the responses of populations to  
58 increasing temperature variability and extremes induced by climate change, especially in a  
59 community context, remains a key research frontier in marine population dynamics, community  
60 ecology, and fisheries science.

61         Directly, temperature variability can impact populations of species in a variety of ways,  
62 including by altering the rates of fundamental processes that determine population size,  
63 extinction risk, and productivity. Increases in the frequency or duration of exposure to extreme  
64 temperatures can induce physiological shock leading to depressed somatic growth or lower  
65 survival [20,21]. Temperature variability and extremes above cold or warm events, in contrast to  
66 mean temperature conditions, can also alter environmental cues that induce or suppress  
67 reproductive cycles leading to skip spawning [22], development [23,24], or hatching [23] that  
68 change the number of offspring (i.e. recruitment in fish) or cause reproductive failure. Theory  
69 and empirical work shows species' performance responds non-linearly and asymmetrically to

70 environmental temperature, including intrinsic growth rates and other fitness proxies. This  
71 relationship is known as a thermal performance curve (TPC) [8,25,26]. Because of this non-  
72 linearity, changes in temperature variance can affect demographic rates differently than changes  
73 in mean temperature alone, due to non-linear averaging and Jensen's inequality ( i.e., that the  
74 mean of a concave function is smaller than the concave function of a mean, and vice versa for  
75 convex functions, see Fig. 1; put in an ecological context *reviewed in* [19]). This also means that  
76 if species are well-adapted to the mean conditions, such that their thermal optimum is close to  
77 the average environmental temperature (i.e., in the concave part of the thermal performance  
78 curve), then increases in temperature variation around the mean are predicted to reduce a  
79 species' performance (e.g., growth rate) [20,27,28]. These impacts scale from individuals to  
80 population growth rates [29,30]. Similarly, nonlinear TPCs suggest that higher frequency or  
81 duration of exposure to temperature extremes, rather than longer-term temperature averages,  
82 shape growth and mortality [31] due to species' asymmetric responses to higher temperatures  
83 and extremes [20]. Collectively, these nonlinear responses and intermittent exposures to thermal  
84 extremes suggest that temperature variability can alter population dynamics in complex ways not  
85 explained by warming of average temperatures alone [7,30,32].

86 Simultaneously, temperature can indirectly affect populations through species interactions,  
87 thus community and ecosystem responses to temperature variability are complex to predict.  
88 Species interactions mediate how temperature impacts a population's growth, biomass, and  
89 dynamics. Because species that interact can respond differently to temperature [33,34], species-  
90 specific thermal performances can alter interspecific interactions and resulting population  
91 dynamics. For instance, if temperature increases prey growth while predators net growth increase  
92 less (e.g., due to increased metabolism for larger bodied-species,[35,36]), prey can outgrow

93 predation windows raising survival [37]. This suggests that if prey thrive directly in response to  
94 temperature variation when predators are heat suppressed, prey may flourish in response to  
95 heatwaves, and *vice versa*. Understanding the consequences of temperature variability for marine  
96 communities therefore requires considering species interactions, because some species benefit  
97 from variable temperatures while others lose (Fig. 1).

98         However, the effects of both temperature variability (or extremes) and species  
99 interactions are rarely accounted for in studies of how climate change impacts community  
100 dynamics and ecosystem functioning. On one hand, lab studies that quantify the impacts of  
101 temperature variability on individuals and populations often focus on the direct physiological  
102 effects on performance (e.g., [8,30,32]), with few considering both variation and interactions (*but*  
103 *see* [7,38,39]). On the other hand, most experimental and theoretical studies investigating  
104 warming effects on species interactions and their indirect effects do so under different levels of  
105 average temperature conditions (e.g.,[15,37]), with less emphasis on variability and extremes  
106 (*but see* e.g., [7]). However, when demographic rates depend non-linearly on temperature and  
107 interacting species differ in their thermal responses, we anticipate that the net effect of these  
108 processes can lead to unexpected outcomes for population dynamics and stability. Indeed, the net  
109 effect of temperature variability could be more positive or negative than considering either effect  
110 in isolation.

111         In this paper, we examine how different temperature regimes impact the dynamics of  
112 interacting predators and prey, with a focus on multiple types of temperature variability,  
113 including increases in temperature variability associated with climate change. We theoretically  
114 investigate when considering the combined direct and indirect effects of temperature variability  
115 (“net effect”) alters predictions for population productivity, stability, and trajectories through

116 time, relative to considering a constant environment and/or warming average temperatures alone.

117 Specifically, we ask:

- 118 1) How does increasing temperature variability affect population size through time,  
119 occurrence of collapse, and stable coexistence of both predator and prey, relative to a  
120 constant environment?
- 121 2) How do these effects depend on the predator's and prey's TPCs relative to the  
122 temperature variability regime, and relative to one another?
- 123 3) What are the net *versus* direct effects of temperature variability on these properties when  
124 species interact, and when are direct versus net effects acting in opposite directions?
- 125 4) How do effects of temperature variability compare to and/or modify the effects of  
126 increasing mean temperatures?

127 We hypothesize that the extent to which the effects of temperature variability shift predictions  
128 about population growth, size, and stable coexistence beyond warming average conditions will  
129 depend on the 1) thermal variability regime, 2) strength in species interactions, and 3) overlap in  
130 TPCs of interacting species (Fig. 1). We motivate our theoretical investigation with a marine  
131 predator-prey system, though the model applies more generally to predator-prey systems  
132 experiencing both temperature variability and rising temperatures.

