

1 **A framework for understanding climate change impacts through non-compensatory intra-**
2 **and interspecific climate change responses**

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27 **Abstract**

28 Understanding and predicting population responses to climate change is a crucial challenge. A
29 key component of population responses to climate change are cases in which focal biological
30 rates (e.g. population growth rates) change in response to climate change due to non-
31 compensatory effects of changes in the underlying components (e.g. birth and death rates)
32 determining the focal rates. We refer to these responses as non-compensatory climate change
33 effects. As differential responses of biological rates to climate change have been documented in
34 a variety of systems and arise at multiple levels of organization within and across species, non-
35 compensatory effects may be nearly ubiquitous. Yet, how non-compensatory climate change
36 responses combine and scale to influence the demographics of populations is often unclear and
37 requires mapping them to the birth and death rates underlying population change. We provide a
38 flexible framework for incorporating non-compensatory changes in upstream rates within and
39 among species and mapping their consequences for additional downstream rates across scales to
40 their eventual effects on population growth rates. Throughout we provide specific examples and
41 potential applications of the framework. We hope this framework helps to enhance our
42 understanding of and unify research on population responses to climate change.

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44

45 **Introduction**

46 Global climate change is altering mean temperatures, temperature variances, precipitation
47 regimes, and extreme weather events (IPCC 2021). Understanding how species respond to these
48 changes is crucial for managing and forecasting the ecological impacts of climate change.
49 Furthermore, understanding species' responses to climate change is also critical due to the
50 potential consequences for ecosystem services, disease transmission, and food production (IPCC
51 2022). However, predicting species responses to climate change remains difficult because this
52 requires an understanding of both direct physiological effects and impacts on intra- and
53 interspecific interactions (Blois *et al.* 2013; Gilman *et al.* 2010; Sutherst *et al.* 2007).

54 Our goal here is to provide a framework for understanding and predicting how
55 populations will respond to climate change through non-compensatory effects of climate change
56 on rates determining species' population demographics. We define a **non-compensatory effect**
57 as the case in which a focal 'downstream' rate of interest changes because changes in 'upstream'
58 processes influencing the focal rate do not cancel one another out (see Box 1 for an in-depth
59 explanation and mathematical definition, and see Box 2 for a glossary of terms in bold
60 throughout the manuscript). Non-compensatory effects with respect to climate change are those
61 in which the 'upstream' components respond in a non-compensatory manner to some aspect of
62 climate (e.g. precipitation, temperature, pH, etc.) to drive a change in a 'downstream' focal rate.
63 For example, changing temperatures can alter population growth rate (a downstream rate)
64 through non-compensatory effects of changes in birth and death rates (upstream rates;
65 Amarasekare & Savage 2012). Such non-compensatory effects can occur at any level of
66 biological organization, from the molecular level to population growth rate, and a key to

67 understanding them is to identify a focal rate, to evaluate how upstream components combine to
68 generate the focal rate, and to assess the response of upstream components to climate change.

69 We focus on non-compensatory climate change effects for two principal reasons. First, at
70 the population level, a crucial climate change response is the extent to which a population might
71 grow or decline in response to climate change. In general, barring changes in immigration or
72 emigration, changes in population abundances must reflect non-zero population growth rates (i.e.
73 birth rates minus death rates; note that our framework can be expanded to incorporate the
74 climate-dependence of immigration and emigration, but we do not discuss these here for the sake
75 of simplicity). For example, a change to a negative growth rate from a positive one with a change
76 in the environment implies that birth and death rates have changed with the environment such
77 that the death rate now exceeds the birth rate. Thus, this fundamental non-compensatory effect is
78 central to understanding population demographic changes in response to climate change, as well
79 as all other dynamic changes in population abundance. Second, there exists a large and growing
80 list of so-called ‘asymmetries’ and ‘mismatches’ that have been identified both within and
81 among species. These asymmetries and mismatches describe cases in which multiple biological
82 rates respond differently to climate change, suggesting that non-compensatory climate change
83 effects could be nearly ubiquitous (See Box 3: Non-compensatory Effects, Asymmetries, and
84 Mismatches for a critical comparison of the three concepts). For example, studies have identified
85 asymmetric responses to temperature: among different rates within species (Bozinovic *et al.*
86 2020; Huey & Kingsolver 2019; Johnson *et al.* 2023; Jørgensen *et al.* 2022; Pawar *et al.* 2024;
87 Wang *et al.* 2020), in consumer-resource interactions (Álvarez-Codesal *et al.* 2023; Bideault *et*
88 *al.* 2021; Dell *et al.* 2014; Gibert *et al.* 2022; Gilbert *et al.* 2014), and in host-parasite systems
89 (Cohen *et al.* 2017; Kirk *et al.* 2022; Mordecai *et al.* 2013, 2019; Taylor *et al.* 2019). However,

90 we currently lack a cohesive framework with which to conceptualize how these responses might
91 lead to non-compensatory climate change effects and how those effects fit together and interact
92 to ultimately produce changes in populations. Furthermore, a common framework to understand
93 these non-compensatory effects across systems would provide a powerful tool for synthesizing
94 climate change impacts.

95 Below, we first provide an in-depth explanation of a framework for understanding non-
96 compensatory climate change effects that provides a flexible, hierarchical approach for linking
97 multiple non-compensatory effects, tracking their consequences for populations, and connecting
98 both intra- and interspecific processes. Throughout our explanation of the framework, we
99 provide empirical examples of non-compensatory climate change effects across single-species
100 systems, consumer-resource interactions, parasite-host interactions, and others to illustrate the
101 generality of the framework and how it can be applied to understanding climate change
102 responses in particular systems. We then conclude by providing some suggestions for how
103 researchers might apply this framework in their own systems and offer guidance on how future
104 studies might combine this framework with experiments and observational data to better
105 understand species' responses to climate change.

106 **A framework for Non-compensatory Effects and Climate Change Impacts**

107 *A minimal, rate-hierarchy model of emergent climate change effects*

108 Our framework (Figure 1) starts with the recognition that the most concerning species' responses
109 to climate change generally come in the form of changes in population size through the
110 population growth rate. Thus, we focus primarily on the population growth rate (r ; note that this
111 is the net growth rate encompassing births and all sources of mortality rather than a maximum or
112 intrinsic growth rate). All factors that feed into population growth within our framework are also

113 rates. By definition, in a closed population, changes in growth rates are driven by changes in the
114 demographic rates of births (b) and deaths (d). Thus, a **demographic non-compensatory effect**
115 arises when birth and death rates respond to some aspect of climate change (e.g., temperature) in
116 a non-compensatory way thus altering the population growth rate. Demographic non-
117 compensatory effects form the top-level effect and all other non-compensatory effects must feed
118 into the demographic non-compensatory effect to affect the population growth rate.

119 Changes in birth rates arise through two general pathways. First, net resource uptake (of
120 any form from light to prey; designated as u) determines the amount of energy and biosynthetic
121 metabolites available for allocation to reproduction (b), organismal growth (g), and maintenance
122 (d_i , with allocations described by dashed lines in Figure 1). Allocation of resources to
123 reproduction is a principal driver of birth rates, given variation in life history that determines
124 offspring size, fecundity, and reproductive effort. Indirectly, birth rates at the population level
125 are also determined by the timing of maturation based on development rate. Thus, organismal
126 growth feeds into the rate of births at the population level by influencing the number of adults.

127 Changes in death rates (d) arise through both internal (d_i) and external forces (d_e).
128 External forces include risks from environmental conditions, competitors, predators, or
129 pathogens generating a rate of extrinsic mortality. Internal forces, such as aging, will generate an
130 intrinsic rate of mortality. This intrinsic rate will depend on the allocation of resources to
131 maintenance, including repair, immune function, and basal metabolic costs. Intrinsic and
132 extrinsic death rates are, in principle, additive. Although one could influence the other through
133 density dependence and compensatory mortality (i.e., when extrinsic mortality reduces density-
134 dependent mortality; Anderson & Burnham 1976).

135 This minimal model represents a single species and can be broken into life stages if
136 needed as different life stages may have different responses to climate variables and accounting
137 for stage structure may be necessary to understand overall population patterns (Coulson *et al.*
138 2001; Davidson *et al.* 2024; Johnson *et al.* 2023). It can also be connected to other species via
139 connecting rates, such as the predator functional response, which, for example, would link the
140 uptake rate for the predator and the extrinsic death rate for the prey (see Interspecific Non-
141 compensatory Effects below). Species interactions can connect two or more rate hierarchies in a
142 variety of ways, depending on whether the interaction alters mortality, resource uptake, or
143 allocation of resources. For example, a vector-borne pathogen may be connected to both the
144 vector and the host through the rate at which the vector bites hosts.

145 Critically, the framework is intended to be a minimal but general depiction of how core
146 organismal-level rates interact to drive change in population size, in service of simplifying our
147 representation of how non-compensatory effects arise and may interact. All populations have
148 individuals that uptake and allocate resources for maintenance, growth, and reproduction. These
149 allocations, in all cases, are used to support physiological processes determining development
150 rates, fitness, and demographics. Thus, we intend that any species can be described through the
151 minimal model, with appropriate expansions of rates and processes as needed for a particular
152 problem. For example, a prey species with anti-predator defenses may require an allocation
153 arrow from the uptake rate to extrinsic mortality, or if one is studying multiple sources of
154 extrinsic mortality and their responses to climate change, one may need to split up the extrinsic
155 mortality rate into multiple rates. Note, this model is not a food-web model or a network; the
156 arrows describe how upstream rates lead to downstream rates following a chain of effects from

157 resource uptake to the change in population growth rates. Thus, we refer to this structure as a rate
158 hierarchy.

