

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

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9 Running title: Asymmetric climate change responses
10

11 Keywords (up to 10): predator-prey; mutualism; host-parasite; life history; demographic change;
12 population growth/decline; community; temperature; thermal performance; mismatch
13

14 Article type: Review
15

16 Number of words in abstract: 204, number of words in main text: 7004, number of words in text
17 box 1: 436
18

19 Number of references: 82
20

21 Number of figures, tables, and text boxes: 10 total -- 9 figures, 1 text box.
22

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28 Statement of Authorship: All authors developed and refined the framework for understanding
29 asymmetric climate change responses. KEC led the writing of the manuscript with all authors
30 contributing.
31

32 Data Accessibility Statement: There are no data associated with this study.

33 **Abstract**

34 A crucial challenge in ecology is understanding and predicting population responses to climate
35 change. A key component of population responses to climate change are asymmetries in which
36 focal intra- or interspecific rates (e.g. population growth rates) change in response to climate
37 change due to non-compensatory changes in the underlying components (e.g. birth and death
38 rates) determining the focal rates. Asymmetric climate change responses have been documented
39 in a variety of systems and arise at multiple levels of organization within and across species. Yet,
40 how these asymmetries combine to influence the demographics of populations is often unclear,
41 as identified asymmetries are typically not mapped back to the fundamental demographic
42 asymmetry – the differential changes in a species' birth and death rates – that underlies
43 population and community change. We provide a flexible framework incorporating asymmetric
44 effects of changes in upstream rates within and among species and mapping their consequences
45 for additional downstream rates across scales to their eventual effects on population growth rates.
46 Throughout we provide specific applications of the framework. We hope this framework helps to
47 unify research on asymmetric climate change responses, provides researchers with a common
48 language to discuss asymmetric responses, and enhances our ability to understand how
49 populations are responding to climate change.

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51

52 **Introduction**

53 Global climate change is driving changes in mean temperatures, temperature variance,
54 precipitation regimes, and extreme weather events, among other environmental effects (IPCC
55 2021). Understanding how species respond to these changes is crucial for managing and
56 forecasting the ecological impacts of climate change. Furthermore, understanding species'
57 responses to climate change is also critical due to the potential consequences for ecosystem
58 services, disease transmission, and food production (IPCC 2022). However, predicting species
59 responses to climate change remains difficult because this requires an understanding of both
60 direct physiological effects and impacts on intra- and interspecific interactions (Blois *et al.* 2013;
61 Gilman *et al.* 2010; Sutherst *et al.* 2007).

62 Our goal here is to provide a framework for understanding and predicting how
63 populations will respond to climate change through the asymmetric effects of climate change on
64 rates determining species' population demographics. We define an asymmetry as a case in which
65 some focal rate changes because of differential, non-compensatory changes in the components
66 determining the focal rate (see Box 1 for an in-depth explanation and a mathematical definition).
67 Asymmetries with respect to climate change are those in which the components respond to some
68 aspect of climate (e.g. precipitation, temperature, pH, etc.) and drive a change in what we call the
69 'downstream' focal rate. For example, changes in population growth rate (a downstream rate)
70 with temperature can be caused by the differential effects of changes in birth rates and death
71 rates (upstream rates) with temperature (Amarasekare & Savage 2012). Asymmetries can occur
72 at any level of biological organization, from the molecular level to population growth rate, and a
73 key to understanding them is to identify the downstream rate, evaluate how upstream
74 components combine to generate the downstream rate, and to assess the response of upstream

75 components to climate change. Note that the literature often treats so-called mismatches and
76 asymmetries as synonymous (Álvarez-Codesal *et al.* 2023; Cohen *et al.* 2017), but we view these
77 as distinct but interrelated concepts (see “Clarifying Asymmetries and Mismatches”).

78 We focus on asymmetric climate change effects for two principal reasons. First, at the
79 population level, the ultimate response to climate change that we are often most interested in is
80 whether and to what extent a population might grow or decline in response to climate change. In
81 general, barring changes in immigration or emigration, changes in population abundances must
82 reflect non-zero population growth rates (i.e. birth rates minus death rates; note that our
83 framework can incorporate the climate-dependence of immigration and emigration, but we do
84 not discuss these here for the sake of simplicity). For example, a change to a negative growth
85 rate from a positive one with a change in the environment implies that birth and death rates have
86 changed with the environment in a manner such that the death rate now exceeds the birth rate.
87 Thus, this fundamental asymmetry is central to understanding population changes in response to
88 climate change, as well as all other dynamic changes in population abundance. Second, there
89 exists a large and growing list of asymmetric climate change effects that have been identified
90 both within and among species. For example, studies have identified asymmetric effects of
91 temperature among different rates within species (Bozinovic *et al.* 2020; Huey & Kingsolver
92 2019; Johnson *et al.* 2023; Jørgensen *et al.* 2022; Pawar *et al.* 2024; Wang *et al.* 2020) in
93 consumer-resource interactions (Álvarez-Codesal *et al.* 2023; Bideault *et al.* 2021; Dell *et al.*
94 2014; Gibert *et al.* 2022; Gilbert *et al.* 2014), and in host-parasite systems (Cohen *et al.* 2017;
95 Kirk *et al.* 2022; Mordecai *et al.* 2013, 2019; Taylor *et al.* 2019). Although the ubiquity of
96 asymmetric climate change effects is becoming clear, we currently lack a cohesive framework
97 with which to conceptualize how these asymmetries are likely to fit together and interact to

98 ultimately produce changes in populations. Furthermore, a common framework to understand
99 asymmetries across systems would provide a powerful tool for synthesizing climate change
100 impacts.

101 Below, we first provide an explanation for our distinction between asymmetries and
102 mismatches and clarify our language to avoid confusion given the current ambiguity with which
103 these terms are used in the literature. We then give an in-depth explanation of a framework for
104 understanding asymmetric climate change effects that provides a flexible, hierarchical approach
105 for linking asymmetries, tracking their consequences for populations, and connecting both intra-
106 and interspecific processes. Throughout our explanation of the framework, we provide empirical
107 examples of asymmetries and climate change effects across single-species systems, consumer-
108 resource interactions, parasite-host interactions, and others to illustrate the generality of the
109 framework and how it can be applied to understanding climate change responses in particular
110 systems. Last, we provide some suggestions for how researchers might apply this framework in
111 their own systems and give some guidance on how future studies might combine this framework
112 with experiments and observational data to understand species' responses to climate change.

113 **Clarifying Asymmetries and Mismatches**

114 A current difficulty in navigating the literature on asymmetries, mismatches, and climate change
115 is the ambiguity with which these terms are used. For example, asymmetries and mismatches are
116 often treated as synonymous, and the term mismatch is used to refer to several distinct effects of
117 climate change (cf. Cohen *et al.* 2017; Stenseth & Mysterud 2002). Here, we hope to clarify the
118 language that is used around asymmetries and explain why we think our definition provides a
119 more useful definition for an asymmetric effect of climate change.

120 Asymmetry in the context of climate change responses is currently widely used in two
121 contexts. First, asymmetry is used to describe when two or more rates have different thermal
122 sensitivities (Gibert *et al.* 2022). Second, asymmetry is also used to describe the case where the
123 thermal performance curves of two species are not equivalent (also referred to by some authors
124 as mismatch; e.g. Cohen *et al.* 2017). We believe that these definitions are inadequate when the
125 goal is to understand how a process of interest is likely to change with climate due to changes in
126 component processes or rates. Therefore, our definition focuses not on whether the components
127 change in the same manner or not with climate change, but whether the changes in the
128 components with climate change subsequently alter a process of interest (Box 1). This is because
129 it is possible that the components change with the environment proportionally in exactly the
130 same way and generate effects on a rate of interest (Figure 1a), and for the components to change
131 with the environment in different ways and generate no effect on a process of interest (Figure
132 1b). Crucially, it is how these components specifically combine that determine whether their
133 changes generate an asymmetric effect on a focal process.

134 We also believe that asymmetry is a more appropriate term for this situation than
135 mismatch. We view the term mismatch as implying that there must be some optimum
136 constituting a ‘match’, with a ‘mismatch’ describing when this optimum is not occurring
137 (Cushing 1990; Cushing & Dickson 1977). This definition fits the case where mismatch is used
138 in the climate change literature to describe when some interaction process was ‘matched’ at some
139 point in time, but climate change has led to the development of a discrepancy (e.g. phenological
140 mismatches). However, we believe that using mismatch to describe, for example, differences in
141 thermal performance curves among species, generates confusion because: 1) it conflates multiple
142 usages of the word mismatch, 2) what would often be a ‘match’ in terms of an optimum for one

143 species is likely to be a ‘mismatch’ for the other species if they interact antagonistically, and 3)
144 the optimal situation for one species (aka a ‘match’) may often be to have a ‘mismatch’ in terms
145 of, say, thermal optima (Casas Goncalves & Amarasekare 2021; Smith & Amarasekare 2018). If
146 differences lead to downstream effects, we believe referring to this as an ‘asymmetry’ or
147 ‘asymmetric effect’ provides greater clarity by forcing one to specify, for example, exactly how
148 differences in thermal performance are related to a focal process of interest.