## 133 **Methods**

### 134 ***Model***

135 We model a predator-prey system in which a subset of key parameters depend upon  
136 temperature. In line with prior investigations of how temperature affects community dynamics  
137 [40–43], we use a Rosenzweig-MacArthur model with a prey population  $x(t)$  and predator  
138 population  $y(t)$  changing as a function of time  $t$ :

139 
$$\frac{dx(t)}{dt} = r(T(t))x(t) \left(1 - \frac{x(t)}{K}\right) - y(t)f(x(t), y(t), T(t)), \quad (1)$$

140 
$$\frac{dy(t)}{dt} = (cf(x(t), y(t), T(t)) - m)y(t). \quad (2)$$

141 Here,  $r$  is the temperature-dependent intrinsic growth rate of the prey population,  $K$  their  
142 carrying capacity,  $T(t)$  is temperature at time  $t$ ,  $m$  the density-independent mortality in the  
143 predator, and  $f$  denotes the Holling type II functional response of the predator:

144 
$$f(x(t), y(t), T(t)) = \frac{a(T(t))x(t)}{a(T(t))hx(t)+1}. \quad (3)$$

145 Here  $a$  denotes attack rate, which depends on temperature;  $h$  is handling time; and  $c$  is  
146 conversion efficiency.

147 In the absence of temperature effects, this Rosenzweig-MacArthur model has three  
148 equilibria: joint extinction, extinction of the predator with the prey at carrying capacity, and a  
149 coexistence equilibrium. The coexistence equilibrium is defined by:

150 
$$x^* = \frac{m}{a(c-mh)}, \quad y^* = \frac{r}{a} \left(1 - \frac{x^*}{K}\right) (ahx^* + 1), \quad (4)$$

151 which requires that  $aK(c - mh) > m$ . We use this equilibrium to set the starting conditions, in  
152 terms of the populations levels (abundances), to provide consistent initial conditions under which  
153 there are no transitory dynamics in the absence of temperature-dependence.

154 We focus on understanding how temperature variability influences population dynamics  
155 via impacts to the predator and the prey species. Particularly, we model how both the attack rate  
156 ( $a$ ) of the predator [44] and the intrinsic growth ( $r$ ) of the prey [8] depend on temperature.  
157 Following current theory and empirical studies, we assume  $r(T)$  and  $a(T)$  follow unimodal non-  
158 linear relationships, with maxima at  $T_r^*$  and  $T_a^*$ , respectively (Fig. 1). Although the shape of  
159 thermal performance curves (TPCs) will vary among species, populations, and life stages, TPCs  
160 are generally considered to have a steep, negative drop-off in performance above optimal

161 temperatures, but rapid gains in performance at lower temperatures (Fig. 1) [33,45,46]. In our  
162 model, we use species-specific asymmetric hump-shaped TPC following Gårdmark et al. (in  
163 prep) and [47,48]; see SI for details.

164 We focus on the temperature-dependence of these two parameters, attack rate  $a$  and prey  
165 growth rate  $r$ , but recognize that temperature also could influence other parameters in our model  
166 (e.g., carrying capacity  $K$ , handling time  $h$ , and mortality rate  $m$ ) [44,49]. We choose to examine  
167 the temperature dependence of  $a$  and  $r$  because these are the parameters for which we have the  
168 most unequivocal information (*see* [50]). For example, carrying capacity may also vary with  
169 temperature [49], but that parameter is not mechanistic in the Rosenzweig-MacArthur model.  
170 That is,  $K$  may be determined by many factors including primary productivity, nutrient supply,  
171 and habitat availability, and temperature may affect each of these in different and complex ways  
172 that are more likely linked to exogenous factors that this model does not incorporate.

173

## 174 ***Simulations***

175 The way in which temperature variability affects growth and attack rates depends on the  
176 distribution of temperatures to which species are exposed and the species' TPCs. Because TPCs  
177 for a prey and its predator are likely to differ (Fig. 1), we explore how overlap of TPCs and their  
178 relation to temperature distributions affect population dynamics for both species. Thus, we  
179 conduct several simulations that combine and vary both: the temperature regime and how  
180 species' TPCs relate to one another. For each simulation, we examine how the temperature  
181 regime influences average temperature-dependent demographic rates ( $r$  and  $a$ ), long-run  
182 population means for both predator and prey, and the equilibrium type (either extinction or  
183 coexistence with either fixed densities or cycling dynamics). Here, we define '*long-run*' predator



184 and prey populations based on the last 10% of the simulated time steps (final 200 out of the 2000  
185 time steps), which provides time required to reach a stationary distribution (Fig. S1), if one  
186 exists.

187

## 188 **Temperature regimes**

### 189 *Scenarios of temperature regimes for means and variability*

190 The temperature regimes we consider are (1) temperature variability of different  
191 amplitudes, but constant mean temperature ('variability-only'), (2) increasing mean temperature,  
192 but no variability ('warming-only'), (3) increasing mean temperatures and constant temperature  
193 variability of different amplitudes ('warming-and-constant variability') and (4) both increasing  
194 mean temperatures and increasing temperature variability ('warming-and-increasing variability').

