

1 **Are we underestimating the ecological and evolutionary effects of warming?**
2 **Interactions with other environmental drivers may increase species vulnerability to**
3 **high temperatures**

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14

15 **Abstract**

16

17 Warming, the most prominent aspect of global environmental change, already affects
18 most ecosystems on Earth. In recent years, biologists have increasingly integrated the effects
19 of warming into their models by capturing how temperature shapes their physiology, ecology,
20 behavior, evolutionary adaptation, and probability of extirpation/extinction. The more
21 physiologically-grounded approaches to predicting ectotherms' responses use thermal
22 performance curves (TPCs) obtained by measuring species performance (e.g. growth rate)
23 under different temperatures. TPCs are typically measured while other factors are held
24 constant at benign levels to 'isolate' the effects of temperature. Here we highlight that this
25 practice paints a misleading picture because TPCs are *functions* of other factors, including
26 global change stressors. We review evidence that resource limitation, pH, oxygen and CO₂
27 concentration, salinity, water availability, parasites and mutualists, all influence TPC shape
28 and thermal traits such as optimum temperature for growth. Evidence from a wide variety of
29 organisms – phytoplankton, protists, plants, insects, and fish – points towards such
30 interactions increasing organisms' susceptibility to high temperatures (reducing it in the case
31 of mutualists). Failing to account for these interactions is likely to lead to erroneous
32 predictions of performance in nature and an underestimation of the risks of warming. We
33 discuss the general patterns and possible consequences of such interactions for ecological
34 communities. But importantly, interactions with TPCs share common features that we can
35 learn from. Incorporating these interactions into population and community models should
36 lead to deeper insights and more accurate predictions of species' performance in nature – as
37 well as strategies for managing natural and agricultural ecosystems in the face of warming.

38

39 **Keywords:** Thermal performance curve (TPC), optimum temperature, stressor interaction,
40 resource limitation, global environmental change, warming.

41 **Introduction**

42 The next 100 years are expected to see temperature increases of at least 2 to 3°C both
43 on land and in the ocean, and the planet will likely continue to warm beyond that time frame
44 (IPCC 2021). Understanding and predicting the consequences of this change has been a
45 major, defining goal of biological research for nearly a generation – and will continue to be,
46 for decades to come. A multitude of approaches has been used to understand what warming
47 and associated environmental changes means for organisms, communities, and ecosystems:
48 from experiments in the lab, mesocosm and field, correlative analyses on expression patterns,
49 genes, species, communities and ecosystems, from local to global scales, theoretical models
50 ranging from the abstract and simple to the detailed and specific. To make this problem
51 tractable, a substantial proportion of this work – especially the experimental and theoretical
52 parts – has focused on isolating the effects of temperature change alone on populations and
53 communities and maintaining other environmental factors at benign (e.g., high nutrient/food
54 levels) levels. We argue that this approach must change. By ignoring or oversimplifying how
55 temperature interacts with other factors to influence populations and communities, we draw
56 conclusions and make projections that are likely to be heavily biased.

57 Here we briefly describe how temperature shapes the growth of ectotherms, then
58 discuss the available evidence on temperature interactions with other environmental factors,
59 and the consequences of such interactions for predicting the effects of rising temperatures on
60 species and communities. The strongest existing evidence is for the effects of resource
61 limitation on the temperature response because this has received the most careful study, but
62 we also provide examples of how other abiotic and biotic factors affect thermal performance
63 curves.