149 Last, we note that mismatches, such as phenological mismatches, may arise due to
150 asymmetric climate change effects and can generate additional asymmetries in the framework we
151 introduce below. For example, the timing of the peak activity of predators and prey, such as birds
152 and insects, may show differential responses to temperature generating a phenological mismatch
153 (Damien & Tougeron 2019; Reed *et al.* 2013; Figure 2a). This phenological mismatch could then
154 alter bird feeding rates through the asymmetric effects of peak activity changes in birds and
155 insects on the abundance of insects experienced by the birds through reduced temporal overlap
156 (Figure 2b). Lowered feeding rates, in turn, may lead to asymmetric effects between birth and
157 death rates in bird or insect populations thus generating yet another asymmetry (see below).

158 **A framework for Asymmetries and Climate Change Impacts**

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

160 Our framework (Figure 3) starts with the recognition that the most concerning *species*’ responses
161 to climate change generally come in the form of changes in population size through the
162 population growth rate. Thus, we focus primarily on the population growth rate (r). All factors
163 that feed into population growth within our framework are also rates. By definition, in a closed
164 population, changes in growth rates are driven by changes in the demographic rates of births (b)
165 and deaths (d). Thus, a **demographic asymmetry** arises when birth and death rates respond to

166 some aspect of climate change (e.g., temperature) in a non-compensatory way (a table of
167 definitions of specific asymmetries identified herein is provided in Table S1.1). Demographic
168 asymmetries form the top-level asymmetry and all other asymmetries must feed into the
169 demographic asymmetry to affect population change.

170 Changes in birth rates arise through two general pathways. First, resource uptake (of any
171 form from light to prey; designated as u) generates energy and biosynthetic metabolites that are
172 allocated to reproduction (b), organismal growth (g), and maintenance (d_i , with allocations
173 described by dashed lines in Figure 3). The allocation of resources to reproduction is a principal
174 driver of birth rates, given variation in life history that determines offspring size, fecundity, and
175 reproductive effort. Indirectly, birth rates at the population level are also determined by the
176 timing of maturation based on development rate. Thus, organismal growth feeds into the rate of
177 births at the population level by influencing the number of adults.

178 Changes in death rates (d) arise through both internal (d_i) and external forces (d_e).
179 External forces can be any sort of risk from environmental conditions, competitors, predators, or
180 pathogens generating a rate of extrinsic mortality. Internal forces, such as aging, will generate an
181 intrinsic rate of mortality. This intrinsic rate will depend on the allocation of resources to
182 maintenance, including repair, immune function, and basal metabolic costs. These two rates of
183 death are in principle additive, although one could influence the other through density
184 dependence and compensatory mortality (i.e., when extrinsic mortality reduces density-
185 dependent mortality; Anderson & Burnham 1976).

186 This minimal model represents a single species and can be broken into life stages if
187 needed as different life stages may have different responses to climate variables and accounting
188 for stage structure may be necessary to understand overall population patterns (Coulson *et al.*

189 2001; Davidson *et al.* 2024; Johnson *et al.* 2023). It can also be connected to other species via
190 connecting rates, such as the predator functional response, which, for example, would link the
191 uptake rate for the predator and the extrinsic death rate for the prey (see Interspecific
192 Asymmetries). Species interactions can connect two or more models in a variety of ways,
193 depending on whether the interaction alters mortality, resource uptake, or allocation of resources.
194 For example, a vector borne pathogen may be connected to both the vector and the host through
195 the rate at which the vector bites hosts.

196 Critically, the framework is intended to be a minimal but general depiction of how core
197 organismal-level rates interact to drive change in population size, in service of simplifying our
198 representation of asymmetries. All populations have individuals that uptake and allocate
199 resources for maintenance, growth, and reproduction. These allocations, in all cases, are used to
200 support physiological processes determining development rates, fitness, and demographics.
201 Metabolic losses due to heat can be added with another ‘allocation’ arrow, but this is generally
202 not critical to the issue of asymmetries. Thus, we intend that any species can be described
203 through the minimal model, with appropriate expansions of rates and processes as needed for a
204 particular problem. Note, this model is not a food-web model or a network; the arrows describe
205 how upstream rates lead to downstream rates following a chain of effects from resource uptake
206 to the change in population growth rates. Thus, we refer to this structure as a rate hierarchy.

207 **Intraspecific Asymmetries**

208 Within the rate-hierarchy framework, asymmetries affecting population growth rate can arise at
209 multiple levels of biological organization. At the highest level are the aforementioned
210 demographic asymmetries that directly change population growth rates (and therefore also mean
211 fitness; Lande 1982) when there are non-compensatory responses of birth or death rates to

212 climate change. Population growth will be promoted when birth rates increase faster with climate
213 change than death rates, while population declines will result when death rates increase faster
214 with climate change than birth rates. Given the nonlinearity or unimodality of some climate
215 change responses, such as many thermal functions, population growth may increase or decrease
216 with changes in climate. A commonly assumed form of the demographic asymmetry comes from
217 Amarasekare and Savage (2012), in which birth rates are a unimodal function of temperature and
218 death rates are an exponentially increasing function of temperature (Fig 4a). The difference
219 between these two functions generates the canonical left-skewed population growth rate thermal
220 performance curve (TPC; Amarasekare & Savage 2012; Ratkowsky *et al.* 1982, 1983) and a
221 demographic asymmetry through the non-compensatory effects of temperature on birth and death
222 rates.

223 The proportional allocation of resources acquired through uptake rates to organismal
224 growth, maintenance, and reproduction may shift in response to changing environmental
225 conditions (Atkinson 1994; Brett *et al.* 1969; Roff 2001). These changes will often manifest in
226 life history trade-offs, and their potential consequences may be complex, as resources are split
227 into multiple competing ends. It is worth noting that an allocation change may not immediately
228 result in a change in a specific rate, if changes in uptake rates counteract the effect of the
229 allocation, and we do not propose that a change in proportional allocations is an asymmetry
230 *sensu stricto*. Below we discuss the two asymmetries at lower levels in our rate hierarchy,
231 fecundity-maturation and growth-maintenance asymmetries, which arise from resource uptake
232 rates and allocation changes.

233 A **fecundity-maturation asymmetry** arises due to changes in the birth rate driven by
234 non-compensatory changes in the upstream rates of resource allocation to reproduction and

235 maturation (Fig 4b). This asymmetry can be seen through the lens of an expression describing
236 how the birth rate is generated:

$$237 \quad b = AF = A \frac{u_r}{c}.$$

238 The total birth rate (b) is the product of the number of mature adults A and the fecundity per time
239 of individuals F . The number of mature adults in the population depends on the organismal
240 growth rate (or inversely, maturation time). Faster development and shorter maturation times
241 resulting from increases in resource acquisitions and allocations to organismal growth will lead
242 to a subsequent increase in the number of reproducing adults, so one of the upstream contributors
243 to b passes through organismal growth to a change in A . Fecundity (F) is determined by a
244 combination of factors including resource allocations to reproduction (u_r) and the costs per
245 offspring (c), following a typical Smith-Fretwell quantity-quality trade-off (Smith & Fretwell
246 1974). Thus, the other upstream contributor to b is straight from the uptake rate given the
247 fraction of the uptake rate allocated to reproduction. Given that the cost per offspring could also
248 be climate-dependent, there are at least three ways in which birth rates change due to asymmetric
249 effects of the upstream component rates (i.e. the number of adults, resource allocation to
250 reproduction, and cost per offspring).

251 A common example of potential maturation-fecundity asymmetries in ectotherms is the
252 relationship between temperature, size at maturity, and fecundity. At cooler temperatures,
253 ectotherms tend to grow more slowly, reach maturity at a larger size, and due to their larger size
254 produce a larger number of eggs (Atkinson 1994; Roff 2001). Thus, birth rates may change with
255 temperature because of the simultaneous changes in A and F . Whether or not these changes lead
256 to a decrease in birth rates with temperature can be complex, depending on, for example, whether
257 the relationship between size and fecundity itself is temperature dependent (Arendt 2011). In

258 general, maturation-fecundity asymmetries could be difficult to detect if changes in maturation
259 and fecundity counterbalance each other and only result in a demographic and life history shift in
260 the population.

261 A **growth-maintenance asymmetry** arises due to changes in the death rate driven by
262 non-compensatory changes in the organismal growth rate and the rate of allocation to
263 maintenance (Fig 4c). As with the fecundity-maturation asymmetry, the rate of allocation of
264 resources to maintenance (u_m) influences the likelihood of survival in concert with the rate of
265 growth and maturation that sets expected lifespan by setting the age and size at maturation. This
266 asymmetry can be seen through the lens of an expression that clarifies how survival is generated:

$$267 \quad s \propto B \frac{u_m}{c_m}.$$

268 The mortality rate is the inverse of survival, and survival depends on the allocation of resources
269 to maintenance and the size B of the organism that is being maintained. Thus, survival is
270 proportional to the product of the per mass availability of maintenance resources (u_m / c_m) and the
271 mass of the organism. In this way, maturation and growth form one part of the upstream rate
272 effect on mortality, and allocation of resources forms the other part. As body mass may change
273 with climate, for example, through the impact of temperature on growth, and allocation decisions
274 and overall uptake rates may vary with temperature, there are several ways in which the climate
275 dependence of upstream rates will have non-compensatory effects on survival.