195 We generate the temperature variability and warming regimes as follows. In the  
196 variability-only regime, temperatures oscillate linearly between a maximum  $T_{max}$  and minimum  
197  $T_{min}$ , completing one cycle per time period (see SI) to reflect seasonality. In this scenario,  
198 increases in temperature variability do not affect the mean temperature  $\bar{T}$ . In the warming-only  
199 regime, temperatures increase linearly from  $T_{min}$  to  $T_{max}$  over the course of the simulation. To  
200 facilitate comparison, all warming-only scenarios share the same  $\bar{T}$ , such that the variability-only  
201 and warming-only regimes have the same overall distribution of temperatures for a given  $T_{min}$   
202 and  $T_{max}$ . We generate these regimes for different sets of  $T_{min}$  and  $T_{max}$ , which we refer to as  
203 "amplitudes." Finally, the warming-and-variability scenarios combine the linear warming and  
204 linear oscillation effects with different amplitudes, where both warming and variability share a  
205 specified amplitude (see SI).

206

207 *Scenarios with stochastic events driving temperature variability*

208           In addition to the deterministic temperature changes in the form of seasonal variation,  
209 warming, or both, we also simulate temperature variability that is stochastic, to test the  
210 sensitivity of our results. We examine two types of stochastic temperature changes (see SI  
211 section 1.2). First, we examine major “events” modeled after El Niño; when such an event  
212 occurs, the temperature shifts up during a given year. Second, we examine smoother stochastic  
213 variability in the form of a Gaussian process with squared exponential covariance function,  
214 allowing for both variance and autocorrelation to increase through time. In both cases, we add  
215 these stochastic temperature deviations on top of our baseline scenario of oscillating (seasonal)  
216 temperatures – enabling us to focus solely on the two types of variability rather than the  
217 combination of variability and warming.

218

219 *Examining how predator-prey TPC overlap and trophic structure modulates effects of*  
220 *temperature*

221           To investigate the extent that TPC overlap between predator and prey species determines  
222 the impact of temperature on each population and their coexistence, we systematically vary the  
223 extent of TPC overlap between predator and prey species for each temperature scenario. For each  
224 temperature regime, we consider a range of configurations of species’ TPCs, defined by the  
225 offset  $T^* - \bar{T}$  (in degrees Celsius) between each species’ optimal temperature and the mean  
226 environmental temperature (see Fig. 1). Specifically, we consider cases where the TPCs for the  
227 predator and prey have offsets of the same magnitude but opposite sign, so that the location of  
228 both TPCs is defined in terms of the prey offset (as in Fig 1). When that offset is zero, the  
229 predator and prey TPCs overlap exactly. Table S1 defines parameters for these simulations.

230 Finally, we conduct an additional set of analyses in which we introduce a second prey  
231 species with different thermal affinities than the first prey. To do so, we use a multispecies  
232 Holling type II functional response [51], to maintain the same functional form assumptions as  
233 above, in order to isolate the effect of adding an additional prey on stable coexistence. To test the  
234 influence of multiple prey species with different TPCs on co-existence of predator and prey  
235 species, we shifted the first prey TPC and the predator TPC in opposite directions as before, but  
236 fixed the second prey TPC at the environmental mean, to facilitate comparison with the single  
237 prey case.

238

### 239 *Calculating direct effects versus net effects of temperature via species interactions*

240 To quantify the importance of accounting for species interactions when studying the  
241 effects of temperature variability, we contrast the direct and net effects (direct plus indirect) of  
242 temperature variability on the predator population. For each combination of temperature regime  
243 and species' TPCs, we track the predator population for three simulations, with growth and  
244 attack rates set to (i)  $r(\bar{T})$  and  $a(\bar{T})$ ; (ii)  $r(\bar{T})$  and  $a(T)$ ; and (iii)  $r(T)$  and  $a(T)$ ; rates defined  
245 either at the actual temperature  $T$  or at the mean temperature  $\bar{T}$  ignoring variability. Thus,  
246 simulation (1) ignores all effects of temperature variability, simulation (2) ignores the effects of  
247 variability on prey growth, and simulation (3) examines the effects of temperature variability on  
248 both species. We define the net effect of temperature variability as the difference in long-run  
249 predator population between simulations (3) and (1), while the direct effect is defined by the  
250 difference between simulations (2) and (1).

251

## 252 **Results**

253 *Effects of temperature variability on long-run populations*

254       Increases in temperature variability produce either stable coexistence, predator-prey cycles,  
255 or extinctions (Fig. 2), depending on the difference in predator and prey TPCs and parameters  
256 relating to species interactions (predator conversion efficiency and attack rate) (Figure 1; Figure  
257 S1). When TPCs for predator and prey coincide (i.e., are identical), variable temperatures can  
258 drive the predator extinct from an equilibrium that is stable under conditions without temperature  
259 variability (Figure 2b; Fig S1). For higher parameter values of predator conversion efficiency  
260 ( $c = 0.3$  in Fig. 2a versus  $c = 0.1$  in Fig. 2b), however, increasing temperature variability can  
261 stabilize the system, causing a shift from cyclic dynamics (limit cycle) to a stable equilibrium  
262 point (fixed point) (Fig 2a). The opposite effects can arise when the TPCs for the two species are  
263 offset so that the prey's temperature optimum is higher. Specifically, when peak attack rates are  
264 high, variability can save the predator from extinction, if the prey has a much higher optimum  
265 temperature than the predator, or destabilize an otherwise stable equilibrium by inducing cyclic  
266 dynamics when the difference in TPCs between predator and prey is less (Fig. 2c). Even when  
267 variability does alter the type of equilibrium that arises, equilibrium population levels can be  
268 driven up or down.