159 **Intraspecific Non-compensatory Effects**

160 Within the rate-hierarchy framework, non-compensatory effects altering population growth rate
161 can arise at multiple levels of biological organization. At the highest level are the
162 aforementioned demographic non-compensatory effects that directly change population growth
163 rates (and therefore mean fitness; Lande 1982) when climate change alters birth and death rates
164 in a way that does not cancel. Population growth will be promoted when birth rates increase
165 faster with climate change than death rates, while population declines will result when death
166 rates increase faster with climate change than birth rates. Given the nonlinearity or unimodality
167 of some climate change responses, such as many thermal functions, population growth may
168 increase or decrease with changes in climate. A commonly assumed form of the demographic
169 non-compensatory effect comes from Amarasekare and Savage (2012), in which birth rates are a
170 unimodal function of temperature and death rates are an exponentially increasing function of
171 temperature (Fig 2a). The difference between these two functions generates the canonical left-
172 skewed population growth rate thermal performance curve (TPC; Amarasekare & Savage 2012;
173 Ratkowsky *et al.* 1982, 1983) through the non-compensatory changes in birth and death rates
174 with temperature.

175 At lower levels of the rate hierarchy, the proportional allocation of resources acquired
176 through uptake rates to organismal growth, maintenance, and reproduction also may shift in
177 response to changing environmental conditions (Atkinson 1994; Brett *et al.* 1969; Roff 2001).
178 These changes often will manifest in life history trade-offs, and their potential consequences may
179 be complex, as resources are split into multiple competing ends. It is worth noting that an

180 allocation change may not immediately result in a change in a specific rate if changes in uptake
181 rates counteract the effect of the allocation. Below we discuss the two non-compensatory effects
182 at lower levels in our rate hierarchy, fecundity-maturation and growth-maintenance non-
183 compensatory effects, which arise from resource uptake rate and allocation changes.

184 A **fecundity-maturation non-compensatory effect** arises due to changes in the birth
185 rate driven by non-cancelling changes in the upstream rates of resource allocation to
186 reproduction and maturation (Fig 2b). This asymmetry can be seen through the lens of a
187 simplified expression describing how the birth rate is generated:

$$188 \quad b = AF = A \frac{u_r}{c}.$$

189 The total birth rate (b) is the product of the number of mature adults (A) and the fecundity per
190 time of individuals (F). The number of mature adults in the population depends on the
191 organismal growth rate (or inversely, maturation time). Faster development and shorter
192 maturation times resulting from increases in resource acquisitions and allocations to organismal
193 growth will lead to a subsequent increase in the number of reproducing adults, so one of the
194 upstream contributors to b passes through organismal growth to a change in A . Fecundity (F) is
195 determined by a combination of factors including resource allocations to reproduction (u_r) and
196 the costs per offspring (c), following a typical Smith-Fretwell quantity-quality trade-off (Smith
197 & Fretwell 1974). Thus, the other upstream contributor to b is straight from the uptake rate given
198 the fraction of the uptake rate allocated to reproduction. Given that the cost per offspring could
199 also be climate-dependent, there are at least three ways in which birth rates change due to non-
200 compensatory effects on the upstream component rates (i.e. the number of adults, resource
201 allocation to reproduction, and cost per offspring).

202 A common example of potential fecundity-maturation non-compensatory effects in
203 ectotherms is the relationship between temperature, size at maturity, and fecundity. At cooler
204 temperatures, ectotherms tend to grow more slowly, reach maturity at a larger size, and, due to
205 their larger size, produce a larger number of eggs (Atkinson 1994; Roff 2001). Thus, birth rates
206 may change with temperature because of the simultaneous changes in A and F . Whether or not
207 these changes lead to a decrease in birth rates with increasing temperatures can be complex,
208 depending on, for example, whether the relationship between size and fecundity itself is
209 temperature dependent (Arendt 2011).

210 A **growth-maintenance non-compensatory effect** arises due to changes in the death rate
211 driven by non-cancelling changes in the organismal growth rate and the rate of allocation to
212 maintenance (Fig 4c). As with the fecundity-maturation non-compensatory effect, the rate of
213 allocation of resources to maintenance (u_m) influences the likelihood of survival in concert with
214 the rate of growth and maturation that sets expected lifespan by setting the age and size at
215 maturation. This non-compensatory effect can be seen through the lens of another simplified
216 expression that clarifies how survival is generated:

$$217 \quad s \propto B \frac{u_m}{c_m}.$$

218 The mortality rate is the inverse of survival, and survival depends on the allocation of resources
219 to maintenance and the size of the organism that is being maintained. Thus, survival (s) is
220 proportional to the product of the per mass availability of maintenance resources (u_m / c_m :
221 allocation of resources to maintenance over maintenance cost) and the mass of the organism (B).
222 In this way, maturation and growth form one part of the upstream rate effect on mortality, and
223 allocation of resources forms the other part. As body mass may change with climate, for
224 example, through the impact of temperature on growth, and allocation decisions and overall

225 uptake rates may vary with temperature, there are several ways in which the climate dependence
226 of upstream rates will have non-compensatory effects on survival.

227 For example, across ectothermic taxa, increases in environmental temperatures drive
228 elevated maintenance metabolic rates, up to a point, influencing the cost of maintenance (c_m),
229 and correspondingly necessitate higher rates of resource allocation requirements for maintenance
230 (u_m ; Amarasekare & Savage 2012). If not compensated for by changes in the uptake rate,
231 increasing metabolic rates will result in concurrent decreases in resource allocation to organismal
232 growth. Huey and Kingsolver (2019) proposed the “metabolic meltdown hypothesis” suggesting
233 that growth-maintenance non-compensatory effects will frequently arise, given direct negative
234 effects of climate change on resource and nutrient availability or indirectly by negative effects of
235 higher temperatures on locomotion and foraging rates. This hypothesis is supported by empirical
236 studies demonstrating combined negative effects of temperature and resource availability on
237 organismal and population growth rates (Brett *et al.* 1969; Thomas *et al.* 2017).

238 **Interspecific Non-compensatory Effects**

239 Although intraspecific physiological and life history responses to climate change play an
240 important role in how populations will respond to climate change, it is also necessary to
241 understand how the interactions among species are likely to change and how these changes can
242 feed into the intraspecific rates. To understand how non-compensatory changes occurring among
243 interacting species will impact populations, we expand our framework from the single species to
244 multi-species cases. To do so, we connect two or more species' rate hierarchies via an
245 appropriate connecting rate (e.g. predator functional response, mosquito biting rate, plant
246 pollination rate) dictating their interactions. Critically, changes in connecting rates will have
247 cascading consequences across pairs of species that can result in demographic shifts in one or

248 both interacting species. Furthermore, the connecting rate itself can depend on possible non-
249 compensatory changes in upstream mechanisms that generate the rate. Below, we show how the
250 addition of connecting rates can allow us to examine how non-compensatory climate change
251 responses might influence predator-prey, host-parasite, and mutualistic interactions and the
252 resultant consequences for populations.

253 *Predator-prey interactions*

254 Feeding rates connect predators and prey as they determine the uptake rate of the predator
255 and influence the extrinsic death rate of the prey. We define a **predator-prey non-**
256 **compensatory effect** as the case when the foraging rate changes with climate due to the non-
257 cancelling effects of upstream factors related to both the predator/consumer (x_c) and
258 prey/resource (x_r) that respond to climate (Figure 3). As predation events depend on movement
259 and encounters between predator and prey, the detection of prey by the predator, and the
260 successful attack by the predator (DeLong 2021; Jeschke *et al.* 2002; Wootton *et al.* 2023), there
261 are many ways in which climate change may alter the emergent foraging rate (f).

262 One of the earliest recognized drivers of climate change effects on interspecific
263 interactions are phenological mismatches, which can be viewed as a predator-prey non-
264 compensatory climate change effect. Predators and prey must be in the same area at the same
265 time for predation to occur, and environmental factors like temperature may influence the
266 likelihood of this co-occurrence, especially in highly seasonal habitats (Damien & Tougeron
267 2019). In a classic case of phenological mismatch, differential changes in the timing of breeding
268 activity of insectivorous great tits (*Parus major*) and their caterpillar prey affects foraging rates
269 of the birds (Reed *et al.* 2013). The migration of great tits is triggered by daylength and
270 temperature, but caterpillar phenology advances more quickly with warming than egg laying

271 phenology of the birds (Burgess *et al.* 2018; Reed *et al.* 2013), resulting in non-compensatory
272 phenological changes that reduce availability of prey during peak resource demand for the birds.
273 As foraging rates depend on prey availability through the functional response, this disparity in
274 timing lowers the foraging rates and can also generate a demographic non-compensatory effect
275 for the birds by reducing reproductive rates and/or increasing death rates due to resource
276 shortage. As phenological changes are widely documented with climate change, this may be a
277 common source of predator-prey non-compensatory climate change effects.