276 For example, across ectothermic taxa, increases in environmental temperatures drive
277 elevated maintenance metabolic rates, up to a point, influencing the cost of maintenance (c_m),
278 and correspondingly necessitate higher rates of resource allocation requirements for maintenance
279 (u_m ; Amarasekare & Savage 2012). If not compensated for by changes in the uptake rate,
280 increasing metabolic rates will result in concurrent decreases in resource allocation to organismal

281 growth. Huey and Kingsolver (2019) proposed the “metabolic meltdown hypothesis” that
282 suggests that growth-maintenance asymmetries will frequently arise, given direct negative
283 effects of climate change on resource and nutrient availability or indirectly by negative effects of
284 higher temperatures on locomotion and foraging rates. This hypothesis is supported by empirical
285 studies demonstrating combined negative effects of temperatures and resource availability on
286 organismal and population growth rates (Brett *et al.* 1969; Thomas *et al.* 2017).

287 **Interspecific Asymmetries**

288 To understand how asymmetric responses that might occur among interacting species will impact
289 populations, we can expand our framework from the single species to multi-species cases. To do
290 so, we connect two or more species via an appropriate connecting rate (e.g. predator functional
291 response, mosquito biting rate, plant pollination rate) dictating their interactions. Critically,
292 changes in connecting rates will have cascading consequences across pairs of species that can
293 result in demographic shifts in one or both interacting species. Furthermore, the connecting rate
294 itself can depend on possible asymmetric effects of upstream mechanisms that generate the rate.
295 Below, we show how the addition of connecting rates can allow us to examine how asymmetric
296 climate change responses might influence predator-prey, host-parasite, and mutualistic
297 interactions and the resultant consequences for populations.

298 *Predator-prey interactions*

299 Feeding rates connect predators and prey as they determine the uptake rate of the predator
300 and influence the extrinsic death rate of the prey. We define a **predator-prey asymmetry** as the
301 case when the foraging rate changes with climate due to the non-compensatory effects of
302 upstream factors related to both the predator/consumer (x_c) and prey/resource (x_r) that respond to
303 climate (Figure 5). As predation events depend on movement and encounters between predator

304 and prey, the detection of prey by the predator, and the successful attack by the predator
305 (DeLong 2021; Jeschke *et al.* 2002; Wootton *et al.* 2023), there are many ways in which climate
306 change may alter the emergent foraging rate (f).

307 One of the earliest recognized drivers of climate change asymmetries are phenological
308 mismatches. Predators and prey must be in the same area at the same time for predation to occur,
309 and environmental factors like temperature may influence the likelihood of this co-occurrence,
310 especially in highly seasonal habitats (Damien & Tougeron 2019). In a classic case of
311 phenological mismatch, differential changes in the timing of breeding activity of insectivorous
312 great tits (*Parus major*) and their caterpillar prey affects foraging rates of the birds (Reed *et al.*
313 2013). The migration of great tits is triggered by daylength and temperature, but caterpillar
314 phenology advances more quickly with warming than egg laying phenology of the birds
315 (Burgess *et al.* 2018; Reed *et al.* 2013), resulting in reduced availability of prey during peak
316 resource demand for the birds. As foraging rates depend on prey availability through the
317 functional response, this disparity in timing lowers the foraging rates (a change in x_r) and can
318 also generate a demographic asymmetry for the birds by reducing reproductive rates and/or
319 increasing death rates due to resource shortage. As phenological changes are widely documented
320 with climate change, this may be a common source of climate change asymmetries.

321 Foraging rates also can depend on changes in the climate and particularly temperature
322 through a **movement asymmetry**. Predation depends on the encounter rate between predator and
323 prey, and local movement patterns determine the probability that prey are in close enough
324 proximity for detection by predators. This encounter rate process is often captured via the idea of
325 a relative velocity and described mathematically by combining the velocities of consumers and
326 resources through their mean root square,

327 $V_{rel} = \sqrt{V_R^2 + V_C^2}$

328 where V_{rel} is the relative velocity of predators and prey, V_R is the velocity of the prey, and V_C is
329 the velocity of the predator (Aljetlawi *et al.* 2004; Dell *et al.* 2014; Pawar *et al.* 2012). A
330 movement asymmetry may arise when predator foraging rates change due to the predator and
331 prey having different thermal sensitivities of movement (i.e., upstream changes in x_c and x_r ; Dell
332 *et al.* 2014). Such movement sensitivities to climate change may be due to differences in average
333 searching velocities of predator relative to prey, but also may be caused by changes in activity
334 patterns or attack or escape speeds. For example, Öhlund *et al.* (2015) showed how an
335 asymmetry in the relationships between temperature, pike attack speeds, and trout escape speeds
336 generated an overall temperature dependence of attack rates of pike on trout. A specific form of
337 the movement asymmetry can be caused by differences in thermy among predators and prey
338 (Gibert *et al.* 2022), in which one species is an endotherm while the other is an ectotherm. In this
339 scenario, the endotherm would show minimal change in searching velocity while the ectotherm
340 would have a greater thermal sensitivity, creating a change in encounter rates that alters the
341 foraging rate and potentially leads to a demographic asymmetry for both species.

342 Predation events also depend on the ability of predators to detect prey. Climate change
343 may alter the ability of predators to detect prey or for prey to avoid detection by predators. For
344 example, changes in temperature regimes can alter the effectiveness of camouflaging
345 phenotypes, creating a camouflage mismatch that changes the risk of predation. In a classic case,
346 snowshoe hares (*Lepus americanus*) change coat color to blend in with the seasonally changing
347 environment, with a white coat in the winter to reduce contrast with the snowy ground and a
348 brown coat in the summer to reduce contrast with soils and plants. The timing of the color switch
349 is temperature independent, but changing precipitation patterns resulting in delayed snowfall and

350 early snowmelt result in windows during which hare have a visual mismatch with the
351 background, causing easier detection by predators such as lynx (*Lynx canadensis*) (Ferreira *et al.*
352 2023). Thus, the mismatch increases foraging rates because of an effect on the upstream process
353 of detecting prey (x_c), which depends on both predator and prey traits. Climate change also may
354 alter prey detection of predators in chemically mediated interactions (Roggatz *et al.* 2022). For
355 example, increases in acidity in aquatic environments can alter the olfactory ability of fish to
356 detect predators or alarm cues potentially making fish more susceptible to predation (Ou *et al.*
357 2015; Porteus *et al.* 2018).

358 *Host-parasite interaction*

359 For a host-parasite interaction, the connection between species may or may not involve a
360 connecting rate, and, given the diversity of types of host-parasite interactions, hosts and parasites
361 may be connected in a variety of ways. For any kind of parasite that primarily draws off
362 resources of the host (e.g. tick, tapeworm, etc.), the connection between the rate hierarchy of the
363 host and the parasite would be directly through the two uptake rates (Figure 6). That is, the
364 parasite gathers resources out of the host's resource stream, impacting the host's available
365 resources. We thus draw an arrow toward the hosts uptake rate from the parasites uptake rate.
366 The host's realized uptake rate, then, is generated by the interacting effects of their own resource
367 gathering activity and the parasite's resource extracting behavior (f). In this way, an **uptake rate**
368 **asymmetry** can arise due to the non-compensatory effects of host and parasite foraging. If
369 warming, for example, increases the rate of resource uptake of a parasite more quickly than that
370 of its host, there would be a net decline in the realized uptake rate of the host. This change in
371 uptake rate would cascade up to host demography and also potentially feedback to alter the
372 demography of the parasite. Further, a transfer of resources from host to parasite might be

373 disproportionate or not depending on whether the fraction of resources passing through the gut
374 varies with resource flow. A parasite that has an uptake rate that saturates with increasing flow
375 through would have a different proportional effect on host resource assimilation, and emergence
376 of an asymmetry would depend on whether or not host uptake rate was altered by climate
377 change. Additionally, parasite induced anorexia or hyperphagy in its host (Hite *et al.* 2020; Hite
378 & Cressler 2019) could also mediate an uptake rate asymmetry.

379 Outside of effects of parasites on host uptake, endoparasites also may increase host
380 extrinsic mortality directly by triggering cell death, releasing toxins, or instigating extreme
381 immune responses (Figure 5). As parasite pathogenicity and host immune responses can both be
382 dependent on the environment (Thomas & Blanford 2003; Wright & Cooper 1981),
383 environmental changes could lead to asymmetries that alter the death rate of the host. In sub-
384 lethal infections, the presence of the endoparasite could necessitate increased host allocations to
385 immune function, leading to fecundity-maturation or growth-maintenance asymmetries. In
386 particular, all of these processes could be temperature dependent if the host's decision to tolerate
387 or fight the endoparasite depends on temperature, or if the host is an ectotherm making uptake,
388 allocation, and demographic processes temperature dependent.