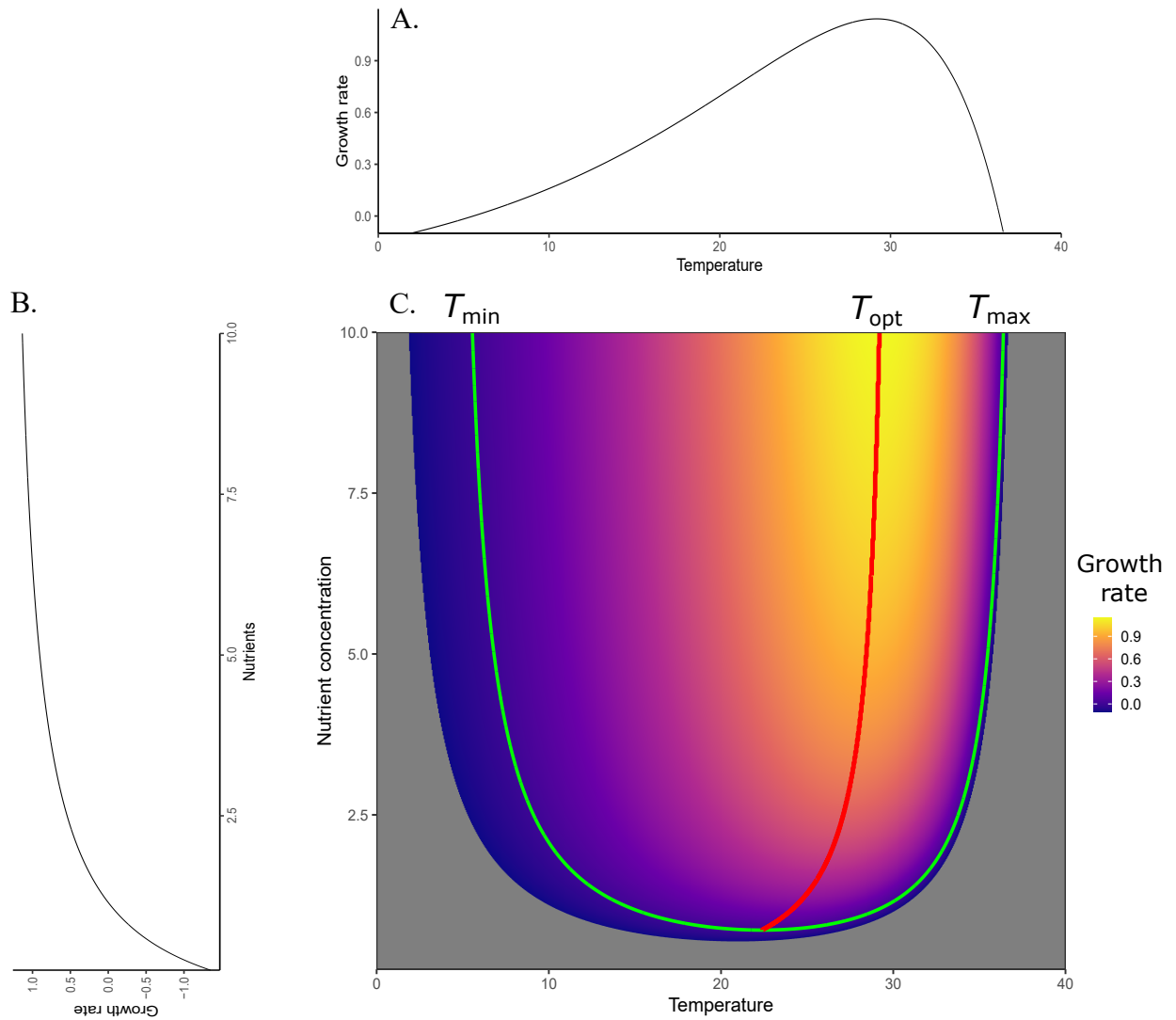
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65 **Thermal performance curves (TPCs)**

66 At a fundamental level, temperature affects organisms by changing chemical reaction
67 rates. Accelerating reaction rates with increasing temperature from a low baseline tends to
68 increase organismal performance and vital rates. As summarized in the Metabolic Theory of
69 Ecology, increasing temperature drives exponential increases in rates of growth, death,
70 movement, consumption, reproduction, mutation and more (Brown et al. 2004). This in turn
71 causes global variation in a host of traits and life history strategies. For any particular
72 biochemical reaction, however, the exponential increase in reaction rate with increasing
73 temperature does not continue indefinitely: it slows, stops, and reverses rapidly. At a high
74 enough temperature, enzyme conformations begin to fail and they bind with unintended
75 target molecules. In all ectotherms, from bacteria to reptiles, this manifests at the organismal
76 and population level as performance being a left-skewed unimodal function of temperature
77 (Fig. 1A). There are also additional thermodynamic, metabolic and physiological processes
78 that control thermal limits (Tomanek 2008, Ritchie 2018).