278 Foraging rates also can depend on changes in the climate and particularly temperature
279 through a **non-compensatory movement effect**. Predation depends on the encounter rate
280 between predator and prey, and local movement patterns determine the probability that prey are
281 in close enough proximity for detection by predators. This encounter rate process is often
282 captured via the relative velocity of searching movements and described mathematically by
283 combining the velocities of consumers and resources through their mean root square,

$$284 V_{rel} = \sqrt{V_R^2 + V_C^2}$$

285 where V_{rel} is the relative velocity of predators and prey, V_R is the velocity of the prey, and V_C is
286 the velocity of the predator (Aljetlawi *et al.* 2004; Dell *et al.* 2014; Pawar *et al.* 2012). A
287 movement non-compensatory effect arises when predator foraging rates change due to the
288 predator and prey having different thermal sensitivities of movement (i.e., upstream changes in
289 x_c and x_r ; Dell *et al.* 2014). Such movement sensitivities to climate change may be due to
290 differences in average searching velocities of predator relative to prey, but also may be caused by
291 changes in activity patterns or attack or escape speeds. For example, Wootton *et al.* (2023) show
292 how differences among predators in relationships between activity levels and temperature can
293 cause different relationships between temperatures and feeding rates among predators. A specific

294 form of the movement non-compensatory effect can be caused by differences in thermy among
295 predators and prey (Gibert *et al.* 2022), in which one species is an endotherm while the other is
296 an ectotherm. In this scenario, the endotherm would show minimal change in searching velocity
297 while the ectotherm would have a greater thermal sensitivity, creating a change in encounter
298 rates that alters the foraging rate and potentially leads to a demographic non-compensatory effect
299 for both species.

300 Predation events also depend on the ability of predators to detect prey. Climate change
301 may alter the ability of predators to detect prey or for prey to avoid detection by predators. For
302 example, changes in temperature regimes can alter the effectiveness of camouflaging
303 phenotypes, creating a camouflage mismatch that changes the risk of predation. In a classic case,
304 snowshoe hares (*Lepus americanus*) change coat color to blend in with the seasonally changing
305 environment, with a white coat in the winter to reduce contrast with the snowy ground and a
306 brown coat in the summer to reduce contrast with soils and plants. The timing of the color switch
307 is temperature independent, but changing precipitation patterns resulting in delayed snowfall and
308 early snowmelt result in windows during which hare have a visual mismatch with the
309 background, causing easier detection by predators such as lynx (*Lynx canadensis*) (Ferreira *et al.*
310 2023). Thus, the mismatch increases foraging rates because of an effect on the upstream process
311 of detecting prey (x_c), which depends on both predator and prey traits. Climate change also may
312 alter prey detection of predators in chemically mediated interactions (Roggatz *et al.* 2022). For
313 example, increases in acidity in aquatic environments can alter the olfactory ability of fish to
314 detect predators or alarm cues potentially making fish more susceptible to predation (Ou *et al.*
315 2015; Porteus *et al.* 2018).

316 *Host-parasite interaction*

317 Given the diversity of types of host-parasite interactions, hosts and parasites may be
318 connected in a variety of ways resulting in several types of host-parasite-specific non-
319 compensatory effects. For example, for parasites that primarily draw off resources of the host
320 (e.g. tick, tapeworm, etc.), host and the parasite rate hierarchies would be directly connected
321 through the two uptake rates, without need for a distinct intermediate connecting rate (Figure 4).
322 That is, the parasite gathers resources out of the host's resource stream, impacting the host's
323 available resources. Thus, we draw an arrow toward the hosts uptake rate from the parasites
324 uptake rate. The host's realized net uptake rate, then, is generated by the interacting effects of
325 their own resource gathering activity and the parasite's resource extracting behavior (f). In this
326 way, a **non-compensatory uptake rate effect** can arise when the changes in host and parasite
327 foraging do not cancel. If warming, for example, increases the rate of resource uptake of a
328 parasite more quickly than that of its host, there would be a net decline in the realized net uptake
329 rate of the host. This change in uptake rate would cascade up to host demography and also
330 potentially feed back to alter the demography of the parasite. Further, a transfer of resources
331 from host to parasite may or may not be compensatory depending on whether the fraction of
332 resources passing through the gut varies with resource flow. A parasite that has an uptake rate
333 that saturates with increasing flow through would have a different proportional effect on host
334 resource assimilation, and the emergence of a non-compensatory effect would depend on
335 whether or not host uptake rate was altered by climate change. Additionally, parasite induced
336 anorexia or hyperphagy in its host (Hite *et al.* 2020; Hite & Cressler 2019) could also mediate a
337 non-compensatory uptake rate effect.

338 Outside of direct effects of parasites on host uptake rates, endoparasites also may increase
339 host extrinsic mortality directly by triggering cell death, releasing toxins, or instigating extreme

340 immune responses (Figure 4). As parasite pathogenicity and host immune responses can both be
341 dependent on the environment (Thomas & Blanford 2003; Wright & Cooper 1981),
342 environmental changes could lead to non-compensatory changes that alter the death rate of the
343 host. In sub-lethal infections, the presence of the endoparasite could necessitate increased host
344 allocations to immune function, leading to non-compensatory fecundity-maturation or growth-
345 maintenance effects. In particular, all of these processes could be temperature dependent if the
346 host's decision to tolerate or fight the endoparasite depends on temperature, or if the host is an
347 ectotherm, making uptake, allocation, and demographic processes temperature dependent.

348 For ectoparasites that are vectors (e.g. mosquitos), the presence of a vectored pathogen
349 generates new possible avenues of non-compensatory changes (Figure 5). Here the biting rate
350 would serve as an intermediate connecting rate between the host, pathogen, and vector. This is an
351 expansion of the non-compensatory uptake rate effect, as some form of 'biting' would be
352 involved in any such host-parasite interaction. Thus, the biting rate could cause a demographic
353 non-compensatory effect by increasing reproduction of the vector, decreasing reproduction of the
354 host, and increasing death rate of the host caused by pathogen transmission, and altering the
355 states (susceptible or infected with pathogen carried by the vector) of individuals in the host
356 population. The biting rate is also a critical connecting rate determining the net reproductive rate
357 (R_0) of vectored pathogens themselves. A seminal study by Mordecai et al. (2013) makes clear
358 how R_0 is dependent on numerous upstream rates (e.g., vector development rate and
359 competence), creating a wide range of potential non-compensatory changes in upstream rates. As
360 most of these upstream rates are dependent on climate, including temperature, the non-cancelling
361 nature of responses in upstream rates make R_0 temperature dependent as well (Mordecai *et al.*
362 2013, 2019).

363 **Mutualistic interactions**

364 As for host-parasite and consumer-resource interactions, we can incorporate mutualistic
365 interactions into the framework through the addition of direct or intermediate connecting rates
366 between the mutualists based on how the mutualism operates. For example, plants and their
367 pollinators can be connected through a visitation rate that links the birth rate of the plant to the
368 uptake rate of the pollinator (often through pollen or nectar consumption for the pollinator;
369 Figure 6). This visitation rate is a downstream rate that could be affected by upstream features of
370 the pollinator (x_{po}) and the plant (x_{pl}), such as pollinator energy demands or plant attractiveness.
371 A protective mutualism, such as ant-acacia mutualisms, would have a connecting rate linking the
372 uptake rate for the ants from resources provided by the acacia to the extrinsic death rate or
373 uptake rate of the acacias as the ants prevent defoliation (Janzen 1966). Endosymbiotic
374 mutualists may have similar or more complex relationships between connecting rates than other
375 mutualisms. For example, the protist *Paramecium bursaria* hosts an algal *Zoochlorella*
376 symbiont. The paramecium in this interaction receives sugars provided from algal photosynthesis
377 while the paramecium both provides protection and nutrients for the algae (Brown & Nielsen
378 1974; Karakashian 1963). Thus, this system might be described by a connecting rate that links
379 the uptake rate of the paramecium and the uptake rate and extrinsic death rate of the algae.

380 There are many ways in which differing responses of mutualistic partners to climate
381 change can lead to **non-compensatory uptake rate effects**, phenological mismatches, or other
382 non-compensatory effects that alter the connecting rate with potential cascading effects for either
383 or both mutualistic partners. In a recent review, Cruz et al. (2023) highlighted how differing
384 thermal performance curves of mutualistic partners in traits related to the interaction among
385 partners can generate an overall mutualism thermal performance curve, making the mutualism

386 itself temperature dependent. Given that mutualistic interactions generally involve connections to
387 rates such as uptake rates and extrinsic death rates, the temperature dependence of mutualisms
388 generated by non-compensatory effects can potentially lead to changes that could scale up to a
389 non-compensatory demographic effect and population growth or decline. For example, in an
390 experimental plant-pollinator system, increasing temperatures led to fewer flowers per plant and
391 lower nectar volume, but higher nectar concentration (de Manincor *et al.* 2023). However, the
392 net effect of these changes with temperatures led to reduced visitation rates and shorter bee
393 handling times with negative consequences for flower seed set under warmer conditions (de
394 Manincor *et al.* 2023). The negative effect on plant reproduction would not have been expected
395 had consequences for pollinators not also been considered. Thus, this example also highlights the
396 importance of accounting for non-compensatory effects arising from interspecific interactions for
397 understanding population responses to climate change.