389 For ectoparasites that are vectors (e.g. mosquitos), the additional player (vectored
390 pathogen) generates new possible avenues of asymmetries (Figure 7). Here the biting rate (bite)
391 would serve as a connecting rate between the host, pathogen, and vector. This is an expansion of
392 the uptake rate asymmetry, as some form of 'biting' would be involved in any such host-parasite
393 interaction. Thus, the biting rate could cause a demographic asymmetry by increasing
394 reproduction of the vector, decreasing reproduction of the host, and increasing death rate of the
395 host caused by pathogen transmission, and altering the states (susceptible or infected with

396 pathogen carried by the vector) of individuals in the host population. The biting rate is also a
397 critical connecting rate determining the net reproductive rate (R_0) of vectored pathogens
398 themselves. A seminal study by Mordecai et al. (2013) makes clear how R_0 is dependent on
399 numerous upstream rates (e.g., vector development rate and competence), creating a wide range
400 of potential asymmetries. As most of these upstream rates are dependent on climate, including
401 temperature, R_0 is temperature dependent as well (Mordecai *et al.* 2013, 2019).

402 **Mutualistic interactions**

403 As for host-parasite and consumer-resource interactions, we can incorporate mutualistic
404 interactions into the framework through a connecting rate or by connecting rates directly
405 between the mutualists. How the players in the mutualism are connected is dependent on how the
406 mutualism operates. For example, plants and their pollinators can be connected through a
407 visitation rate that links the birth rate of the plant to the uptake rate of the pollinator (often
408 through pollen or nectar consumption for the pollinator; Figure 8). This visitation rate is a
409 downstream rate that could be affected by upstream features of the pollinator (x_{po}) and the plant
410 (x_{pl}), such as pollinator energy demands or plant attractiveness. A protective mutualism, such as
411 ant-acacia mutualisms, also might have a mutualism connecting rate that links uptake for the ants
412 from resources provided by the acacia to the extrinsic death rate or uptake rate of the acacias as
413 the ants prevent defoliation (Janzen 1966). Endosymbiotic mutualists may have similar or more
414 complex relationships between connecting rates than other mutualisms. For example, the protist
415 *Paramecium bursaria* hosts an algal *Zoochlorella* symbiont. The paramecium in this interaction
416 receives sugars provided from algal photosynthesis while the paramecium both provides
417 protection and nutrients for the algae (Brown & Nielsen 1974; Karakashian 1963). Thus, this

418 system might be described by a mutualism connecting rate that links the uptake rate of the
419 paramecium and the uptake rate and extrinsic death rate of the algae.

420 There are many ways in which differing responses of mutualistic partners to climate
421 change can lead to **uptake rate asymmetries**, phenological mismatches, or other asymmetries
422 that alter the mutualism connecting rate with potential cascading effects for either or both
423 partners. In a recent review, Cruz et al. (2023) highlighted how differing thermal performance
424 curves of mutualistic partners in traits related to the interaction among partners can generate an
425 overall mutualism thermal performance curve, making the mutualism itself temperature
426 dependent. Given that mutualistic interactions generally involve connections to rates such as
427 uptake rates and extrinsic death rates, the temperature dependence of mutualisms generated by
428 asymmetric responses can potentially lead to changes that could scale up to a demographic
429 asymmetry and population growth or decline. For example, in an experimental plant-pollinator
430 system, increasing temperatures led to fewer flowers per plant and lower nectar volume, but
431 higher nectar concentration (de Manincor *et al.* 2023). However, the net asymmetric effect of
432 these changes with temperatures led to reduced visitation rates and shorter bee handling times
433 with negative consequences for flower seed set under warmer conditions (de Manincor *et al.*
434 2023).

435 Under some circumstances, asymmetric climate change effects on mutualisms may shift
436 these interactions along the so-called mutualism-parasitism continuum (Bronstein 1994; Johnson
437 *et al.* 1997). For example, in the aforementioned *Paramecium bursaria-Zoochlorella* system, at
438 high temperatures ‘ghost’ *Paramecium* without algal symbionts have higher fitness than
439 *Paramecium* that contain *Zoochlorella* symbionts (Salsbery & DeLong 2018). A potential
440 explanation for this is that the paramecia are mixotrophs that receive energy from both their algal

441 symbionts and through bacterivory. At higher temperatures, bacterivory may lead to greater
442 fitness for *Paramecium* without symbionts relative to those with symbionts because the energy
443 gained from the algae at high temperatures is less than the potential energy that could be gained
444 from bacteria. This is because the space within a cell is finite, generating a trade-off between
445 allocating that space to algae or food vacuoles. In this case, changes in the relative potential
446 benefits of bacterivory and photosynthates from the algae with temperature generate an
447 asymmetric effect on uptake rates that switches the presence of algae from beneficial to
448 detrimental. Given the potential for the costs and benefits of symbioses to be environmentally
449 dependent (Bronstein 1994; Cruz *et al.* 2023; Hoeksema & Bruna 2015; Johnson *et al.* 1997),
450 asymmetric climate change effects may play a particularly important role in moving host-
451 symbiont relationships along the mutualism-parasitism continuum.

452 **Asymmetries and Indirect Interactions**

453 Thus far, we have focused on how the framework can be used to understand asymmetric climate
454 change impacts on rates within species and species with direct interactions. By combining
455 modules representing single species or pairwise species interactions, we can apply the
456 framework to larger groups of species and communities more generally. For example, a key
457 indirect interaction in ecology is resource competition (Tilman 1982). Although often modeled
458 phenomenologically as a direct interaction between two species, competition can be understood
459 more mechanistically as two or more consumers using the same resource (Abrams 2022). In our
460 framework, this can be represented by two consumers with uptake rates that are connected to a
461 single resource through feeding rate links for a biotic resource or utilization rate links for an
462 abiotic resource. Armed with this new module, one can then track how asymmetric impacts on
463 rates within and among species might influence the entire competitive system. Similarly, one

464 could construct a module with two resources consumed by a single consumer to examine
465 apparent competition (Holt 1977) or a module with a predator connected to a consumer
466 connected to a resource to examine trophic cascades (Paine 1980).

467 **Asymmetries, Communities, and Ecosystems**

468 Until now, we have focused our discussion of asymmetries around effects of climate change that
469 impact the demographics and the growth or decline of populations. For communities and
470 ecosystems composed of these species, however, asymmetric effects of climate change on
471 species growth rates can propagate to yet another level to cause **community** or **ecosystem**
472 **asymmetries**. These asymmetries occur when there are non-compensatory changes among the
473 constituent species that shape community- or ecosystem-level rates or properties are themselves
474 functions of the rates of change of constituent species in response to climate change that are non-
475 compensatory (Figure 9). Defining community and ecosystem asymmetries allows us to apply
476 our framework to potentially inform predictions about consequences of species-specific changes
477 for aggregate responses across species and ecosystem functioning. As the biodiversity-ecosystem
478 functioning and climate change literature have made clear, species contributions to ecosystem
479 functioning are rarely equal (Huston 1997; Tilman *et al.* 1997), and climate change impacts on
480 species within a community are likely to generate cases of climate change ‘winners’ and ‘losers’
481 (Clucas *et al.* 2014; Kimball *et al.* 2010; Somero 2010; Sorte *et al.* 2013). Therefore, barring a
482 compensatory mechanism such as the portfolio effect, in which diversity in responses across
483 species buffers community properties from change (Doak *et al.* 1998; Tilman *et al.* 1998),
484 asymmetric effects of climate change on community and ecosystem-level properties such as
485 ecosystem functioning are likely to be common.

486 **Conclusions and Future Prospects**

487 Here we provide a framework for understanding how asymmetric responses to climate change in
488 rates within and among species combine to impact populations, communities, and ecosystems.
489 Although most of the examples we used throughout have focused on asymmetric responses to
490 mean temperatures, we believe that this framework is equally applicable to asymmetric
491 responses in other variables likely to be affected by climate change. For example, in a study of
492 Sonoran Desert plant community change over 25 years, Kimball et al. (2010) showed how later
493 winter rains in colder conditions alter germination rates across annual plants leading to
494 community change. When put in the context of our frame work, the germination response to the
495 timing of precipitation of each plant species could be viewed as altering birth rates and causing
496 demographic asymmetries that led to declines or increases in population growth. Our focus on
497 temperature is largely a reflection of the fact that this has been the most widely studied
498 component of climate change, particularly with regard to asymmetries. Expanding research to
499 include asymmetric responses to a greater number of changing climatic features, including the
500 variance of those features (IPCC 2021; Vasseur *et al.* 2014), will provide a more holistic view of
501 how climate change is likely to influence populations.