79 This unimodal function describing the dependence of growth or other process on
80 temperature is called the thermal performance curve (TPC) or thermal reaction norm. It has
81 been at the core of attempts to mechanistically link physiology with species ranges,
82 population dynamics and community composition. While the full TPCs can be incorporated
83 into theoretical models, they can also conveniently be summarized using a few easily-
84 understood parameters such as the optimum, maximum and minimum temperatures (T_{opt} , T_{max}
85 and T_{min}). These parameters can be thought of as traits, and are often used to assess species'
86 vulnerability to high or low temperatures and define their thermal niches (Fig. 1A, Deutsch et
87 al. 2008, Addo-Beddiako et al. 2000, Thomas et al. 2012, Sunday et al. 2011). TPCs and
88 these associated traits capture important patterns in – and constraints on – growth rates and
89 geographic ranges (Sunday et al. 2012, Payne et al. 2016). Therefore, using these TPCs to

90 project how warming will alter species performance and shift their ranges seems feasible with
91 our present level of knowledge. At individual locations, temperature projections through time
92 instead of space can be used to generate expectations of whether species would be able to
93 persist (expected net population growth rate ≥ 0) and whether community composition would
94 remain similar. There are complications that are difficult to address rigorously with this
95 approach at present due to insufficient empirical data on TPC evolution and on how biotic
96 interactions depend on species' TPCs (O'Donnell et al. 2018, Tüzün and Stoks 2018). We
97 focus here on one complication that can and should be addressed: the dependence of TPCs
98 and temperature traits on other environmental drivers such as nutrient/food availability.



99

100 **Figure 1.** The dependence of population growth rate on temperature and nutrient
 101 concentration. A. A typical thermal performance curve (TPC). B. Growth dependence on
 102 nutrient concentration. C. The growth rate surface as a function of temperature and nutrients,
 103 based on a model and data from Thomas et al. (2017). Growth rate is highest when the
 104 temperature is at T_{opt} and nutrient concentration is high. Growth rates below -0.1 are
 105 suppressed to highlight variation in positive values.

106

107 **The dependence of TPCs on environmental factors**

108 **The TPC is not a stable property of species, populations or even individuals.**

109 Temperature interacts with a number of other environmental factors to determine

110 performance; or stated differently, the TPC is itself a function of other factors. Food/nutrient
111 availability, pH, light (for photosynthetic organisms), salinity, water availability, oxygen
112 concentration, as well as biotic interactions such as parasitism or mutualism, all can alter the
113 shape of the TPC (Ern et al. 2016, Thomas et al. 2017, Aldea-Sánchez et al. 2021, Hector et
114 al. 2021).

115 The available evidence suggests that TPC dependence on various environmental
116 factors is widespread. The pattern that emerges across taxa and environmental factors is that
117 T_{opt} and T_{max} (as well as maximum growth rate) decline in stressful conditions such as
118 resource limitation (Fig. 1C). In other words, organisms are more sensitive to high
119 temperatures when deprived of resources or subjected to extremes in other environmental
120 dimensions. In phytoplankton, major oceanic primary producers, nutrient limitation has been
121 shown to not only decrease their maximum population growth rates but also lower their T_{opt}
122 by 3 - 15°C (Boyd 2019, Thomas et al. 2017, Bestion et al. 2018). Light limitation also
123 decreases T_{opt} in phytoplankton by about 4°C on average (Edwards et al. 2016) and as much
124 as 18°C in well-resolved cases (Kovács et al. 2016); it also increases vulnerability to high
125 temperature in seagrasses (Kendrick et al. 2019). In kelp, nitrogen limitation reduced high
126 temperature tolerance (Fernández et al. 2020). In maize, one of the world's most important
127 crops, high temperatures reduced yield three-fold more per °C with increasing water
128 limitation (30%, vs 10% at higher water availability) (Anderson et al. 2015). In another
129 study, irrigated maize was not negatively affected by high temperatures (Carter et al. 2016),
130 though this is partly due to cooling by evaporation (Siebert et al. 2017).