398 Under some circumstances, non-compensatory climate change effects on mutualisms may
399 shift these interactions along the so-called mutualism-parasitism continuum (Bronstein 1994;
400 Johnson *et al.* 1997). For example, in the aforementioned *Paramecium bursaria-Zoochlorella*
401 system, at high temperatures ‘ghost’ *Paramecium* without algal symbionts have higher fitness
402 than *Paramecium* that contain *Zoochlorella* symbionts (Salsbery & DeLong 2018). A potential
403 explanation for this is that the paramecia are mixotrophs that receive energy from both their algal
404 symbionts and through bacterivory. At higher temperatures, bacterivory may lead to greater
405 fitness for *Paramecium* without symbionts relative to those with symbionts because the energy
406 gained from the algae at high temperatures is less than the potential energy that could be gained
407 from bacteria. This is because the space within a cell is finite, generating a trade-off between
408 allocating that space to algae or food vacuoles. In this case, changes in the relative potential

409 benefits of bacterivory and photosynthates from the algae with temperature generate a non-
410 compensatory effect on uptake rates that switches the presence of algae from beneficial to
411 detrimental. Given the potential for the costs and benefits or symbioses to be environmentally
412 dependent (Bronstein 1994; Cruz *et al.* 2023; Hoeksema & Bruna 2015; Johnson *et al.* 1997),
413 non-compensatory climate change effects may play a particularly important role in moving host-
414 symbiont relationships along the mutualism-parasitism continuum.

415 **Non-compensatory Effects and Indirect Interactions**

416 Thus far, we have focused on how the framework can be used to understand non-compensatory
417 climate change impacts on rates within species and species with direct interactions. By
418 combining modules representing single species or pairwise species interactions, we can apply the
419 framework to larger groups of species and communities more generally. For example, a key
420 indirect interaction in ecology is resource competition (Tilman 1982). Although often modeled
421 phenomenologically as a direct interaction between two species, competition can be understood
422 more mechanistically as two or more consumers using the same resource (Abrams 2022). In our
423 framework, this can be represented by two consumers with uptake rates that are connected to a
424 single resource through feeding rate links for a biotic resource or utilization rate links for an
425 abiotic resource. Armed with this new module, one can then track how non-compensatory
426 changes in rates within and among species might influence the entire competitive system.
427 Similarly, one could construct a module with two resources consumed by a single consumer to
428 examine apparent competition (Holt 1977) or a module with a predator connected to a consumer
429 connected to a resource to examine trophic cascades (Paine 1980).

430 **Applying the framework**

431 If one is simply interested in whether a population is declining or increasing in response to
432 climate change, it may suffice to monitor population sizes and growth rates and examine trends
433 over time or space. However, if one wants to know why a population is changing in response to
434 climate change and therefore develop possible interventions, then it is necessary to know how
435 the rates that ultimately determine birth and death rates come together to lead to non-
436 compensatory demographic effects. Therefore, we built the framework presented here with that
437 goal in mind.

438 We can imagine a number of ways in which the framework presented here can be
439 combined with data to either predict how a species might respond to ongoing and future climate
440 change or to dissect why populations are currently increasing or declining with climate change.
441 For many species – especially those amenable to experimental study – the climate change
442 dependence of upstream rates within the framework can be measured directly. For example,
443 studies of arthropods have measured the temperature dependence of a variety of intraspecific
444 upstream rates such as maturation rates, mortality rates, and organismal growth rates in the
445 laboratory that can be combined with mathematical models of population growth to examine
446 how these rates combine and potential responses to climate change (Johnson *et al.* 2023; Richard
447 *et al.* 2023; Simon & Amarasekare 2024.). For interspecific interactions, the dependence of
448 interaction rates on environmental factors likely to change with climate also can be measured
449 experimentally or with observational data both in the lab and field (e.g. Coblentz *et al.* 2022;
450 Englund *et al.* 2011; Kirk *et al.* 2022; Mordecai *et al.* 2019). For species that are not amenable to
451 experimental manipulation, the environmental dependence of upstream rates that ultimately
452 influence population birth and death rates can potentially be measured using appropriate field
453 observations and their dependence spatially or temporally on environmental factors likely to be

454 affected by climate change (e.g. Coulson *et al.* 2001; McLean *et al.* 2016; Wang *et al.* 2020).
455 One also may be able to make assumptions or perform sensitivity analyses regarding particular
456 rates and how they are likely to respond to climate change for rates that are difficult to measure
457 directly. Last, knowing the life history and ecology of one's study system is invaluable in
458 understanding how the minimal framework presented here should be modified to match a
459 particular system and which rates within the rate hierarchy and interactions with other species
460 might be the most important to include or focus on.

461 **Conclusions and Future Prospects**

462 Here we provide a framework for understanding how non-compensatory effects of climate
463 change in rates within and among species combine to impact populations. Although most of the
464 examples we used throughout have focused on non-compensatory responses to mean
465 temperatures, we believe that this framework is equally applicable to other environmental
466 impacts of climate change. For example, in a study of Sonoran Desert plant community change
467 over 25 years, Kimball *et al.* (2010) showed how later winter rains in colder conditions alter
468 germination rates across annual plants leading to community change. When put in the context of
469 our framework, the germination response to the timing of precipitation of each plant species
470 could be viewed as altering birth rates and causing non-compensatory demographic effects
471 leading to declines or increases in population growth. Our focus on temperature is largely a
472 reflection of the fact that this has been the most widely studied component of climate change,
473 particularly with regard to asymmetries in rates and mismatches. Expanding research to include
474 non-compensatory effects in response to a greater number of changing climatic features,
475 including the variance of those features (IPCC 2021; Vasseur *et al.* 2014), will provide a more
476 holistic view of how climate change is likely to influence populations.

477 Our framework makes it apparent that there is potential for non-compensatory effects
478 generated at one level to be canceled out by another rate response to climate change, indicating
479 that caution should be taken when directly interpreting how effects at one level scale to influence
480 population growth or decline. For example, using data across 35 species of birds, (McLean *et al.*
481 2016) showed that warmer temperatures were associated with earlier lay dates and earlier lay
482 dates were associated with higher reproductive rates. However, despite these changes suggesting
483 higher reproduction rates with higher temperatures, they found no relationship between
484 temperature and population growth, suggesting that some negative effect of temperature must be
485 compensating for the increase in reproduction (McLean *et al.* 2016). We believe that the
486 framework herein may be particularly useful in helping to identify where effects cancel and
487 therefore provide target rates to be measured to determine whether a particular non-
488 compensatory effect at one level is likely to influence the population growth rate. Another
489 possible way non-compensatory effects could be canceled out is through feedbacks that are not
490 currently incorporated into the minimal rate hierarchy model. For example, consider a predator-
491 prey interaction in which a non-compensatory climate change effect increases the predator
492 feeding rate which, in turn, increases prey extrinsic mortality and decreases the prey population
493 growth rate and density. As predator feeding rates are increasing functions of prey densities,
494 lower prey densities could feedback to lower predator feeding rates or could lead to reduced
495 density dependence in the prey which could alter birth or death rates. Although this increases the
496 complexity of understanding non-compensatory climate change impacts, applying the framework
497 to think through these possibilities makes clear where these feedbacks might emerge and how
498 they might ultimately affect population growth rates. The framework also facilitates the

499 identification of rates researchers should focus on measuring to understand population-level
500 climate change responses.

501 One impetus for the development of the framework herein was that there is often a
502 disconnect in the literature between traits measured and their inferred effects on downstream
503 climate change responses of interest. For example, differences among species in thermal
504 performance curve properties are often used to suggest the existence of differential responses to
505 temperature that will impact the system (Cohen *et al.* 2017; Gsell *et al.* 2023; Meehan & Lindo
506 2023). Yet, applying the framework here, it becomes clear that the relevance of differences in
507 thermal performance curves and whether they lead to non-compensatory climate change effects
508 is dependent on what trait is being compared among species, where the response of interest
509 occurs within the rate hierarchy, and how ‘performance’ at that position in the rate hierarchy
510 translates to the downstream rate of interest. For example, in seeking to explain the temperature
511 dependence of chytrid prevalence in frogs, Cohen *et al.* (2017) performed an experiment
512 comparing frog preferred temperatures, chytrid growth rates in culture, and chytrid growth rates
513 on frogs. Although chytrid growth rates on frogs are indeed likely to be a determinant of
514 prevalence, applying the framework to this problem would suggest that the temperature
515 dependence of several other processes should also be considered, such as the susceptibility of the
516 frogs to infection and chytrid spore survival. If the temperature dependencies of these processes
517 are well-correlated, these extra considerations may not be necessary, but, in general, this will be
518 an assumption that requires testing. As another example, the relationship between sprint speed
519 and temperature is commonly measured in the literature (Berkum 1988; Hertz *et al.* 1983) and
520 often taken to be correlated with overall organismal performance. However, in our framework,
521 sprint speed is likely to be a trait near the base of the hierarchy that may or may not alter feeding

522 rates depending on how sprint speeds, predator attack or prey escape rates, and their relationships
523 with temperature combine (Öhlund *et al.* 2015). Further, as a rate near the base, taking into
524 account all of the other possible temperature responses in the rate hierarchy, it becomes clear that
525 differences in temperature effects on sprint speeds of predator and prey need not result in non-
526 compensatory demographic effects or be directly correlated with the overall relationship between
527 temperature and population growth (fitness) at the highest level of the hierarchy. Overall, we
528 hope that this framework can help researchers identify which rates are important to measure for a
529 particular process of interest and for making inference on how or if those rates are likely to scale
530 to bring about population-level changes.

531 Throughout, we also have assumed that non-compensatory climate change responses and
532 their potential impacts are constant. However, individual variation in sensitivity to climate
533 change creates the opportunity for natural selection to lead to an eco-evolutionary feedback
534 (Palkovacs & Hendry 2010; Yoshida *et al.* 2003) that in turn could alter the prevalence and
535 consequences of non-compensatory effects. This also highlights the potential role that plasticity
536 may play in moderating non-compensatory climate change effects. As mentioned above, effects
537 on population density from non-compensatory climate change responses could alter the
538 environments to produce additional feedbacks or phenotypic plasticity that counteract or
539 generate new non-compensatory effects. Such changes are likely to depend on the specifics of
540 systems (e.g. is there heritable variation in a particular climate change response involved in
541 affecting a downstream rate?), but studies focusing on these processes will provide important
542 information on how organisms might adapt to the consequences of non-compensatory climate
543 change responses and climate change more generally.