502 Our framework makes it apparent that there is potential for an asymmetry generated at
503 one level to be canceled out by another rate response to climate change, indicating that caution
504 should be taken when directly interpreting how an asymmetry at one level influences population
505 growth or decline. For example, using data across 35 species of birds, McLean et al. (2016)
506 showed that warmer temperatures were associated with earlier lay dates and earlier lay dates
507 were associated with higher reproductive rates. However, despite these changes suggesting
508 higher reproduction rates with higher temperatures, they found no relationship between
509 temperature and population growth, suggesting that some negative effect of temperature must be

510 compensating for the increase in reproduction (McLean *et al.* 2016). We believe that the
511 framework herein may be particularly useful in helping to identify where compensating
512 asymmetric effects might occur and therefore provide target rates to be measured to determine
513 whether a particular asymmetry is likely to scale to influence the population. Another possible
514 way in which asymmetries could be canceled out is through feedbacks that are not currently
515 incorporated into the minimal rate hierarchy model. For example, consider a predator-prey
516 asymmetry in which climate change increases the predator feeding rate, increases prey extrinsic
517 mortality, and decreases the prey population growth rate and density. As predator feeding rates
518 are increasing functions of prey densities, lower prey densities could feedback to lower predator
519 feeding rates or could lead to reduced density dependence in the prey which could alter birth or
520 death rates. Although this increases the complexity of understanding asymmetric climate change
521 impacts, applying the framework to think through these possibilities makes clear where these
522 feedbacks might emerge and how they might ultimately affect population growth rates. The
523 framework also facilitates the identification of rates researchers should focus on measuring to
524 understand the population effects of asymmetric climate change responses.

525 One impetus for the development of the framework herein was that there is often a
526 disconnect in the literature between climate change responses used to infer asymmetries and their
527 effects on systems and the climate change response itself. For example, given the ubiquity of
528 thermal performance curves, differences among species in thermal performance are often used to
529 suggest the existence of asymmetries that will impact the system (Cohen *et al.* 2017; Gsell *et al.*
530 2023; Meehan & Lindo 2023). Yet, applying the framework here, it becomes clear that the
531 relevance of differences in thermal performance curves for asymmetries is dependent on what
532 metric of performance is being compared among species, where in the rate hierarchy the

533 asymmetry of interest occurs, and how ‘performance’ translates to the downstream rate of
534 interest. For example, in seeking to explain the temperature dependence of chytrid prevalence in
535 frogs, Cohen et al. (2017) performed an experiment comparing frog preferred temperatures,
536 chytrid growth rates in culture, and chytrid growth rates on frogs. Although chytrid growth rates
537 on frogs are indeed likely to be a determinant of prevalence, applying the framework here to this
538 problem would suggest that the temperature dependence of several other processes should also
539 be considered, such as the susceptibility of the frogs to infection, chytrid spore survival, etc. If
540 the temperature dependence of all of these processes are well-correlated, these extra
541 considerations may not be necessary, but, in general, this will be an assumption that requires
542 testing. As another example, a commonly measured potential climate change response in the
543 literature is the relationship between sprint speed and temperature (Berkum 1988; Hertz *et al.*
544 1983), which is often taken to be correlated with overall organismal performance. However, in
545 our framework, sprint speed is likely to be a low-level rate on the hierarchy that could, for
546 example, alter feeding rates depending on how sprint speeds, predator attack or prey escape
547 rates, and their relationships with temperature combine (Öhlund *et al.* 2015). However, taking
548 into account all of the other possible temperature responses in the rate hierarchy, it becomes clear
549 that sprint speed responses need not be directly correlated with the overall relationship between
550 temperature and population growth (fitness) at the highest level of the hierarchy. Overall, we
551 hope that this framework can help identify which rates are important to measure for a particular
552 process of interest and for making inference on how or if those rates are likely to scale to bring
553 about population changes.

554 Throughout, we also have assumed that the climate change responses that generate
555 asymmetries and their potential impacts are constant. However, if individuals differ in their

556 climate responses, this creates the opportunity for natural selection that could cause the evolution
557 of responses and lead to an eco-evolutionary feedback, which then alters the asymmetry and its
558 likely consequences. This also highlights the potential role that plasticity may play in moderating
559 the effects of climate change response asymmetries. As mentioned above, feedback effects from
560 asymmetric climate change responses could alter the environments to produce additional
561 feedbacks or phenotypic plasticity that counteract or generate new asymmetries. Such changes
562 are likely to depend on the specifics of systems (e.g. is there heritable variation in a particular
563 climate change response involved in an asymmetry?), but studies focusing on these processes
564 will provide important information on how organisms might adapt to the consequences of
565 climate change response asymmetries and climate change more generally.

566 Understanding how species are responding to climate change is pressing. Many species
567 responses involving changes in population size are likely due to how asymmetric effects of
568 changes in intra- and interspecific rates with climate change scale to the level of birth and death
569 rates with subsequent effects on population growth rates. Here we provide a broadly applicable
570 and flexible framework that can incorporate asymmetric climate change responses in rates within
571 and among species. Our hope is that this framework will allow researchers to identify critical
572 areas and traits within their study systems in which asymmetric climate change effects may occur
573 and to place identified asymmetries within the framework to predict when asymmetries will
574 influence population, community, and ecosystem level responses to climate change.

575

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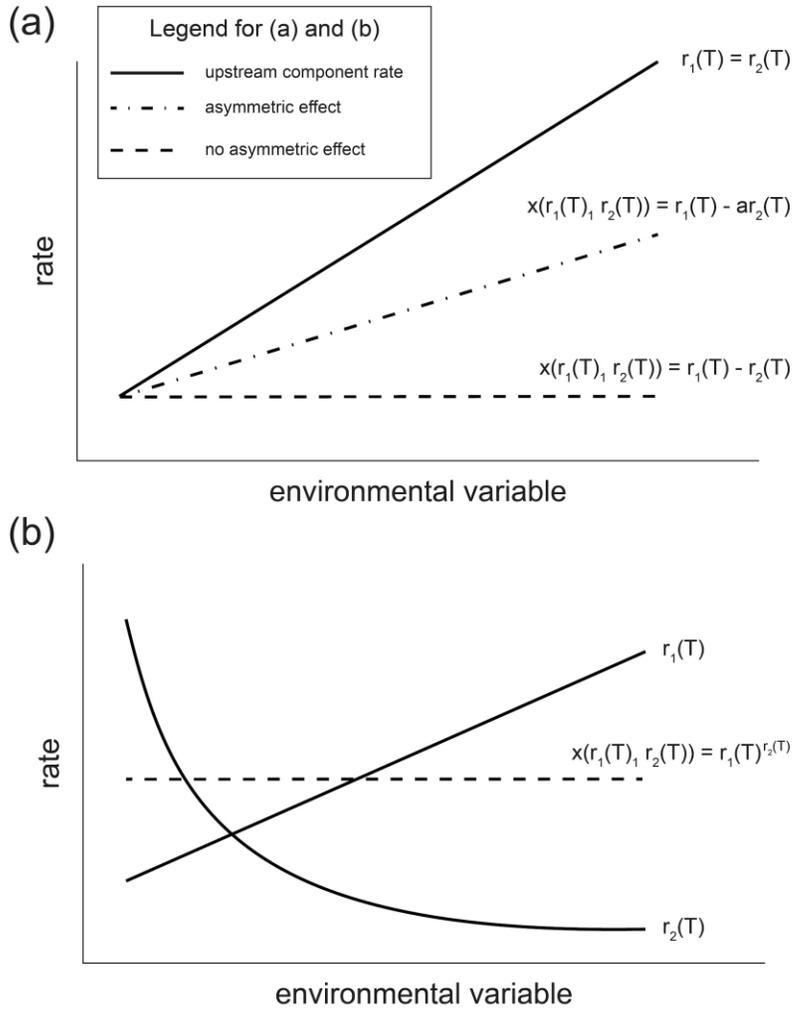
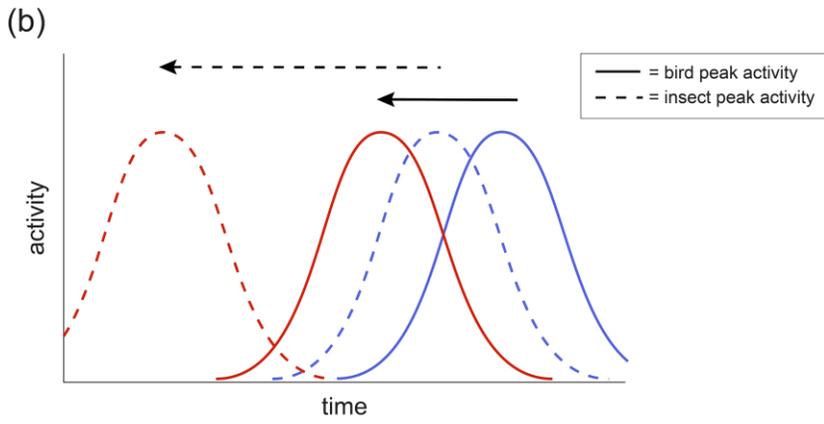
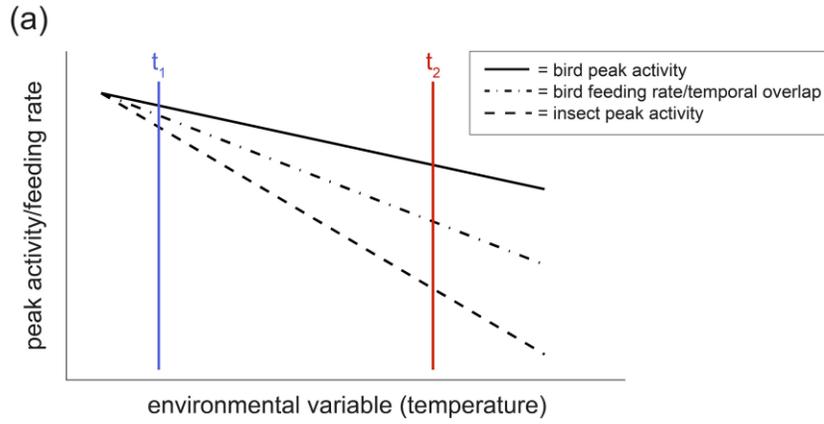
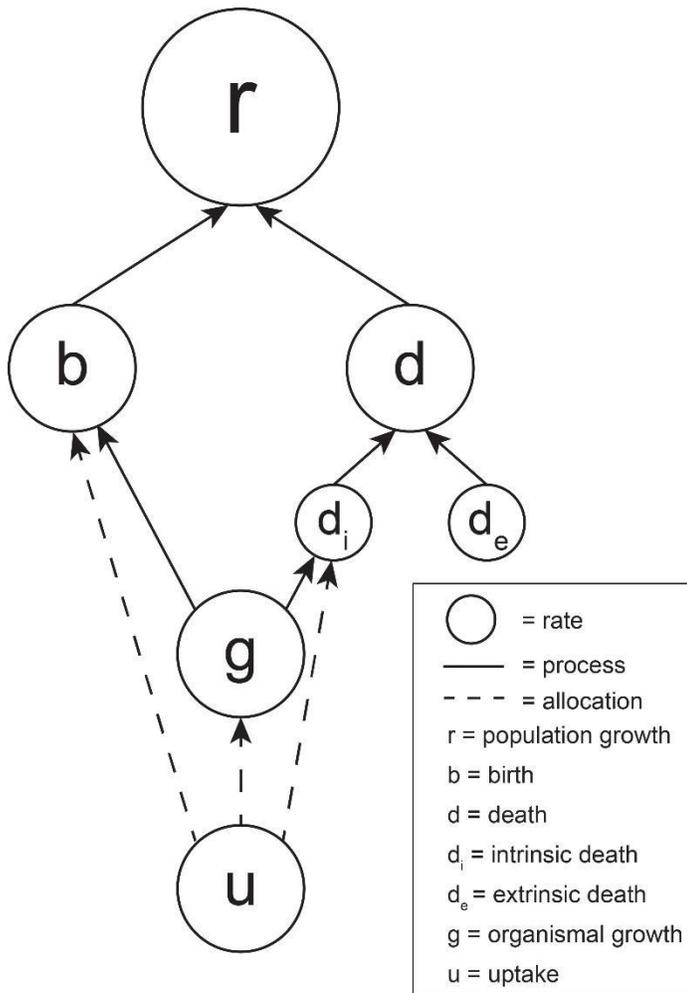