131 This resource-dependence of temperature responses is not limited to photosynthetic
132 organisms. Food reduction decreased T_{opt} and T_{max} by approximately 3-7°C in the freshwater
133 ciliate *Urotricha farcta* (Weisse et al. 2002) and the marine flagellate *Oxyrrhis marina*
134 (Kimmance et al. 2006). The decline in optimum temperature occurs in fish as well: at low

135 food availability, T_{opt} for somatic growth declines by approximately 10°C in salmon (Brett
136 1971) and several degrees in coral reef damselfish larvae (precise values could not be
137 quantified) (McLeod et al. 2013). The salmon study also showed a decrease in T_{max} of
138 approximately 10°C. Food limitation also decreased T_{opt} and T_{max} for population growth rate
139 by about 6°C in mosquitoes (Huxley et al. 2021). In some studies, however, a zooplankter
140 *Daphnia*'s survival at high temperature was higher when fed low phosphorus algae or poor
141 food quality cyanobacteria (Starke et al. 2021, Sarrazin and Sperfeld 2022), suggesting that
142 the effects of resource limitation may differ depending on the temporal scale of responses
143 (Sarrazin and Sperfeld 2022).

144 Other environmental drivers and biotic interactions modify TPCs in a manner that is
145 often similar to the effects of resource limitation. Salinity reduction lowered T_{opt} and T_{max} in
146 phytoplankton from an estuary by 2 - 10°C (Bill et al. 2016). Frogs infected by chytrid
147 pathogens had a reduced tolerance for high temperatures, experiencing spasms at
148 temperatures ~4°C lower than uninfected frogs (Greenspan et al. 2017). Reductions in high-
149 temperature tolerance were also found in *Daphnia* infected by bacterial pathogens, in both
150 short- and long-term experiments (Vale et al. 2008, Hector et al. 2019, Laidlaw et al. 2020).
151 We note that some of these biotic interaction experiments used short-term assays that are
152 substantially different from those used when studying abiotic interactions, and so some
153 caution in comparing measurements is warranted.

154 In contrast, mutualistic interactions increase heat tolerance in a wide range of taxa. In
155 both wild and crop plants, fungal symbionts increase tolerance of high temperatures as well
156 as other stresses such as drought (Redman et al. 2002, Rodriguez et al. 2008, Hubbard et al.
157 2014). In one extraordinary example, the host plant's heat tolerance is dependent on both a
158 fungal endophyte and a virus that infects the fungus (Márquez et al. 2007). The gut
159 microbiota increased heat tolerance of fruit flies (Jaramillo and Castañeda 2021) and tadpoles

160 (Fontaine et al. 2022), and the symbionts of corals increased the thermal tolerance of
161 holobionts (Berkelmans and van Oppen 2006, Pelosi et al. 2021). While the mechanisms of
162 these interactions are not well understood, they alter high-temperature tolerance in a manner
163 consistent with resource change: deprivation reducing T_{\max} in the case of parasites/pathogens
164 (due to reallocation towards combating infection) and supply increasing T_{\max} in the case of
165 mutualists.