269       The presence of a second prey species with different thermal affinities from the first prey  
270 increases the parameter space with stable coexistence (Fig. S5). Predator feeding on an  
271 alternative prey with TPC at mean temperature stabilizes dynamics and prevents extinction,  
272 especially when the original prey has a much lower optimal temperature than its predator  
273 (negative prey TPC offsets, cf. Fig. 2 and Fig. S5) and for predators with low conversion  
274 efficiency (Fig. S5).

275

276 *Direct versus net effects of temperature variation*

277 Including indirect effects can qualitatively change the impact of temperature variability on  
278 populations (Fig. 3; Fig. S2). The true, ‘net’, effect on long-run population levels can differ from  
279 that suggested by studying the direct effect alone, both in terms of direction of the response (Fig.  
280 3) and effects on the stability of predator-prey dynamics (Fig. S2). In other cases, the direct  
281 effect of temperature variability may imply an unstable equilibrium, but after accounting for  
282 indirect effects, the equilibrium remains stable (Fig. S2).

283

284 *Effects of increased temperature variability versus increased temperature mean*

285 The effects of increasing mean temperature on long-run population sizes without shorter-  
286 term variability are qualitatively different than those of variability without warming, even for an  
287 identical distribution of temperatures experienced during the simulation (Fig. 4). For example,  
288 increasing mean temperature on predator and prey with completely overlapping TPCs can drive  
289 the predator extinct (Fig. 4, *red lines*) as higher temperatures eventually lead to extended periods  
290 of low attack rates (which asymptote towards 0). In contrast, variability with the same  
291 distribution of temperatures can lead to a stable coexistence (Fig. 4, *blue lines*). When mean  
292 temperatures increase and variability is present — whether constant (Fig 4, *purple lines*) or  
293 increasing (Fig 4, *orange lines*) — the predator population survives for longer than under  
294 increasing mean temperature alone.

295 Accounting for stochastic variation in temperature does not change our qualitative  
296 conclusions (Figure S6). While moderate stochastic temperature changes knock population  
297 trajectories out of asymptotic convergence to equilibrium levels, they do not qualitatively change  
298 the means of the long-run population trajectories in response to temperature (Fig. S6)

299

## 300 **Discussion**

301       Increases in temperature variability can influence populations of interacting species in  
302 ways not predicted by considering increases in mean temperatures or the direct physiological  
303 effect of temperature variation alone. First, a focus on mean temperature alone misses the highly  
304 non-linear responses of species' demographic rates to changes in temperature [52]. Temperature  
305 variability, by directly creating complex nonlinear demographic responses, can alter both the  
306 viability and stability of populations in either direction (Fig. 2). Second, the net effect of  
307 temperature variability when species interact can differ from that predicted by the direct effect  
308 of temperature on a single species, and even be of opposite sign (Fig. 3). Thus, ignoring indirect  
309 effects and making predictions about population dynamics solely from individual demographic  
310 rates (e.g. growth) may create erroneous expectations, sometimes in the opposite direction (Fig.  
311 3; Fig. S2). This highlights the importance of considering temperature effects in contexts with  
312 both intra- and inter-specific interactions. Third, results depend on the differences in predator  
313 and prey TPCs (i.e., if the predator TPC is optimized at a higher, identical, or lower temperature  
314 than its prey). Finally, results from our model show ignoring temperature variability could over-  
315 predict negative impacts of warming on population and community trajectories. Even under  
316 warming temperatures, temperature variability results in periods in which temperatures return to  
317 a range under which species can grow (Fig. 4), though our results show that the predator  
318 populations may still eventually collapse as warming intensifies (Fig. 4d). These findings have  
319 important implications for natural communities as temperature variability is predicted to increase  
320 further due to global warming.

321 That temperature variability increases species persistence can also be seen in single species  
322 models, which provide insights into when this ‘rescue effect’ occurs. This ‘rescue effect’  
323 depends on how temperature variability influences temperature-dependent demographic rates for  
324 hump-shaped TPCs. In a single-species logistic model with temperature-dependent growth, the  
325 prey population at time  $t$  depends only on the average growth rate  $\bar{r} = \overline{r(T(t))}$  of that time period  
326 [53]. Depending on the curvature of the TPC over the range of temperatures that a species  
327 experiences, temperature variability can either raise (in convex parts of the TPC) or lower  
328 average growth (in concave parts of the TPC), with concomitant change in population levels  
329 (Fig. 1; *see also* [54, 55]). If warming drives the mean temperature above the prey’s optimal  
330 temperature, then temperature variation will span a convex portion of the species TPC, thereby  
331 raising average growth and prolonging population persistence (as seen in Fig. 4).

332 Similar insights can be gleaned about the effects of variability on average rates for  
333 interacting predator and prey species. Temperature variability is likely to lower average attack  
334 rates when the temperature distribution is centered near the peak of the predator’s TPC (Fig. 2  
335 when TPC offset is around 0), whereas it results in higher average attack rates at lower  
336 temperatures (Fig. 2 when TPC offset is large and positive), such that temperature variation  
337 occurs in the convex part of the predator’s TPC. Temperature variability in these ranges of the  
338 TPC thus promotes predator persistence by resulting in sufficiently high attack rates on average.  
339 In fact, simulations using the average predator attack and prey growth rates that arise under  
340 variable temperatures yield similar overall patterns of stability and coexistence (see Fig. S3 and  
341 SI section S1.3 for details).