Figure 2



792 **Figure 3**

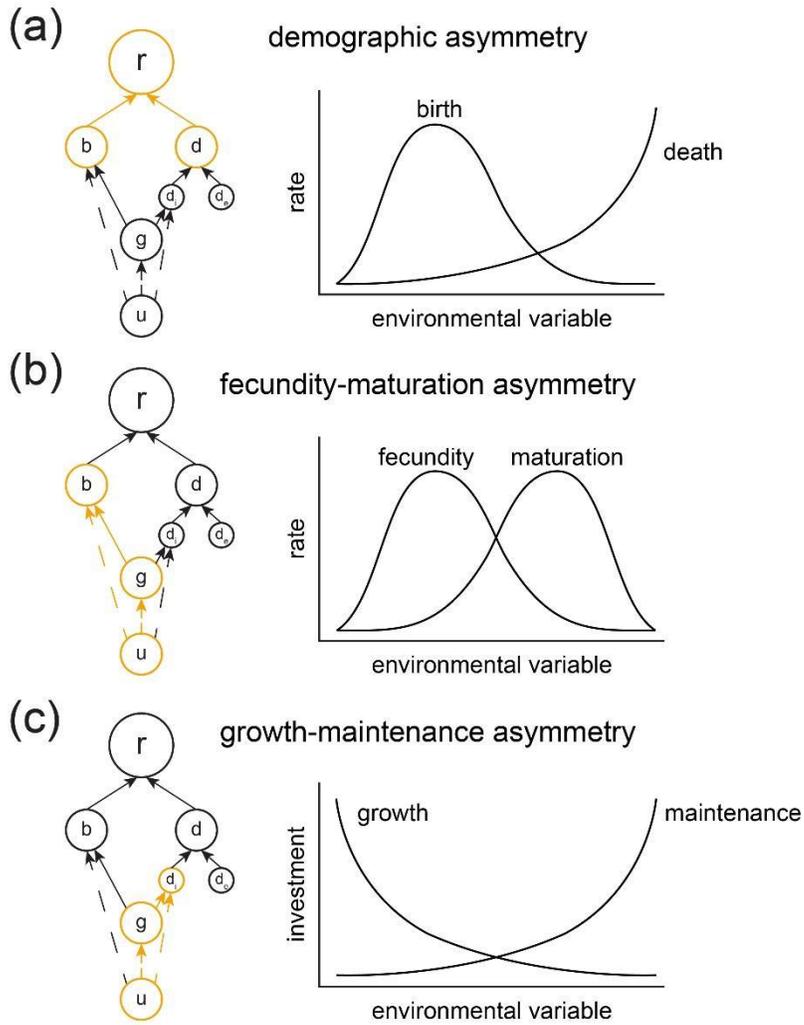


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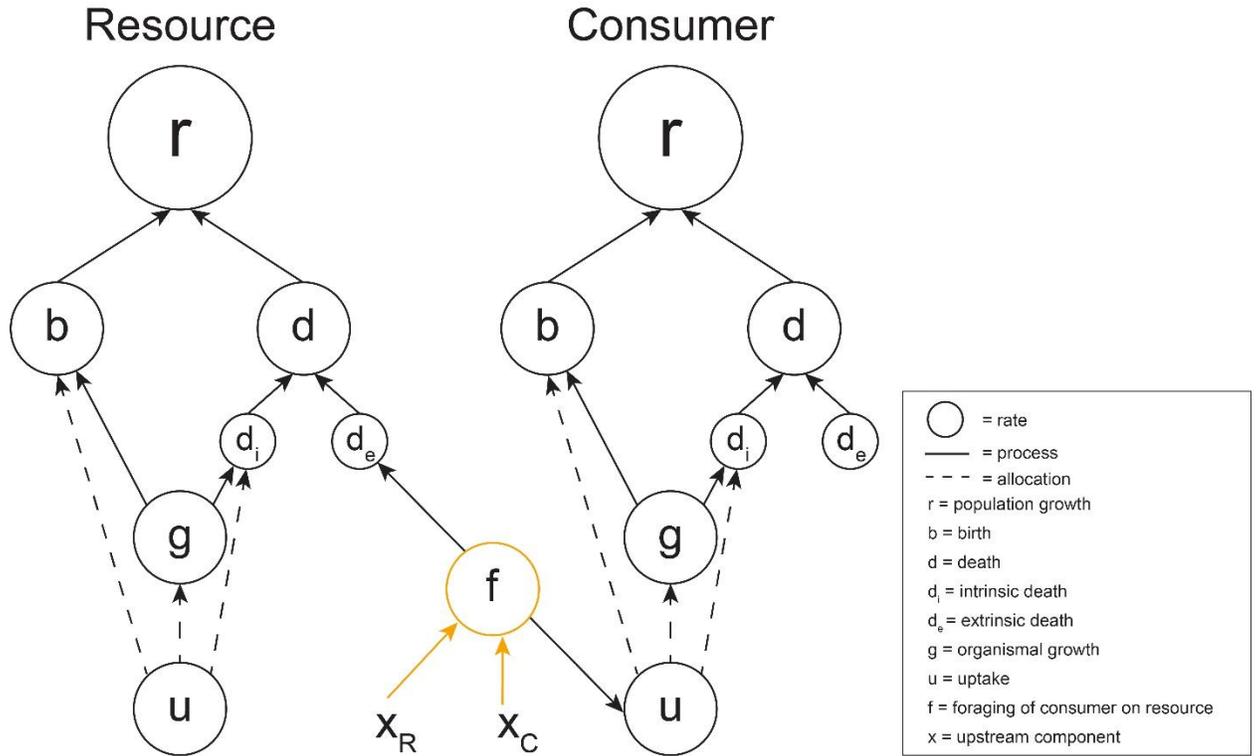
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Figure 4