166 Theoretical investigation of interactions between temperature and other drivers has
167 been limited, but at least two recent models have examined temperature-resource
168 (nutrient/food) interactions influence populations, or equivalently, how resource limitation
169 alters TPCs (Thomas et al. 2017, Huey and Kingsolver 2019). Thomas et al. (2017)
170 developed a simple model of temperature-resource interactions that separates the effects of
171 the two factors on birth and death processes. Huey & Kingsolver (2019) formulated a
172 bioenergetic model that focusses on the thermal sensitivities of energy gain and metabolism.
173 Despite their structural differences, both models come to a similar conclusion: T_{opt} and T_{\max}
174 are saturating functions of resource concentration, consistent with the empirical findings
175 described earlier. Both models also predict that T_{\min} is altered as well, with low resources
176 reducing cold tolerance in a similar manner. Although fewer studies have examined T_{\min} ,
177 high N availability appears to increase cold tolerance in plants (Taulavuori et al. 2014, Toca
178 et al. 2017).

179 **Consequences of interactions of temperature with other environmental factors**

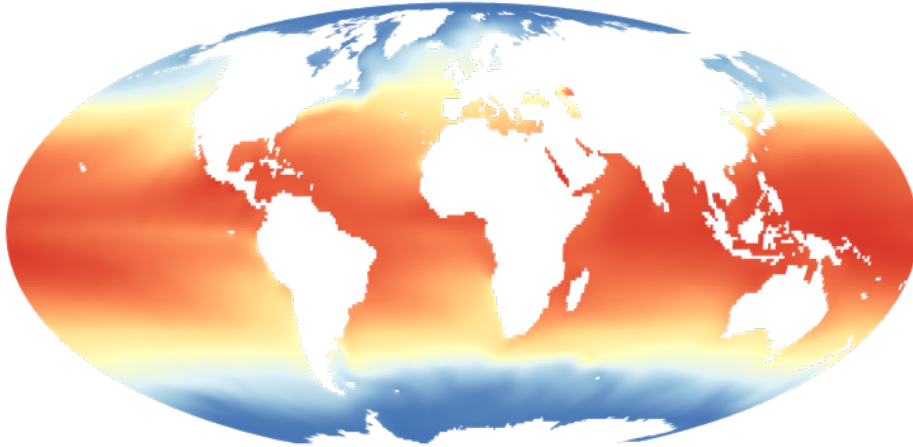
180 Using TPCs obtained in otherwise benign conditions – with no resource limitation or
181 other environmental stress – to predict species survival and shifts in their geographic ranges
182 is likely to underestimate the negative effects of warming. This is because in most habitats,
183 environmental factors are at stressful levels at least part of the time. The observed
184 dependence of thermal traits on other environmental factors has many consequences for

185 organisms, populations and communities that need to be accounted for when predicting the
186 effects of rising temperature and preparing for the future. Here we outline several such
187 consequences that should be investigated.

188 1. Aquatic and terrestrial ecosystems with pronounced resource limitation may be more
189 adversely affected by warming than ecosystems that are not resource-limited. Nutrient
190 (nitrogen, phosphorus or iron) limitation is widespread in the oceans and is predicted to
191 become even more prevalent in the future (Sarmiento et al. 2004, Hayashida et al. 2020). On
192 land, vast regions are also limited by P, N or co-limited by more than one nutrient (Du et al.
193 2020, Hou et al. 2021). Aridification of the land surface is also increasing, especially in the
194 subtropics, thus increasing areas with water limitation (Shi et al. 2021). Because resource
195 limitation decreases T_{opt} and T_{max} (Thomas et al. 2017, Huey and Kingsolver 2019), a
196 simultaneous reduction in resource availability alongside increasing temperatures is likely to
197 be substantially worse than warming alone, affecting broad swathes of the globe (Busseni et
198 al. 2020). Identifying areas that are undergoing changes in temperature as well as the type
199 and degree of resource limitation (Hayashida et al. 2020) could help pinpoint communities
200 that are especially vulnerable to climate change. Fig. 2 shows global ocean nitrate
201 concentration, temperature, and the regions where the lowest nitrate concentration and
202 highest temperatures overlap. Such areas appear predominantly in the tropics. T_{opt} values of
203 tropical phytoplankton measured under replete nutrient conditions are very close to current
204 ambient temperatures (Thomas et al. 2012), and so the declines of T_{opt} due to nutrient
205 limitation are likely to be especially detrimental there, assuming temperatures rise or
206 nutrients decline further in these regions. Tropical terrestrial organisms' T_{opt} values are also
207 close to ambient temperatures (Deutsch et al. 2008), raising the possibility that food declines
208 will reduce heat tolerance on land as well. In terrestrial plants, most studies focus either on
209 the effects of single stressors, namely temperature and water limitation, or on their