544 Understanding how species are responding to climate change is pressing. Non-
545 compensatory effects of climate change on intra- and interspecific biological rates are likely to
546 be playing a critical role in determining consequences for population growth rates. Here we
547 provide a broadly applicable and flexible rate-hierarchy framework that we hope will allow
548 researchers to identify critical areas and traits within their study systems in which non-
549 compensatory climate change effects may occur and to place identified effects within the
550 framework to predict when non-compensatory effects will influence population level responses
551 to climate change.

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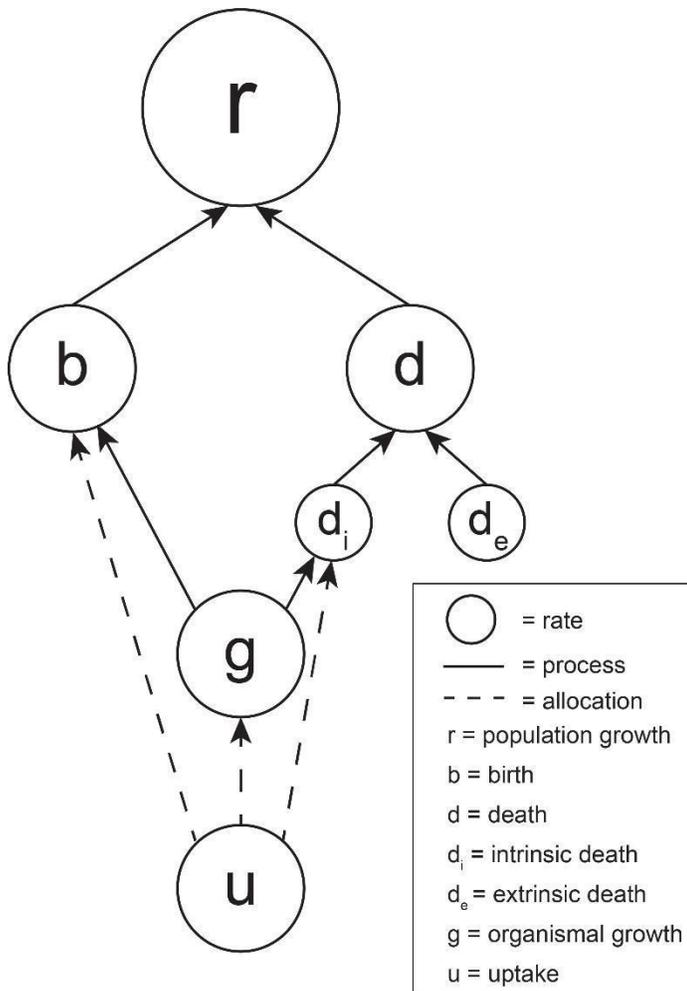
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752 **Figures**

753 **Figure 1**



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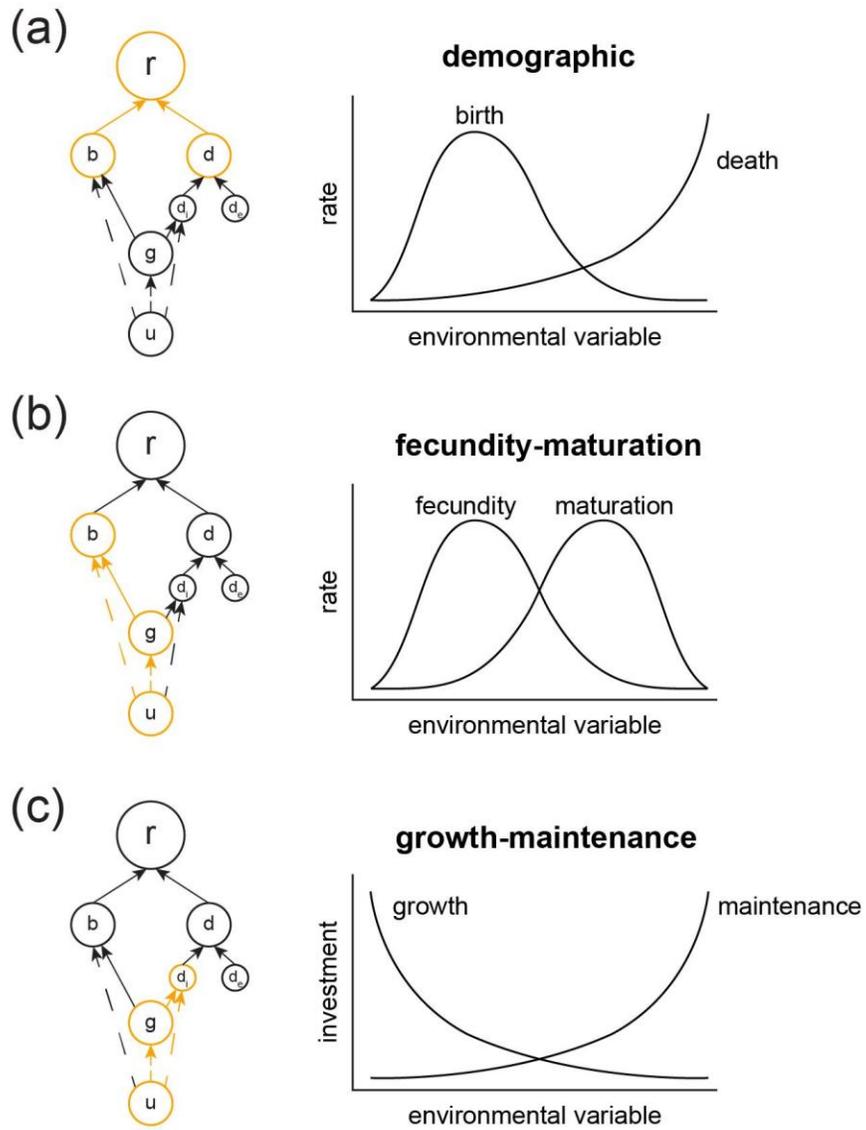
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Figure 2

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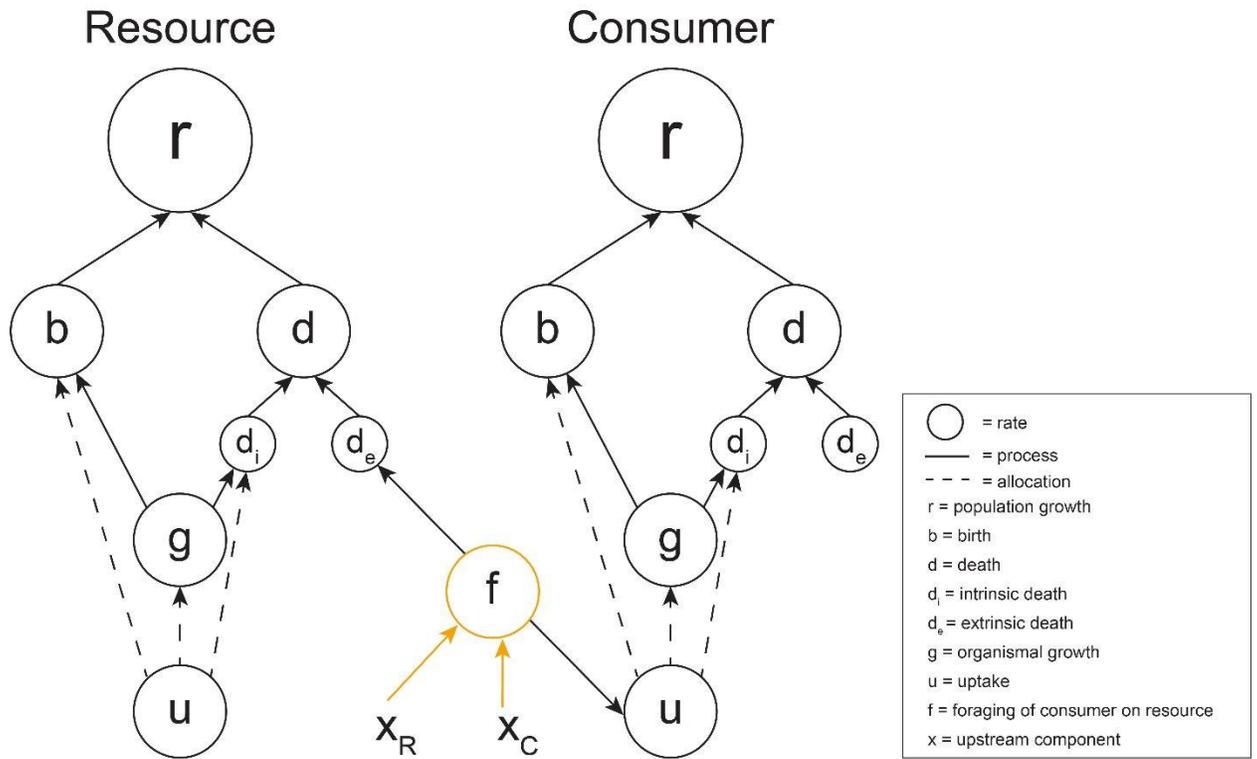
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Figure 3