342 Importantly, our results demonstrate that understanding how a particular temperature regime  
343 affects predator populations requires knowledge of temperature dependencies of *both* species and

344 how they interact. The true ‘net’ effect of temperature variability on predator populations may be  
345 positive or negative; moreover, because of indirect effects, such responses may differ in sign  
346 from predictions made based on changes in attack rate (or other properties in a single species) in  
347 isolation (Fig 3). The potential for indirect effects on equilibrium populations is evident from  
348 equation (4): prey levels are inversely related to attack rates, while predator levels are  
349 proportional to prey growth rates.

350 The difference in TPCs of interacting species dramatically alters the response of ecological  
351 communities to variation in temperature (Fig. 2 & 3). Large differences in temperature optima  
352 from  $\bar{T}$  lead to predator extinction, regardless of which species has the higher optimum  
353 temperature. If prey have lower temperature optima, predator extinction occurs at even lower  
354 levels of temperature variability for the same magnitude of TPC offset, compared to if the  
355 predator has the lower temperature optimum. The rapid decline of the TPCs above a species’  
356 optimum explains this result. Average growth for the prey (or attack rate for predator) is  
357 substantially lower when temperature vary above that species’ optimum temperature compared  
358 to below (i.e. if the temperature optima is shifted downward rather than upward by the same  
359 amount). If the prey has a lower temperature optimum than the predator, high temperature  
360 variability results in prey population depletion by increasing predator attack rates much more  
361 than prey growth rates, eventually leading to predator extinction. These results are consistent  
362 with findings from other contexts showing that imbalances in temperature sensitivities of species  
363 metabolism and ingestion have important consequences for community dynamics. For example,  
364 for invertebrates, metabolism increases faster than ingestion [56,57], which can lead to  
365 starvation, and theoretical analyses indicate that this increases population stability but also the  
366 risk of starvation and extinction of predators [13,40].



367 Comparing the effects of temperature variability with those of warming mean temperatures  
368 reveals their different impacts on species coexistence and stability, even when the distribution of  
369 temperatures under the two regimes is identical. When temperatures warm, long-run predator  
370 populations suffer much more than if the same magnitude of temperature change is experienced  
371 in a cyclical fashion (Fig. 4). Warming eventually drives predator attack rates to low levels,  
372 leading to population declines from natural mortality and a predator population that is not viable.  
373 Prey growth also slows, but with reduced predation, the prey population persists. In contrast,  
374 under a variability-only scenario, periods of low attack rates are intermixed with stretches of  
375 higher attack rates, such that the predator population can survive. Consistent with that intuition,  
376 adding variability to a temperature regime with warming can prolong the existence of the  
377 predator population, though in other parameterizations variability can accelerate collapse.

378 We designed our models to quantify the effects that temperature variability can impose  
379 on interacting species. However, these models include several simplifying assumptions. Our  
380 models assume only the net population growth rate of prey and the attack rate for predators are  
381 affected by temperature, but carrying capacities [58], conversion efficiencies [59], mortalities  
382 [60,61], and handling times [44,60,62] may also depend on temperature. We also include thermal  
383 sensitivity in phenomenological rather than explicitly mechanistic forms. More realistic models  
384 (e.g., size-structured, age-structured, or individual-based models) could parse out how  
385 maturation, fecundity, mortality, individual growth, and consumption simultaneously respond to  
386 thermal regimes in different individuals or size-classes when species interact. For example,  
387 accounting for both the temperature-dependent processes underlying body growth and for  
388 within-population size structure have proven important for understanding how both consumer  
389 populations [35] and food chains [63] vary with temperature. However, while this has been

390 addressed in studies of warming of mean temperatures [35,63,64], it remains to be done for  
391 increasing temperature variability. Both the complex responses to increasing temperature  
392 variability and the importance of accounting also for indirect temperature effects via interacting  
393 species that we demonstrate suggest that predicting how temperature variability would impact  
394 size-structured food webs cannot be done *a priori*. Our study thus calls for addressing  
395 temperature variability effects in food webs with approaches accounting for bioenergetics  
396 processes and the size-dependence of species interactions.

397         We demonstrate that the presence as well as the form of temperature variability influence  
398 species persistence and coexistence and interact with the effects of warming mean temperatures.  
399 Future work could consider the following additional complexities in predicting the effects of  
400 temperature dynamics on interacting species in particular systems. First, thermal variability with  
401 autocorrelation (e.g., persistent heatwaves) can induce not only prolonged shifts in growth but  
402 also mortality, even leading to mass mortality, for instance from oxidative stress shaped by  
403 temperature maxima rather than mean temperature [21]. Mass mortality events may be induced  
404 by short-term exposure to high temperature, and the threshold temperature for mortality can  
405 decrease with greater exposure duration [65], whereas high-frequency variability can also reduce  
406 negative effects, such as coral bleaching [66]. Second, the impacts of these short-term events are  
407 likely to depend on the species' generation time, relative to time scale of the perturbation. For  
408 instance, short-lived species may suffer high mortalities if exposed to unfavorable climate  
409 conditions occurring during its short lifespan, compared to longer-lived organism that may better  
410 buffer against short-term events. Third, acclimatization [67,68], or short-term evolutionary  
411 responses [48,69] to temperature changes could result in inaccurate predictions from models  
412 based on historical observations or experiments that are conditional on the environmental history

413 or genotypes. Nevertheless, our results show temperature variability can alter predictions  
414 compared to accounting for increases in temperature means alone, indicating the need for  
415 considering temperature variability shapes population stability, collapse, and coexistence when  
416 species interact (Fig. 2; Fig. 4).