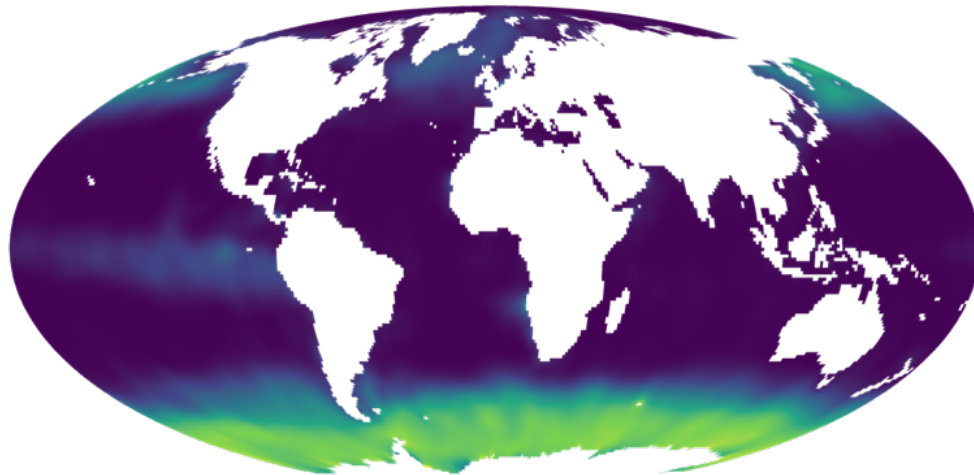
210 interactions (Fahad et al. 2017, El Haddad et al. 2021). The next step should be investigating
211 the effects of nutrient limitation on plant sensitivity to high temperatures, both at high and
212 low water availability.

Temperature

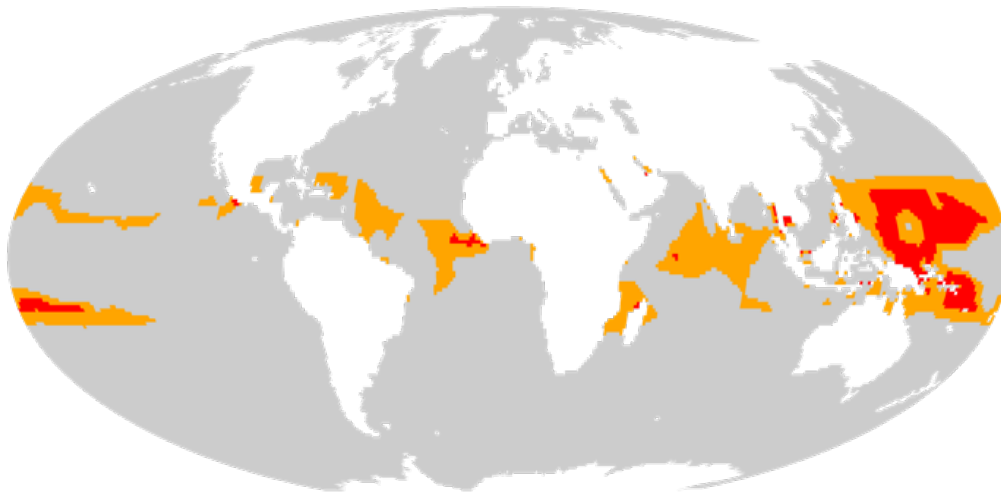


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Nitrate



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215

216 **Figure 2.** Oceanic regions where temperature-nutrient interactions are most likely to be
217 limiting phytoplankton growth and possibly shaping ecosystem dynamics. The bottom map
218 highlights oceanic locations where temperatures are near their maximum and nitrate
219 concentrations near their minimum. Red indicates regions where temperature is in the top
220 10% and nitrate in the bottom 10%. Orange uses a 20% threshold for both instead. For both
221 variables, we use annual mean values and ignore other factors that also shape growth. Data
222 source: World Ocean Atlas 2018 (Garcia et al. 2018, Locarnini et al. 2019).