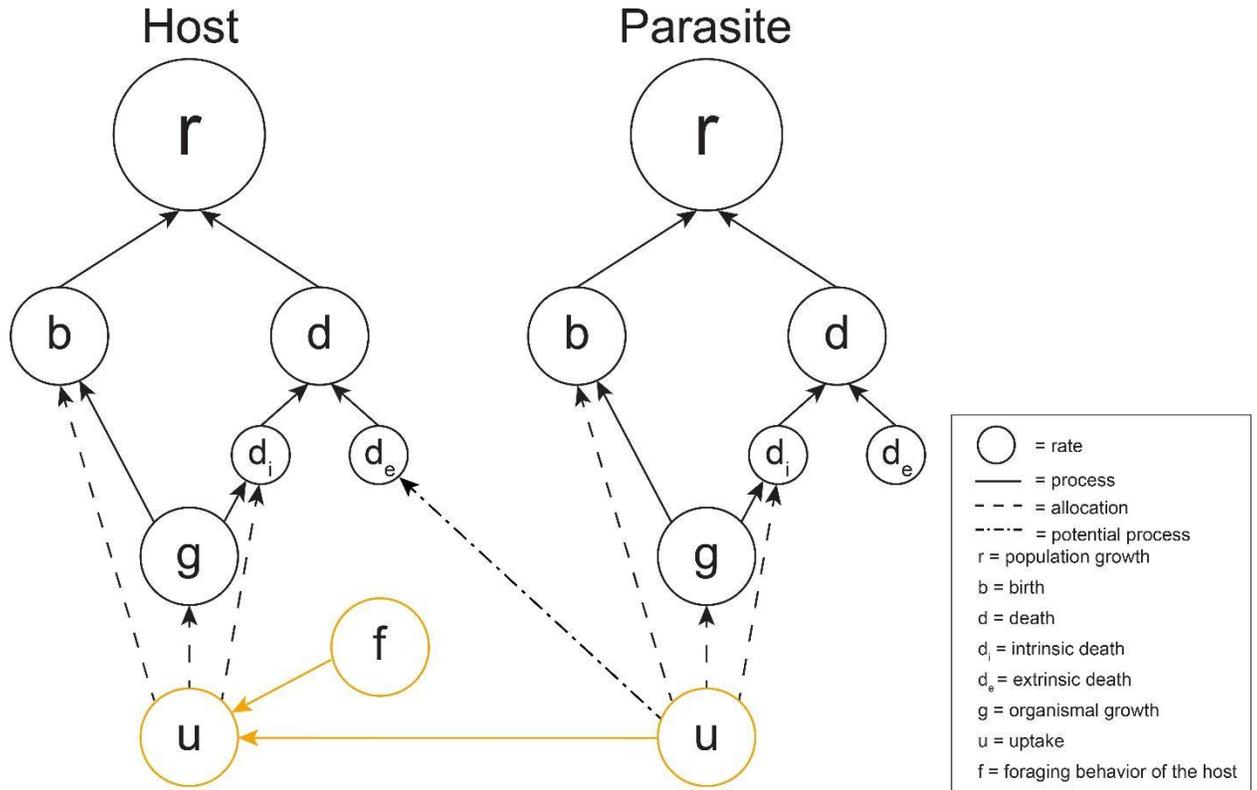


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Figure 4



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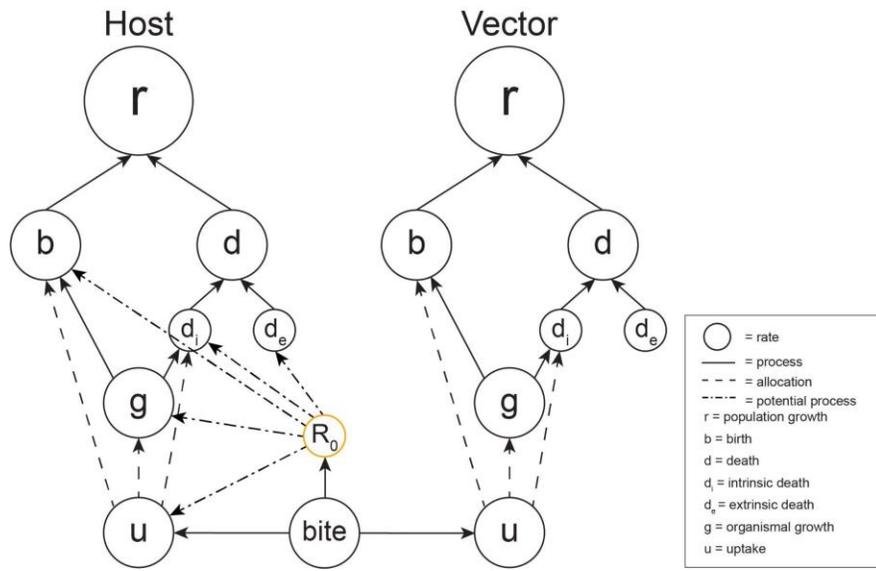
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Figure 5

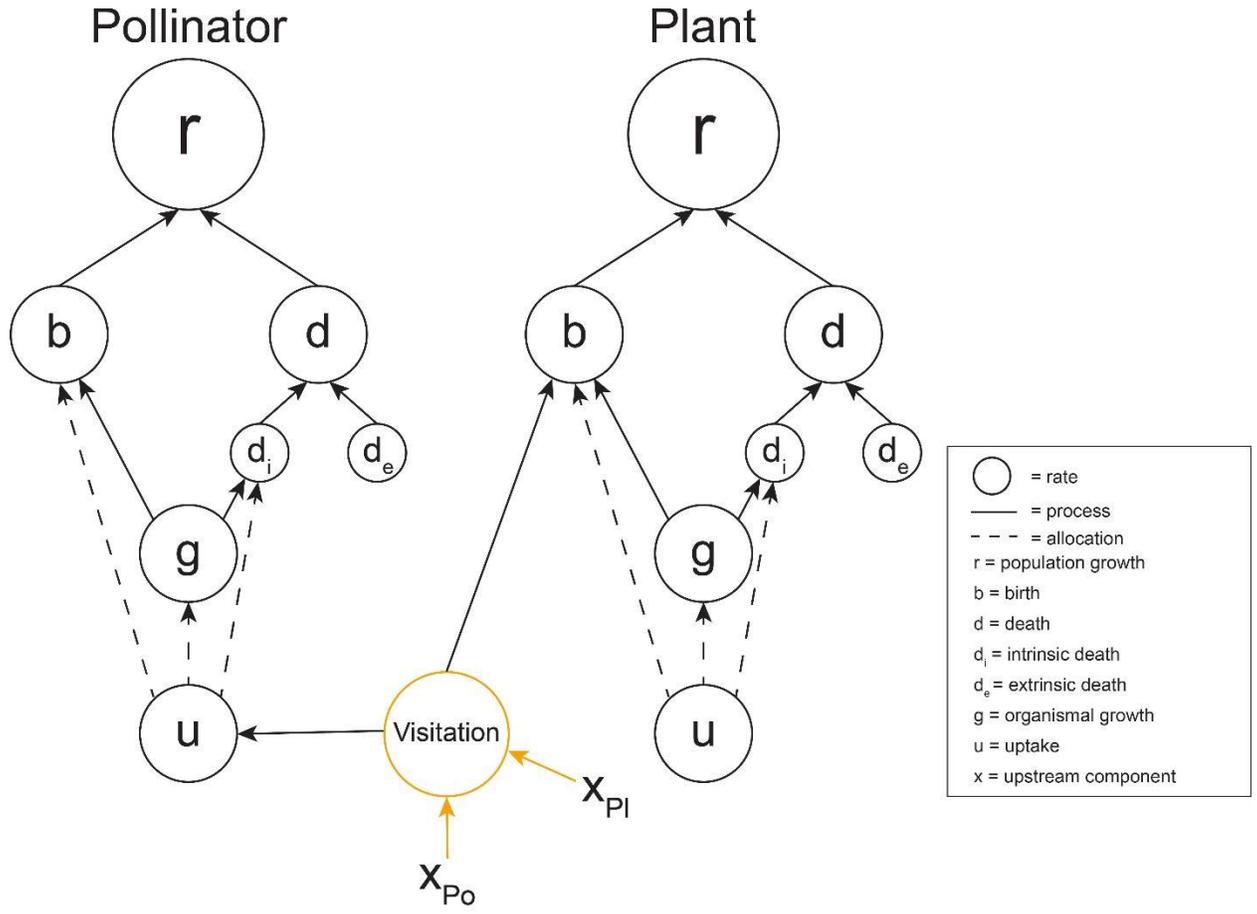
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Figure 6



776 **Figure Legends**

777 **Figure 1.** A single-species depiction of our framework for understanding non-compensatory
778 responses to climate change and their impacts on populations. Each circle represents a rate, and
779 arrows between circles show how rates influence one another. Solid lines represent direct
780 determinations of rates and dashed lines represent allocations of resources to different rates. The
781 top rate r is the rate of change of the focal population (population growth rate). This is
782 determined by the birth rate (b) and the death rate (d). The birth rate is determined by average
783 organismal growth rates in the population (g) and energy allocation to reproduction (b) from
784 resource uptake rates (u). Death rates are determined by both intrinsic death rates (d_i) and
785 extrinsic death rates (d_e). Intrinsic death rates are determined by average organismal growth rates
786 in the population and allocation of energy to maintenance from resource uptake. Last, organismal
787 growth rates (g) are determined by allocation of energy to growth and development from
788 resource uptake.