417 Finally, climate change in the sea is more than warming, variability, and frequency of  
418 extreme temperatures. It also encapsulates changes in dissolved oxygen, pH, surface irradiance,  
419 salinity, and circulation dynamics -- biophysical changes that are often correlated with  
420 temperature fluctuations (IPCC 2019). We chose to focus on temperature dynamics for several  
421 reasons. First, there has been a long history of documenting short and long-term variation in  
422 ocean temperature either *in situ* or using satellite reconstruction. In contrast, for other  
423 biophysical changes, such widespread and high-resolution data collection and reconstructions are  
424 more isolated, sporadic or only recently developed. Second, temperature impacts on physiology  
425 and population dynamics have long been a focus in fisheries ecology. Thus, we focus  
426 on variation in temperature to quantify how variability in abiotic stressors can alter dynamics  
427 with the acknowledgment that other stressors and variability therein are also central in shaping  
428 populations and communities and may exhibit independent and multiplicative stresses on  
429 communities in unpredictable ways. Here we show that the inherent complex direct and indirect  
430 responses of populations and communities to gradual linear temperature changes that  
431 characterizes climate warming versus the non-linear and extreme changes that characterize  
432 climate variability is challenging. This challenge requires that, before including additional and  
433 important complexities, we deeply understand the interplay of climate warming and variability.

434

435 **Conclusions**

436           Climate change is increasing not only mean temperatures but also temperature variability  
437 (IPCC 2019). Understanding the consequences of temperature variability for population  
438 trajectories and dynamics is critical for anticipating how climate change will affect the  
439 productivity and stability of animal communities that support important functions and services.  
440 Here we find that shifts in temperature variability can destabilize, stabilize or lead to predator  
441 collapses, depending on interaction strengths and differences in thermal performance between  
442 predators and prey. Our results also show that impacts on species' growth from concurrent  
443 changes in variability with warming can change predictions from considering warming alone.  
444 Counterintuitively, temperature variability can help a population that would otherwise go extinct  
445 due to warming, when warming negatively impacts population growth, and some forms of  
446 variability can offset these effects. In other cases, however, ignoring increases in temperature  
447 variability associated with climate change leads to underestimation of predator extinction risks.

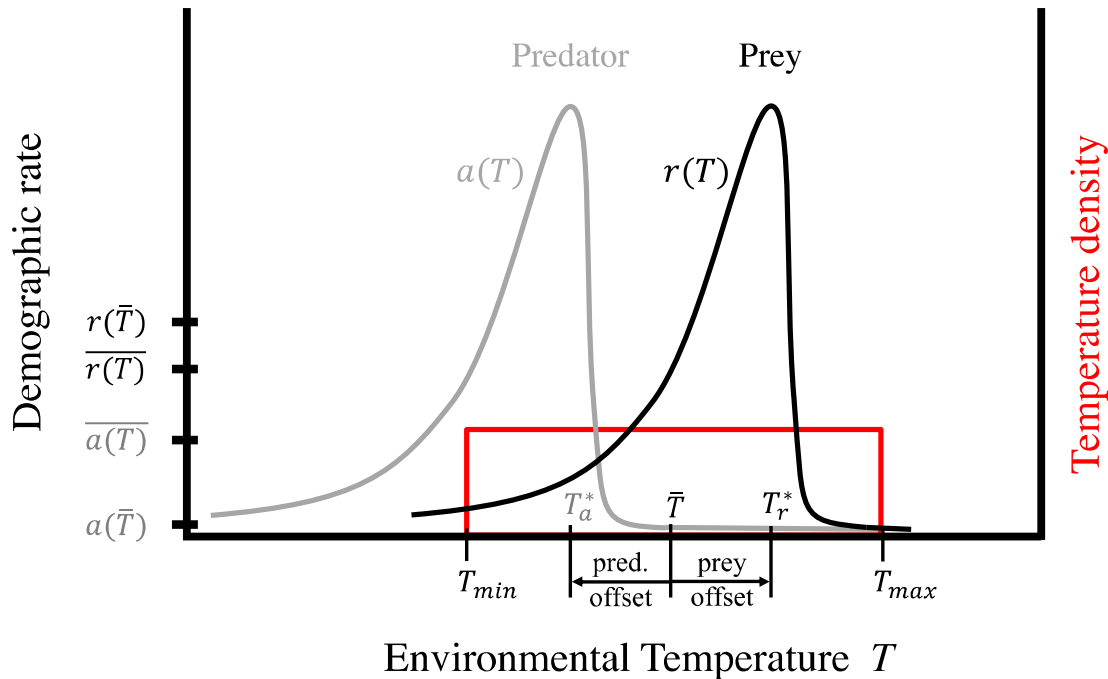
448           Our results contribute to a growing understanding of how temperature variation will alter  
449 life in the oceans, though the theoretical results extend more generally to other predator-prey  
450 systems facing variability. Our findings call for future studies advancing the theory on increasing  
451 temperature variation in foodwebs. In particular, we encourage accounting for within-species  
452 structure and variation in TPCs, as well as testing this in experimental studies in interacting  
453 species (over temperature ranges large enough for the non-linear responses to matter). Moving  
454 beyond a focus on mean temperatures alone, to advance our understanding of the consequences  
455 of temperature variation in complex ecosystems, can improve our ability to inform management  
456 responses that are robust to future climates with increasing variability and extremes.