223

224 2. Heat stress may increase resource requirements while impairing the ability to acquire
225 nutrients/food, such as by damaging nutrient transport mechanisms or reducing time available
226 for foraging. This exacerbates both the harmful effects of resource limitation and high
227 temperatures, causing a harmful positive feedback loop termed a ‘metabolic meltdown’
228 (Gerecht et al. 2018, Giri et al. 2017, Huey and Kingsolver 2019). These feedback loops are
229 underexplored, and may already play an important role in organismal performance in the
230 tropics and during heat waves.

231 3. The available evidence is consistent with a simple prediction: environmental conditions
232 (both abiotic and biotic) that reduce growth rate also reduce T_{opt} and T_{max} , relative to benign
233 conditions. This remains to be tested rigorously across a wide range of conditions. But if true,

234 it would offer us a simple and powerful tool because quantifying changes in growth rate is
235 often cheaper, faster and easier than quantifying T_{opt} and T_{max} directly. Predicting how other
236 environmental changes will shape tolerance of high temperatures would become easier if
237 general ecophysiological patterns such as this exist.

238 4. Because species differ in resource requirements, the same resource levels are limiting to
239 some species and not others (Edwards et al. 2012, Grover 1997). These differences may
240 increase the differences in vulnerability to high temperatures and therefore change
241 community composition. Good nutrient competitors may have their TPCs relatively
242 unchanged by decreases in resources while poor nutrient competitors experience decreases in
243 T_{opt} and T_{max} that make them more sensitive to warming and reduce their relative abundance
244 in the community. An additional source of complexity that we do not discuss here is that
245 resource competitive abilities are also a function of temperature (Tilman et al. 1981,
246 Lewington-Pearce et al. 2019). These feedbacks between temperature and nutrients have not
247 yet been adequately incorporated into our predictions of the global change effects on
248 organisms, populations and communities.

249 5. Within species, populations located in low-resource regions today - such as the oceanic
250 gyres or drylands - may be a valuable source of genetic diversity. Being adapted to low
251 resource levels, they may be better able to tolerate high temperatures under high-nutrient
252 conditions than populations presently living in high-resource regions. They could therefore
253 form a reservoir of (relative) heat tolerance. Heat waves in adjacent high-resource regions
254 may provide opportunities for immigrants from low-resource environments by removing
255 competitors adapted to high-resource conditions. These preadapted genotypes can either
256 disperse into novel environments on their own or be transplanted deliberately to rescue
257 declining populations (Bay et al. 2017).

258 6. Just as species are expected to migrate towards cooler regions, species from hot
259 environments that also experience other stresses at present (low resource availability or low
260 pH, for example) may survive by migrating towards high-resource or moderate pH
261 environments. Such migrations may favour the persistence of otherwise vulnerable taxa. This
262 complicates predictions of extirpation and extinction based solely on thermal limits. It can
263 also lead to more complex spatial and temporal patterns of community reorganization than
264 presently envisioned. A species that persists by migrating towards high-resource or moderate
265 pH environments necessarily competes with resident taxa, possibly causing extirpations. This
266 complex outcome of environmental warming will be hard to predict or model, but properly
267 accounting for interactions is a necessary step towards achieving this.

268 7. The interacting effects of temperature and resources also cascade through food webs. If
269 prey species decline due to warming, this may trigger a similar temperature-food interaction
270 problem in their predators. They may become more sensitive to high temperatures due to
271 resource (food) limitation, and this may amplify the negative effects of warming on
272 consumers. While some studies are starting to address the indirect effects of temperature on
273 food webs (Gibert 2019), we know very little about how resource limitation will shape the
274 TPCs of different trophic levels. We need to incorporate such interactions for multiple
275 trophic levels into food web models to realistically model multiple driver effects on food
276 webs.