789

790 **Figure 2.** A graphical depiction of demographic (a), fecundity-maturation (b), and growth-
791 maintenance (c) intra-specific non-compensatory effects. Upstream rates directly contributing to
792 each non-compensatory effect within our hierarchy are highlighted in yellow. Demographic non-
793 compensatory effects are the highest level effects and are characterized by non canceling
794 changes in birth (b) and death (d) rates occurring in response to environmental change.
795 Fecundity-maturation and growth-maintenance non-compensatory effects occur at the lower
796 levels of our framework and arise due to resource allocation trade-offs between organismal
797 growth and either reproduction or maintenance as climate changes and relationships between
798 organismal growth and birth or death rates.

799 **Figure 3.** The rate hierarchies of a resource (R) and consumer (C) are connected by the foraging
800 rate (f). The foraging rate connects the uptake rate of the consumer and the extrinsic death rate
801 of the resource. Varied non-compensatory climate change effects on upstream factors
802 determining foraging rate (x_R and x_C), such as predator and prey locomotor ability, are
803 highlighted in yellow and can lead to cascading effects up the resource and consumer rate
804 hierarchies to influence their population growth rates.

805

806 **Figure 4.** Example of the directly connected rate hierarchies for a host-parasite interaction in
807 which the parasite feeds directly on the host. Non-compensatory effects of climate change on
808 host and parasite uptake rates (u) (highlighted in yellow), could potentially filter up the rate
809 hierarchies to alter population growth. Some parasites also may have direct effects on the
810 extrinsic death rate of their host, for example, through the development of toxins or direct
811 mortality of cells.

812

813 **Figure 5.** Example rate hierarchies for a host and vector of a pathogen. The uptake rates of the
814 host and vector are connected via the biting rate of the vector. This biting rate is also connected
815 to the R_0 of the pathogen (the basic reproduction number). In turn, R_0 alters the proportion of the
816 population that is infected by or susceptible to the pathogen and potentially a variety of different
817 biological rates in the hierarchy depending how infection shifts rates between infected and non-
818 infected susceptible individuals (indicated by the dot-dashed lines).

819

820 **Figure 6.** Example of a plant-pollinator interaction in which the visitation rate of the pollinator
821 to flowers connects the uptake rate of the pollinator to the birth rate of the plant. Non-

822 compensatory climate change effects on visitation rates can result from non canceling changes
823 in upstream factors determining visitation (x_{Po} and x_{Pl}), such as pollinator behavior and plant
824 attractiveness (highlighted in yellow). These will have potential consequences for pollinator
825 uptake rates and plant birth rates that may also cascade up to have demographic consequences.
826

827 **Boxes**

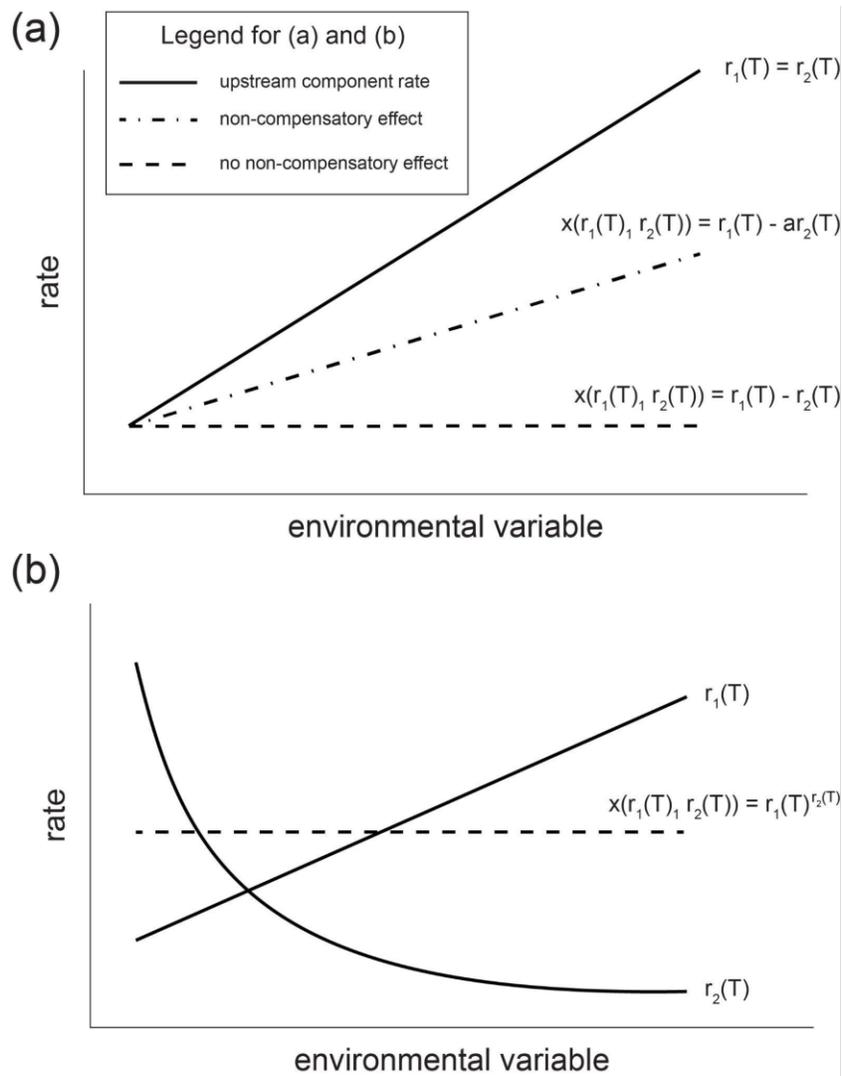
828 **Box 1: What is a non-compensatory effect?**

829 A non-compensatory effect is a case in which some focal rate, say, rate X , changes in response to
830 some driving factor (e.g., temperature) because two or more determining components change in
831 response to that driving factor in such a way that their effects on the focal rate are not canceled
832 out. In contrast, changes in upstream components may lead to no change in a downstream rate if
833 their effects perfectly cancel out in how they determine the downstream rate (Figure 1). Thus,
834 non-compensatory effects focus not on whether changes in the upstream components are
835 proportionally different, but whether the effects of those changes drive further change in the
836 downstream rate. It is both possible that 1) two upstream components respond to a climate driver
837 in the same proportional way but still cause a non-compensatory effect because they come
838 together to influence the downstream rate in different ways (Figure 1A) and that 2) two upstream
839 components change in a disproportionate way and do not lead to a change in the downstream rate
840 because the way they come together cancels out their effects on the downstream rate (Figure 1B).
841 Thus, non-compensatory effects are only detectable in the change in the downstream rate or by
842 knowing how the upstream components combine to determine the downstream rate. We suggest
843 that these special cases will mostly be rare and that differential changes in upstream components
844 will most likely have downstream consequences.

845 To define non-compensatory effects mathematically, assume that our rate X is a function
846 of two or more components r_1, r_2, \dots, r_n that are themselves a function of an environmental
847 variable such as temperature T . Then, a non-compensatory effect will alter X when differences in
848 $r_1(T), r_2(T), \dots, r_n(T)$ between temperatures change the value of $X =$
849 $f(r_{\{1\}}(T), r_{\{2\}}(T), \dots, r_{\{n\}}(T))$. For example, the rate of change in population size is a

850 function of birth and death rates, which vary with temperature (in this case, $\frac{dN}{dt} =$
851 $f(\text{birth rate}(T), \text{death rate}(T)) = \text{birth rate}(T) - \text{death rate}(T)$). So, non-compensatory
852 effects occur between two temperatures when the birth and death rates change differentially with
853 temperature such that $\text{birth rate}(T_1) - \text{death rate}(T_1) \neq \text{birth rate}(T_2) - \text{death rate}(T_2)$.

854 We can consider non-compensatory effects at a single temperature, between two
855 temperatures, or over a range of temperatures. At a single temperature, non-compensatory effects
856 occur if instantaneous changes in $r_1(T), r_2(T), \dots, r_n(T)$ result in $\frac{df(r_1(T), r_2(T), \dots, r_n(T))}{dT} \neq 0$. In the
857 case of a rapid shift between two temperatures, non-compensatory effects occur if
858 $f(r_1(T_1), r_2(T_1), \dots, r_n(T_1)) \neq f(r_1(T_2), r_2(T_2), \dots, r_n(T_2))$. When considering a range of
859 temperatures $[T_1, T_2]$ (or (T_1, T_2) , an open interval between two temperatures), there is a non-
860 compensatory effect if there exists $T_a, T_b \in [T_1, T_2]$ such that $f(r_1(T_a), r_2(T_a), \dots, r_n(T_a)) \neq$
861 $f(r_1(T_b), r_2(T_b), \dots, r_n(T_b))$. In other words, there is no non-compensatory effect over an
862 interval $[T_1, T_2]$ if and only if, over all intervals $(T_a, T_b) \in [T_1, T_2]$, $f(r_1(T_a), r_2(T_a), \dots, r_n(T_a)) =$
863 $f(r_1(T_b), r_2(T_b), \dots, r_n(T_b))$.



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Box 1 Figure. Conceptual representations of non-compensatory effects. We define non-

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compensatory effects of climate change as changes in a focal ‘downstream’ rate (X) due to non-

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cancelling changes in the effects of the ‘upstream’ components (r_i ’s) on the focal

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‘downstream’ rate . This is because components (r_i ’s) can change in the same manner with an

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environmental variable such as temperature (T) and yet may or may not have an effect on the

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focal rate (X) depending on how they combine to determine X (a). Components can also change

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in different ways and yet have no effect on the focal rate (b).