457

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464  
465

466 **Figures**

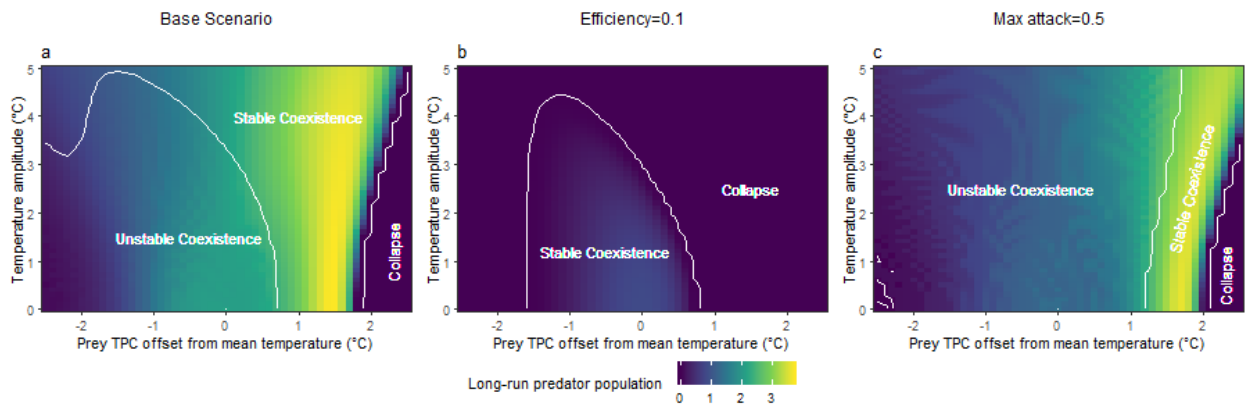


467

468 **Figure 1. Nonlinear responses to temperature.** A conceptual figure of how variable  
 469 temperatures affect demographic rates, e.g., intrinsic per-capita growth rate  $r(T)$  or attack rate  
 470  $a(T)$ , following thermal performance curves (TPCs). Each individual of a species has a  
 471 temperature optimum  $T^*$  at which its performance is maximized, which may be offset from the  
 472 mean environmental temperature  $\bar{T}$ . When temperature varies, average demographic rates  $\overline{r(T)}$   
 473 and  $\overline{a(T)}$  may be higher or lower than demographic rates at the mean temperature ( $r(\bar{T})$  and  
 474  $a(\bar{T})$ ) due to Jensen's inequality. For example, average rates are likely to be smaller for species  
 475 adapted to their average ecosystem temperature, i.e.  $T^* \approx \bar{T}$ . If the range of temperatures  
 476 encompasses both convex and concave regions of the TPC, the net effect is indeterminate but

477 generally nonzero. In experiments, we vary (1) the amplitude of temperature variability ( $T_{max}$  –  
478  $T_{min}$ ), and (2) how far the TPCs are offset from the environmental mean temperature ( $T_r^* - \bar{T}$   
479 and  $T_a^* - \bar{T}$ ). We restrict offsets to be equal in magnitude but have opposite sign, reporting  
480 results in terms of the predator’s TPC offset ( $T_r^* - \bar{T}$ ).