277 8. Phenological shifts can also change resource availability for different trophic levels (Nord
278 and Lynch 2009, Visser and Both 2005) and may therefore increase vulnerability to high
279 temperatures. Flowering plants in peak summer may be an especially important resource for
280 local pollinator communities and their predators. Shifts in flowering times leading to lower
281 resource availability for pollinators (Solga et al. 2014) may make pollinators - especially the

282 specialists - more vulnerable to high temperatures, including heat waves. Changes in fruiting
283 times may also have important effects on consumer species' heat tolerances.

284 9. Selection on temperature tolerance is likely much stronger in nature than anticipated from
285 lab studies, because of the increased heat stress associated with periods of low food and other
286 stresses. Evolutionary adaptation to high temperature may itself be affected by resource
287 availability and other environmental drivers. Under the suboptimal levels of other
288 environmental factors, adaptation to rising temperatures may either be faster due to stronger
289 selection or be slowed down or arrested, if there are trade-offs between temperature
290 tolerances and resource requirements (Aranguren-Gassis et al. 2019), in addition to the
291 simpler reason that population sizes may be reduced. Evolution experiments under different
292 combinations of environmental drivers and temperature would help determine how driver
293 interactions affect thermal adaptation.

294 10. Fertilization practices in agriculture are likely to be especially important to consider as
295 the climate warms. Although excess fertilization is a major environmental concern because of
296 the consequent greenhouse gas emissions (Tian et al. 2020) and aquatic eutrophication
297 (Conley et al. 2009), preventing periods of nutrient limitation in plants could provide
298 protection against heat waves. Nutrient supply has been proposed as a crop cultivation
299 strategy to offset the negative effects of high temperatures (Waraich et al. 2012).

300 11. Because some mutualistic interactions appear to increase high-temperature tolerance (at
301 least in plants), developing and using crop mutualists may alleviate future increases in heat
302 stress. Mutualists from hot environments may improve high-temperature performance of
303 existing crops, a phenomenon known as 'habitat-adapted symbiosis' (Rodriguez et al. 2008).
304 Conversely, disease will likely reduce tolerance for high temperatures. Optimizing crops for
305 future heat waves may require approaches that increase mutualist abundance and resource
306 availability while decreasing disease prevalence. These are likely steps that would be useful

307 even in the absence of warming, but protection from heat stress makes them even more
308 valuable. Possible trade-offs that reduce the possibility of accomplishing these goals are
309 worth investigating to improve crop performance, such as between receptiveness to
310 mutualism and resistance against infection.

311

312 **Conclusions**

313 Across different organisms and ecosystems, a variety of abiotic and biotic drivers
314 modify organisms' ability to tolerate high temperatures. Because these effects appear so
315 widespread, we need to explicitly consider how temperature interacts with other
316 environmental factors, including global change stressors, to develop better predictions of how
317 warming will affect species and communities. So far, most research on the environmental
318 driver interactions with temperature has focused on nutrients and water availability, but the
319 effects of many other environmental factors - especially biotic ones - on TPCs remains
320 underexplored. A focused research agenda to investigate systematically the effects of
321 multiple interacting stressors on species' TPCs from a wide range of habitats in oceanic,
322 freshwater and terrestrial ecosystems (including agricultural systems), would align well with
323 the ongoing efforts to implement the multiple driver/multistressor framework in global
324 change research (Boyd et al. 2019, Wake 2019). Among the key topics to address are: how
325 universal the negative effects of other stressors on the high temperature tolerances are, the
326 magnitudes and the mechanisms of the effects and whether adding more than one or two
327 stressors exacerbates thermal sensitivity even further. The new research would help to better
328 assess the effects of global warming on species growth, future geographic ranges,
329 productivity and biodiversity. Moreover, it is essential for developing predictive models for
330 conservation, agriculture, fisheries and climate change mitigation.

331

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