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Figure 5

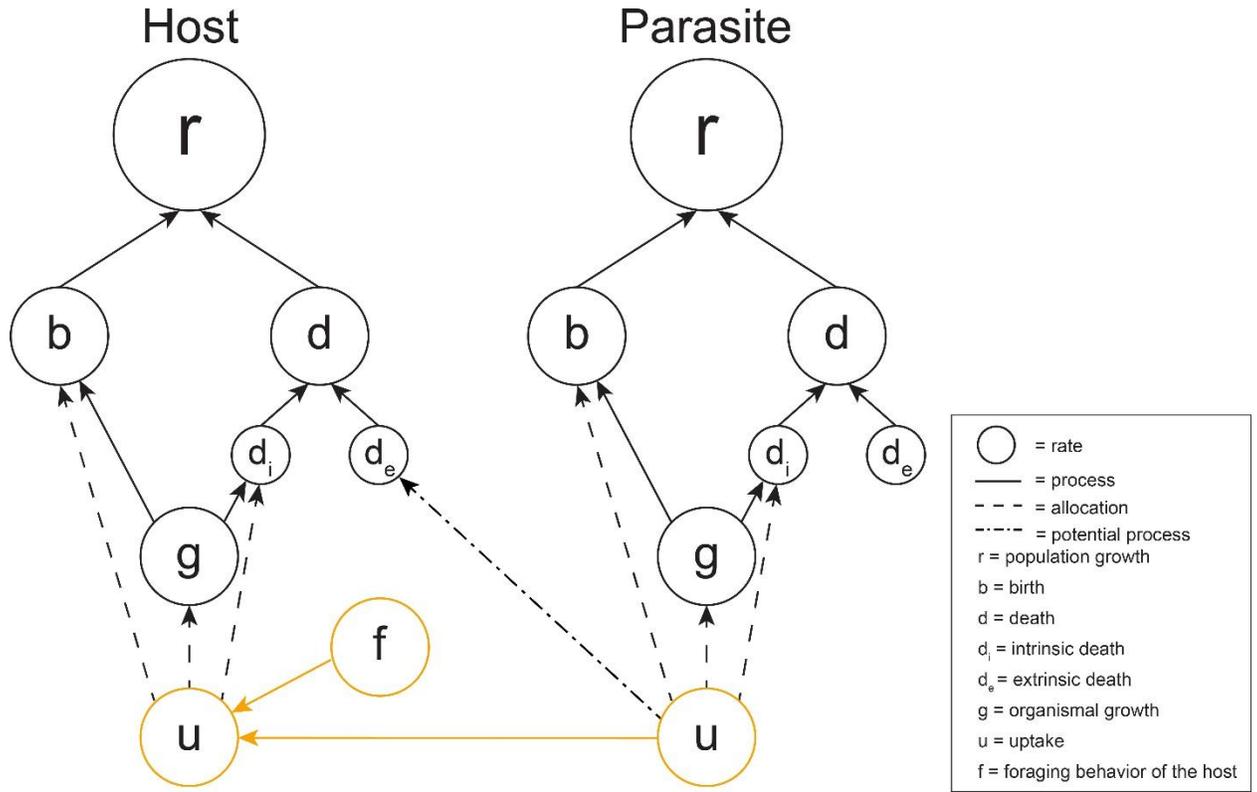


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Figure 6



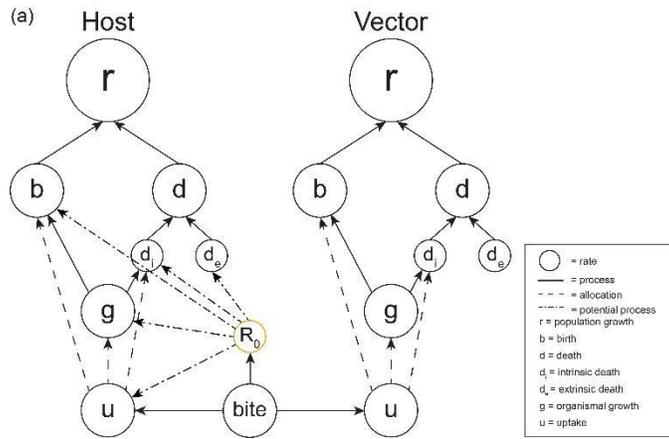
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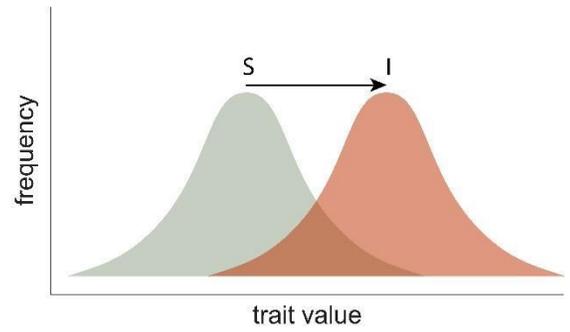
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Figure 7



(b)



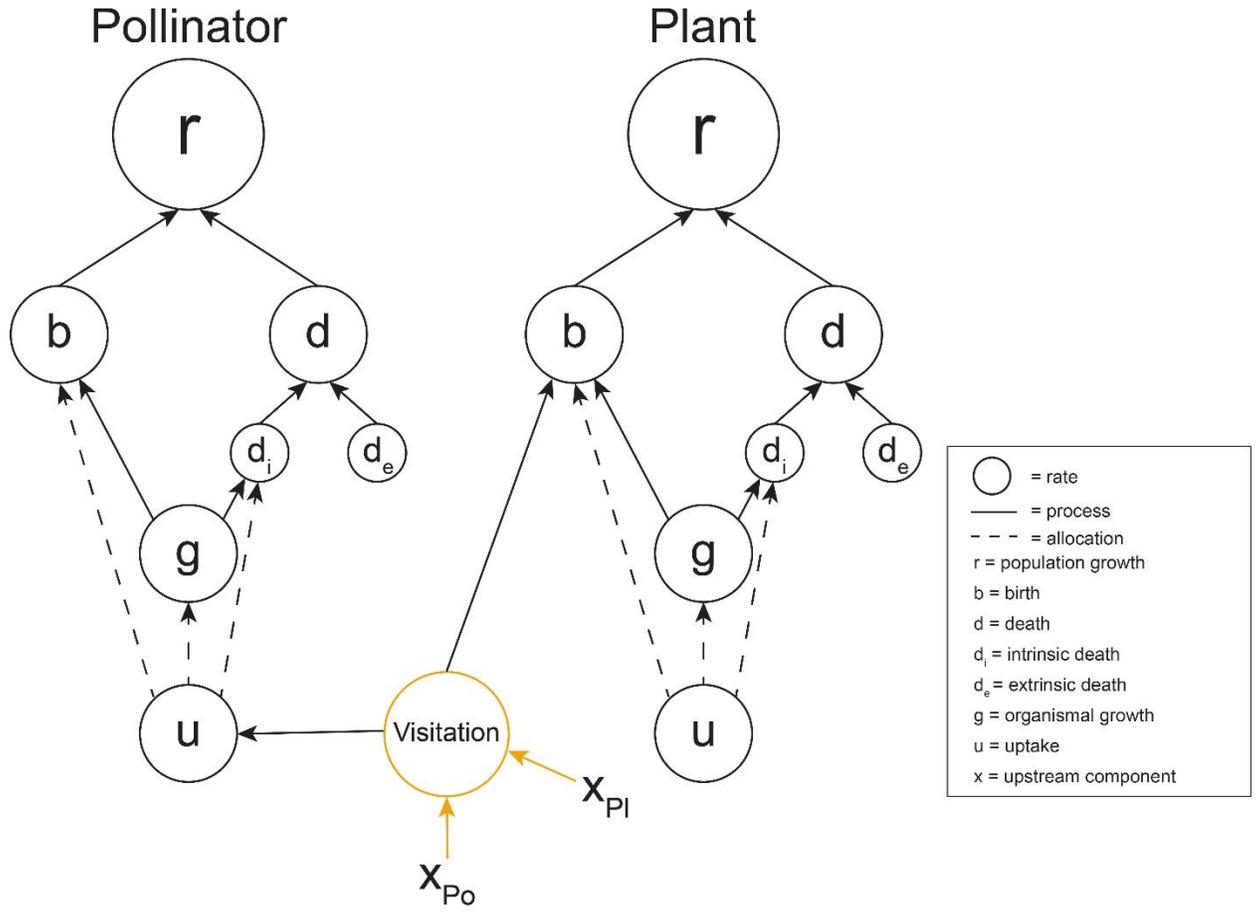
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Figure 8