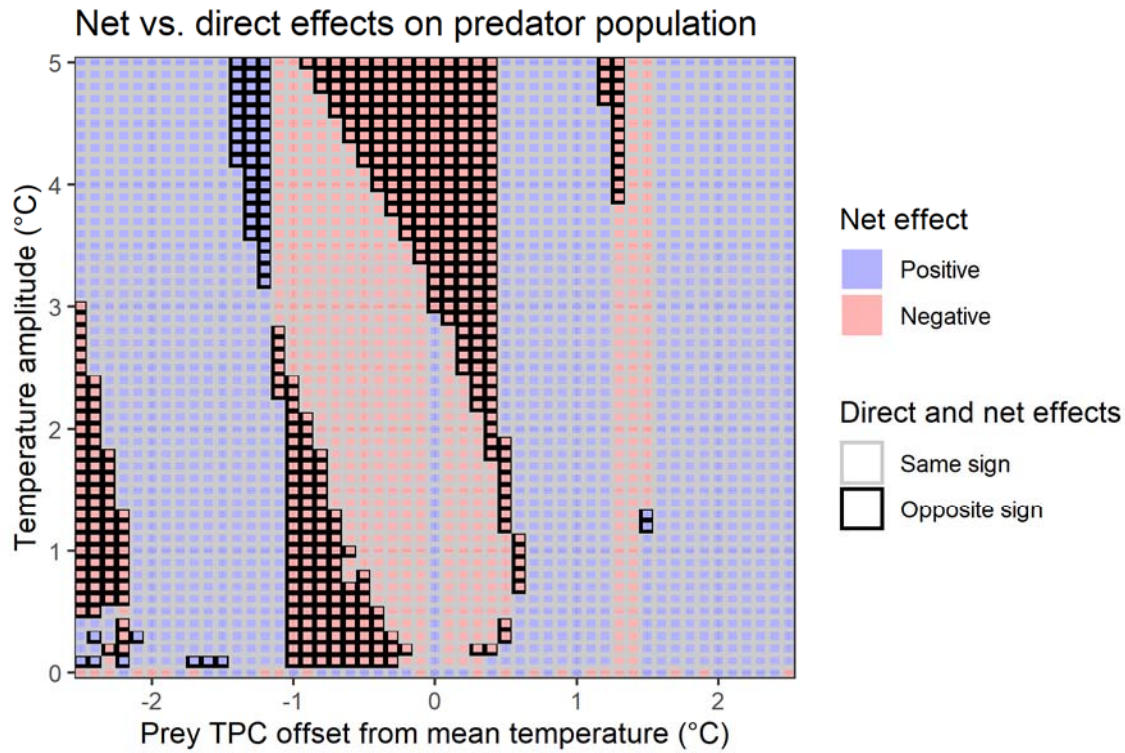
481



482

483 **Figure 2: Stable predator collapse or predator-prey coexistence depends on both the offset**  
484 **in the predator and prey thermal performance curves (TPCs) and amplitude of**  
485 **temperature variability.** Effects of offset in the predator and prey TPCs (x-axis) and amplitude  
486 of temperature variability (y-axis) on predator population abundance (colors) and the type of  
487 equilibrium that arises: predator collapse or predator-prey coexistence, and whether the latter is  
488 stable or unstable (e.g., cycles or oscillatory behavior). Base scenario parameters (a) are  
489 mortality  $m = 0.2$ , carrying capacity  $K = 20$ , conversion efficiency  $c = 0.3$ , maximum attack rate  
490  $a = 0.3$ , and handling time  $h = 0.3$ , whereas species interactions are modified in (b-c) by  
491 lowering conversion efficiency  $c = 0.1$  (B) or increasing attack rate  $a = 0.5$  (C). TPC parameters  
492 are in Table S1.

493



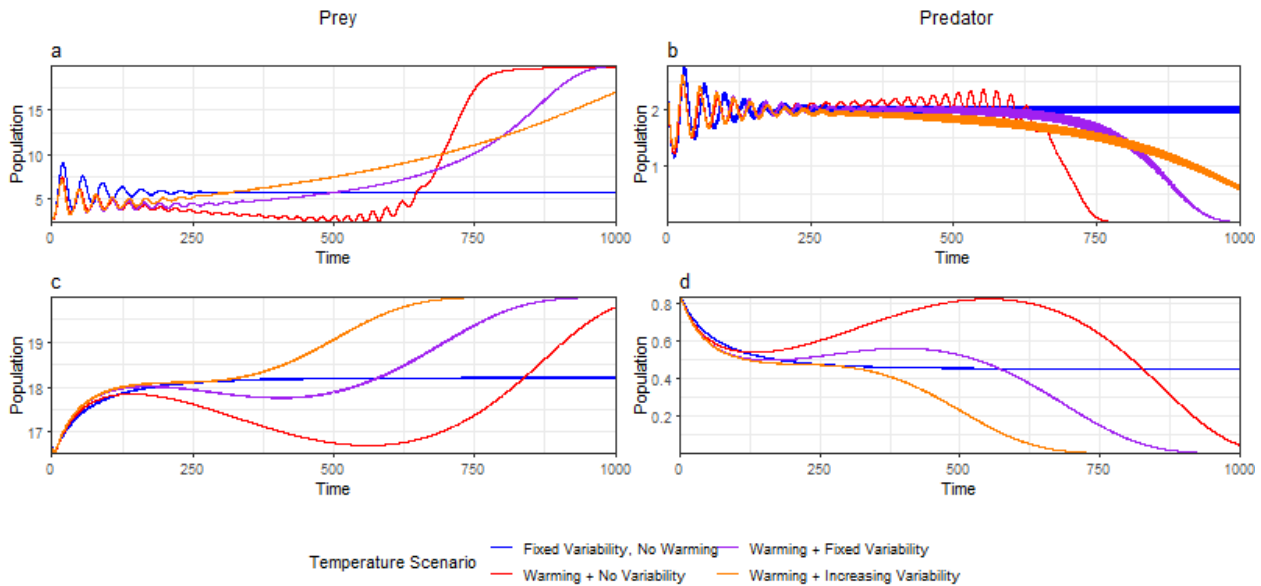
494

495 **Figure 3: The net and direct effects of temperature variability on predator population.**

496 Net effects (blue: positive; red: negative) of temperature variability on long-run population levels  
497 for the predator, as a function of how far the prey TPC is offset relative to the mean temperature  
498 (x-axis) and the amplitude of temperature variability (y-axis). Outlines indicate whether net  
499 effects have the same sign (black outline) or not (light gray outline) as when only considering the  
500 effects of temperature variability on the predator, ignoring the temperature-dependence of its  
501 prey ('direct effects'). For example, red-filled and black-outlined regions indicate  
502 parameterizations where considering only temperature effects on the predator would suggest a  
503 positive effect of temperature variability for the predator population when the true net effect is  
504 negative, due to species interactions. Parameters as in Fig. 2a with TPC parameters in Table S1;  
505 see Fig S4 for results from additional parameterizations.



506



507

508 **Figure 4. Interacting effects of warming and temperature variability.**

509 Population trajectories for the prey (a,c) and predator (b,d) under scenarios of warming

510 (increasing mean temperatures) with no variability (red), constant temperature variability with

511 constant mean temperatures (blue), increases in mean temperatures with constant variability

512 (purple), and increases in both mean temperatures and temperatures variability (orange).

513 Variability on top of warming can either delay (panel b) or accelerate (panel d) predator collapse.

514 Panels a and b reflect model parameters as in Fig 2a with  $T_{max} - T_{min} = 8^\circ C$ ; panels c and d

515 reflect model parameters as in Fig 2b with  $T_{max} - T_{min} = 2^\circ C$  TPC parameters are in Table S1

516 with zero offset.

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