872

873 **Box 2: Glossary**

874 **Non-Compensatory Effect/Response** – A change in a focal downstream rate changes due to
875 non-cancelling changes in the effects of upstream rates on the downstream rate.

876

877 **Asymmetry** – The term asymmetry is used in several ways in the climate change literature: 1)
878 Asymmetry describes when a curve such as a thermal performance curve exhibits skew or is not
879 symmetric around its peak. 2) Asymmetry describes when two rates have different thermal
880 sensitivities. 3) Asymmetry describes when two species' thermal performance curves are not
881 equivalent (differ in their optima). Here we focus on the second and third definitions when using
882 the term.

883

884 **Mismatch** – The term mismatch is used in several ways in the climate change literature: 1)
885 Mismatch describes when the thermal performance curves of two species are not equivalent
886 (differ in their optima). 2) Mismatch describes when a process was 'matched' at some point but
887 has become 'mismatched' with climate change (e.g. phenological mismatches). We note that
888 phenological mismatches can be viewed as non-compensatory effects/responses (see
889 Interspecific Non-compensatory Effects section).

890

891 **Demographic Non-Compensatory Effect/Response** – A non-compensatory effect in which a
892 change in population growth rates occurs due to non-cancelling changes in birth and death rates
893 in response to a change in climate.

894

895 **Fecundity-Maturation Non-compensatory Effect** – A non-compensatory effect that alters
896 population birth rates through non-cancelling changes in the allocation of resources to

897 reproduction or fecundity and organismal growth in response to climate change

898

899 **Growth-Maintenance Non-compensatory Effect** – A non-compensatory effect that alters

900 population death rates through non-cancelling changes in the allocation of resources to

901 organismal growth and maintenance in response to climate change

902 **Predator-Prey Non-compensatory Effect** – A non-compensatory effect in which climate

903 change leads to non-cancelling changes in the underlying processes determining foraging success

904 rates of predators on their prey.

905

906 **Movement Non-compensatory Effect** – A specific form of predator-prey non-compensatory

907 effect that is due to non-cancelling changes in predator and prey movement velocities in response

908 to climate change, which in turn alter predator-prey encounter rates and, thus, foraging rates.

909

910 **Uptake Rate Non-compensatory Effect** – A non-compensatory effect that can occur in host-

911 parasite or mutualistic interactions in which one interaction partner's uptake rate is dependent on

912 the uptake rate of the other interaction partner (e.g. a gut macroparasite and host or

913 photosynthetic symbiont and host) and there are non-cancelling changes in uptake rates of the

914 two species in response to climate change.

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916

917 **Box 3: Non-compensatory Effects, Asymmetries, and Mismatches**

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919 A current difficulty in navigating the literature on asymmetries, mismatches, and climate change
920 is the ambiguity with which these terms are used. For example, asymmetries and mismatches are
921 often treated as synonymous, and the term mismatch is used to refer to several distinct effects of
922 climate change (cf. Cohen *et al.* 2017; Stenseth & Mysterud 2002). Here, we hope to clarify the
923 language that is used around asymmetries and mismatches and explain why we think a focus on
924 non-compensatory effects is more useful in most cases.

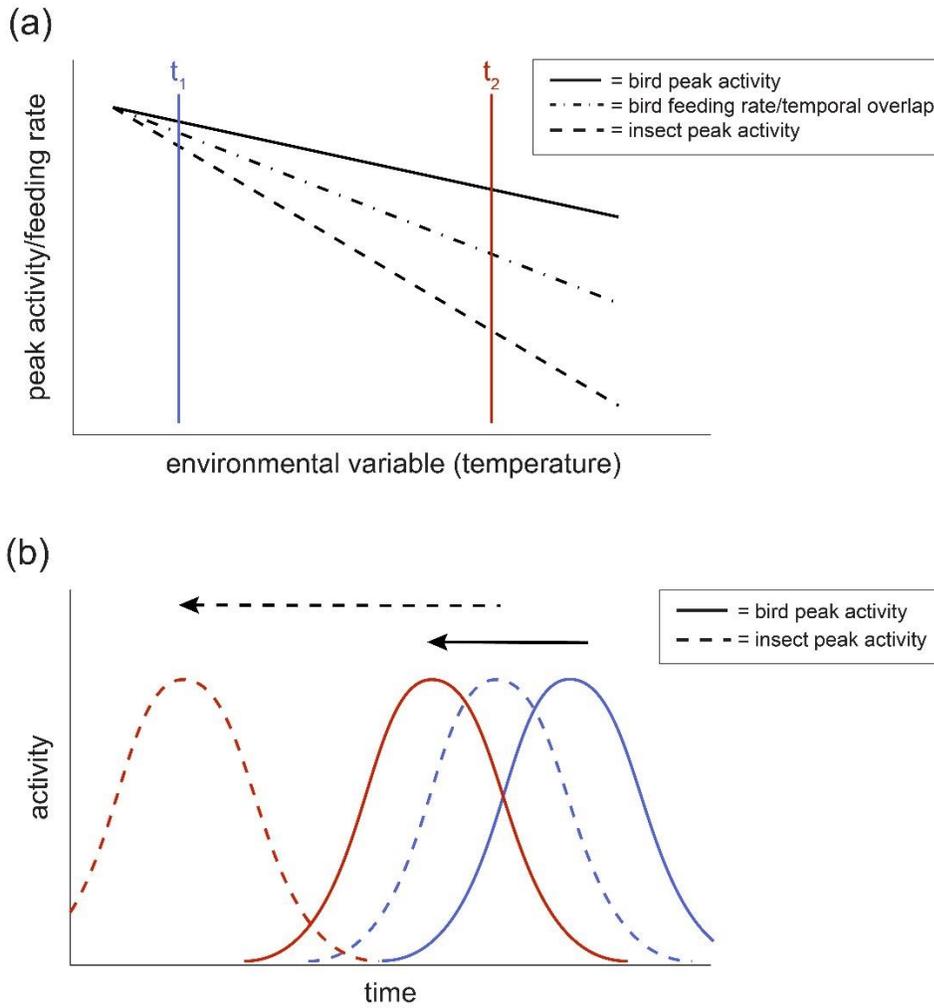
925 Asymmetry in the context of climate change responses is currently widely used in three
926 contexts. First, asymmetry is used to describe when a thermal performance curve is skewed (i.e.
927 non-symmetric around its peak; Buckley *et al.* 2022). Second, asymmetry is used to describe
928 when two or more rates have different thermal sensitivities (Gibert *et al.* 2022). Third,
929 asymmetry is also used to describe the case where the thermal performance curves of two species
930 are not equivalent (also referred to by some authors as mismatch; e.g. Cohen *et al.* 2017). We
931 believe that the first definition is appropriate language for describing thermal performance
932 curves, but that the other definitions are inadequate when the goal is to understand how a process
933 of interest is likely to change with climate due to changes in component processes or rates. Our
934 focus on non-compensatory effects does not depend on whether the components change in the
935 same manner or not with climate change, but whether the changes in the components with
936 climate change subsequently alter a process of interest (Box 1). This is because it is possible that
937 the components change with the environment proportionally in exactly the same way and
938 generate effects on a rate of interest (Box Figure 1a), and for the components to change with the
939 environment in different ways and generate no effect on a process of interest (Box Figure 1b).
940 Crucially, it is how these components specifically combine that determines whether a non-
941 compensatory effect occurs.

942 We also take issue with the use of the term mismatch as a synonym for asymmetry. We
943 view the term mismatch as implying that there must be some optimum constituting a ‘match’,
944 with a ‘mismatch’ describing when this optimum is not occurring (Cushing 1990; Cushing &
945 Dickson 1977). This definition fits the case where mismatch is used in the climate change
946 literature to describe when some interaction process was ‘matched’ at some point in time, but
947 climate change has led to the development of a discrepancy (e.g. phenological mismatches).
948 However, we believe that using mismatch to describe, for example, differences in thermal
949 performance curves among species, generates confusion because: 1) it conflates multiple usages
950 of the word mismatch, 2) what would often be a ‘match’ in terms of an optimum for one species
951 is likely to be a ‘mismatch’ for the other species if they interact antagonistically, and 3) the
952 optimal situation for one species (aka a ‘match’) may often be to have a ‘mismatch’ in terms of,
953 say, thermal optima (Casas Goncalves & Amarasekare 2021; Smith & Amarasekare 2018). If
954 differences in climate change responses lead to downstream effects, we believe that non-
955 compensatory effect is a much better description.

956 Last, we note that mismatches, such as phenological mismatches, may arise due to non-
957 compensatory climate change effects and can generate additional non-compensatory effects in
958 the framework we introduce here. For example, the timing of the peak activity of predators and
959 prey, such as birds and insects, may show differential responses to temperature generating a
960 phenological mismatch (Damien & Tougeron 2019; Reed *et al.* 2013; Box Figure 2a). This
961 phenological mismatch could then alter bird feeding rates through the non-compensatory effects
962 of peak activity changes in birds and insects on the abundance of insects experienced by the birds
963 through reduced temporal overlap (Box Figure 2b). Lowered feeding rates, in turn, may lead to

964 non-compensatory changes in birth and death rates in bird or insect populations thus generating
965 yet another non-compensatory effect.

966



967

968 **Box 3 Figure.** Climate mismatches, such as phenotypic mismatches, can lead to non-
969 compensatory effects. For example, changes in the timing of bird and insect peak activity with
970 temperature (a) can generate a non-compensatory effect on the abundance of and temporal
971 overlap with insects experienced by birds (b) leading to decreased bird feeding rates.