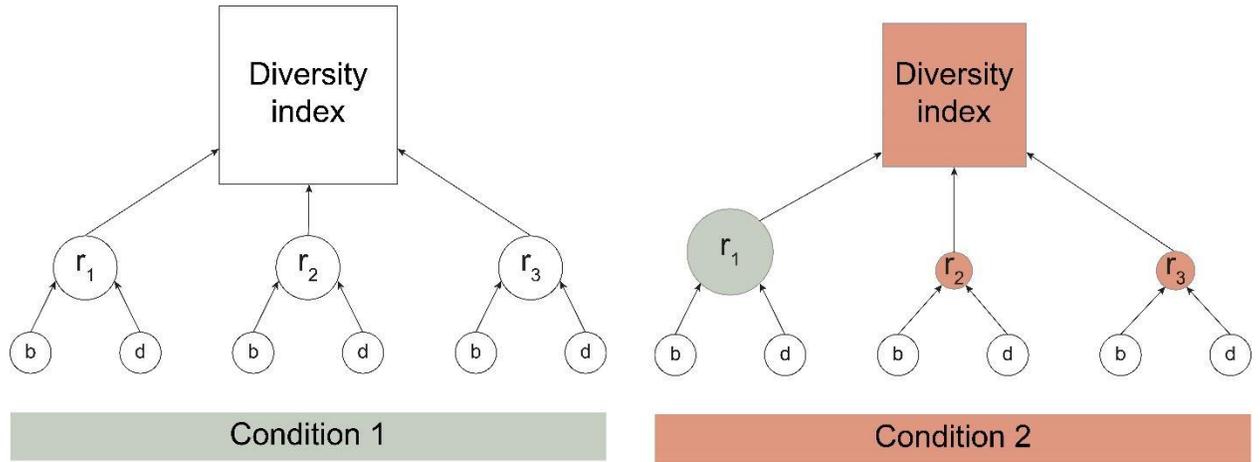


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814

Figure 9



815

816

817 **Figure Legends**

818 **Figure 1.** Conceptual representations of asymmetries. We define asymmetric effects of climate
819 change as changes in a focal rate due to changes in the effects of components determining that
820 rate with climate change. This is because components (r_i 's) can change in same manner with an
821 environmental variable such as temperature (T) and, yet, may or may not have an effect on the
822 focal rate (X) depending on how they combine to determine X (a). Components can also change
823 in different ways and yet have no effect on the focal rate (b).

824

825 **Figure 2.** Climate mismatches, such as phenotypic mismatches, can lead to asymmetric effects.
826 For example, changes in the timing of bird and insect peak activity with temperature can
827 generate an asymmetric effect on the abundance of and temporal overlap with insects
828 experienced by birds leading to decreased bird feeding rates.

829

830 **Figure 3.** A single-species depiction of our framework for understanding asymmetric responses
831 to climate change and their impacts on populations. Each circle represents a rate, and arrows
832 between circles show how rates influence one another. Solid lines represent direct determinations
833 of rates and dashed lines represent allocations of resources to different rates. The top rate r is the
834 rate of change of the focal population (population growth rate). This is determined by the birth
835 rate b and the death rate d . The birth rate is determined by average organismal growth rates in the
836 population (g) and energy allocation to reproduction b from resource uptake rates u . Death rates
837 are determined by both intrinsic death rates d_i and extrinsic death rates d_e . Intrinsic death rates
838 are determined by average organismal growth rates in the population and allocation of energy

839 from resource uptake. Last, organismal growth rates g are determined by allocation of energy
840 from resource uptake.

841

842 **Figure 4.** A graphical depiction of demographic (a), fecundity-maturation (b), and growth-
843 maintenance (c) intra-specific asymmetries. Upstream rates directly contributing to each
844 asymmetry within our hierarchy are highlighted in yellow. Demographic asymmetries are the
845 highest level asymmetry and are characterized by non-compensatory changes in birth (b) and
846 death (d) rates in response to environmental change. Fecundity-maturation and growth-
847 maintenance asymmetries occur at the lower levels of our framework and arise due to resource
848 allocation trade-offs between organismal growth and either reproduction or maintenance as
849 climate changes and relationships between organismal growth and birth or death rates.

850

851 **Figure 5.** The rate hierarchies of a resource (R) and consumer (C) are connected by the foraging
852 rate (f). The foraging rate connects the uptake rate of the consumer and the extrinsic death rate
853 of the resource. Varied asymmetric climate change effects can alter the foraging rate which can
854 lead to cascading effects up the resource and consumer rate hierarchies to influence their
855 population growth rates.

856

857 **Figure 6.** Example of a host-parasite interaction in which the rate hierarchy of the parasite is
858 connected to the host rate hierarchy through its uptake rate reducing the uptake rate of the host.
859 Asymmetric effects of climate change on host and parasite uptake rates could potentially filter up
860 the rate hierarchies to alter population growth. Some parasites also may have direct effects on the
861 extrinsic death rate, for example, through the development of toxins or direct mortality of cells.

862

863 **Figure 7.** Example rate hierarchies for a host and vector of a pathogen. The uptake rates of the
864 host and vector are connected via the biting rate of the vector. This biting rate is also connected
865 to the R_0 of the pathogen (the basic reproduction number). In turn, R_0 alters the proportion of the
866 population that is infected by the pathogen and potentially a variety of different rates in the
867 population depending how infection shifts rates between infected and non-infected individuals
868 (b).

869

870 **Figure 8.** Example of a plant-pollinator interaction in which the visitation rate of the pollinator
871 to flowers connects the uptake rate of the pollinator to the birth rate of the plant. Asymmetric
872 climate change effects on visitation rates thus can alter pollinator uptake rates and plant birth
873 rates potentially cascading up to have demographic consequences.

874

875 **Figure 9.** Demographic asymmetries among species within communities can lead to community
876 and ecosystem asymmetries. As climate change alters environmental conditions (Condition 1 to
877 Condition 2), demographic asymmetries within species can lead to changes in population growth
878 rates among species comprising a community (illustrated by r_i circle size). Community- or
879 ecosystem-level attributes that are dependent on contributions from component species, such as
880 diversity indices, may then experience asymmetric climate change effects due to among-species
881 shifts.

882

883

884 **Text Boxes**

885 **Box 1: What is an asymmetry?** An asymmetry is a case in which some focal rate, say, rate X ,
886 changes in response to some driving factor (e.g., temperature) because two or more determining
887 components change in response to that driving factor in such a way that their effects on the focal
888 rate are not cancelled out. In contrast, changes in upstream components may lead to no change in
889 a downstream rate if their effects perfectly cancel out in the mathematical construct that leads to
890 the downstream rate (Figure 1). Thus, what is asymmetrical about the situation is not that the
891 changes in the upstream components are proportionally different, it is that the effects of those
892 changes drive further change in the downstream rate. It is both possible that 1) two upstream
893 components respond to a climate driver in the same proportional way but still cause an
894 asymmetry because they come together to influence the downstream rate in different ways
895 (Figure 1A) and that 2) two upstream components change in a disproportionate way and do not
896 lead to a change in the downstream rate because the way they come together cancels out their
897 effects on the downstream rate (Figure 1B). Thus, an asymmetry is really only detectable in the
898 change in the downstream rate or by knowing exactly how the upstream components combine to
899 determine the downstream rate. We suggest that these special cases will mostly be rare and that
900 differential changes in upstream components will most likely have downstream consequences.

901 To define an asymmetry mathematically, assume that our rate X is a function of two or
902 more components r_1, r_2, \dots, r_n that are themselves a function of an environmental variable such as
903 temperature T . Then, an asymmetry will alter X when differences in $r_1(T), r_2(T), \dots, r_n(T)$
904 between temperatures change the value of $X = f(r_{\{1\}}(T), r_{\{2\}}(T), \dots, r_{\{n\}}(T))$. For
905 example, the rate of change in population size is a function of birth and death rates, which vary
906 with temperature (in this case, $\frac{dN}{dt} = f(\text{birth rate}(T), \text{death rate}(T)) = \text{birth rate}(T) -$

907 *death rate*(T). So, asymmetries occur between two temperatures when the birth and death
908 rates change differentially with temperature such that $\text{birth rate}(T_1) - \text{death rate}(T_1) \neq$
909 $\text{birth rate}(T_2) - \text{death rate}(T_2)$.

910 We can consider asymmetries at a single temperature, between two temperatures, or over
911 a range of temperatures. At a single temperature, asymmetries occur if instantaneous changes in
912 $r_1(T), r_2(T), \dots, r_n(T)$ result in $\frac{df(r_1(T), r_2(T), \dots, r_n(T))}{dT} \neq 0$. In the case of a rapid shift between two
913 temperatures, asymmetries occur if $f(r_1(T_1), r_2(T_1), \dots, r_n(T_1)) \neq f(r_1(T_2), r_2(T_2), \dots, r_n(T_2))$.
914 When considering a range of temperatures $[T_1, T_2]$ (or (T_1, T_2) , an open interval between two
915 temperatures), there is an asymmetry if there exists $T_a, T_b \in [T_1, T_2]$ such that
916 $f(r_1(T_a), r_2(T_a), \dots, r_n(T_a)) \neq f(r_1(T_b), r_2(T_b), \dots, r_n(T_b))$. In other words, there is no
917 asymmetry over an interval $[T_1, T_2]$ if and only if, over all intervals $(T_a, T_b) \in$
918 $[T_1, T_2]$, $f(r_1(T_a), r_2(T_a), \dots, r_n(T_a)) = f(r_1(T_b), r_2(T_b), \dots, r_n(T_b))$.
919