

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

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32 **Abstract**

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

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50

51 **Introduction**

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

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

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

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

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

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

112 **Clarifying Asymmetries and Mismatches**

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

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

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

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

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

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

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

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

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

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

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

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

188 2001; Davidson *et al.* 2024; Johnson *et al.* 2023). It can also be connected to other species via
189 connecting rates, such as the predator functional response, which, for example, would link the
190 uptake rate for the predator and the extrinsic death rate for the prey (see Interspecific
191 Asymmetries). Species interactions can connect two or more models in a variety of ways,
192 depending on whether the interaction alters mortality, resource uptake, or allocation of resources.
193 For example, a vector borne pathogen may be connected to both the vector and the host through
194 the rate at which the vector bites hosts.

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

206 **Intraspecific Asymmetries**

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

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

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

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

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

$$236 \quad b = AF = A \frac{u_r}{c}.$$

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

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

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

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

266 $s \propto B \frac{u_m}{c_m}$.

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

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

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

286 **Interspecific Asymmetries**

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

297 *Predator-prey interactions*

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

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

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

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

326 $V_{rel} = \sqrt{V_R^2 + V_C^2}$

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

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

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

357 *Host-parasite interaction*

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

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

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

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

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

401 **Mutualistic interactions**

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

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

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

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

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

451 **Asymmetries and Indirect Interactions**

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

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

466 **Asymmetries, Communities, and Ecosystems**

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

485 **Conclusions and Future Prospects**

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

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

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

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

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

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

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

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

574

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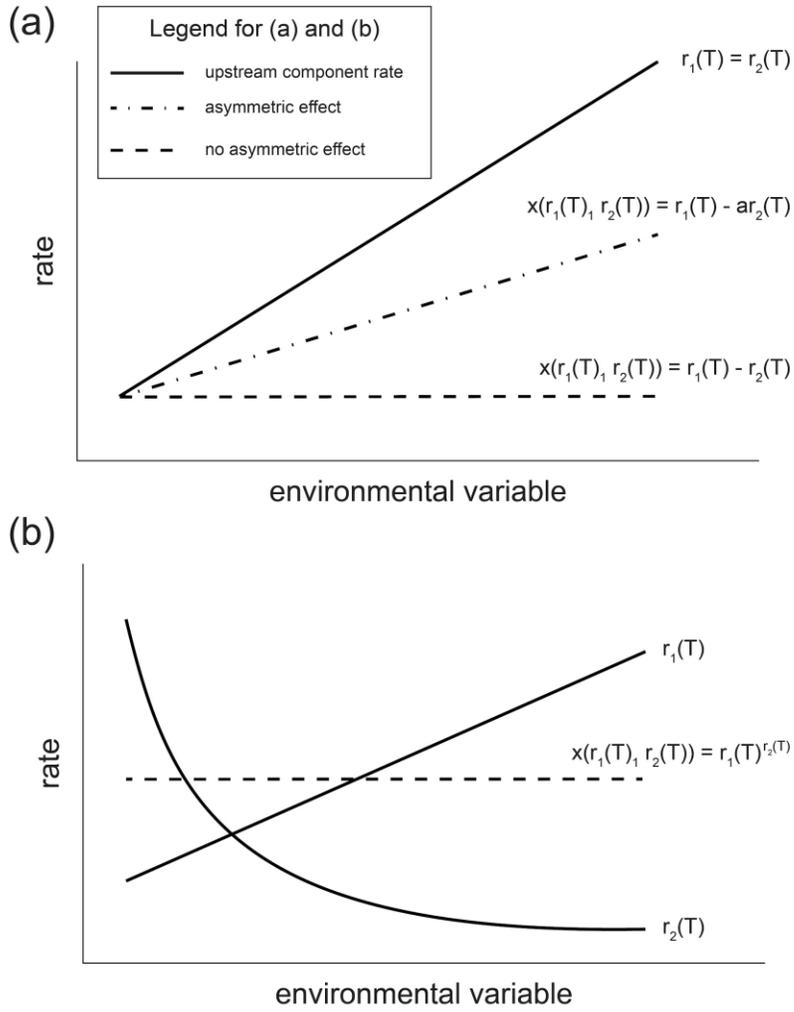
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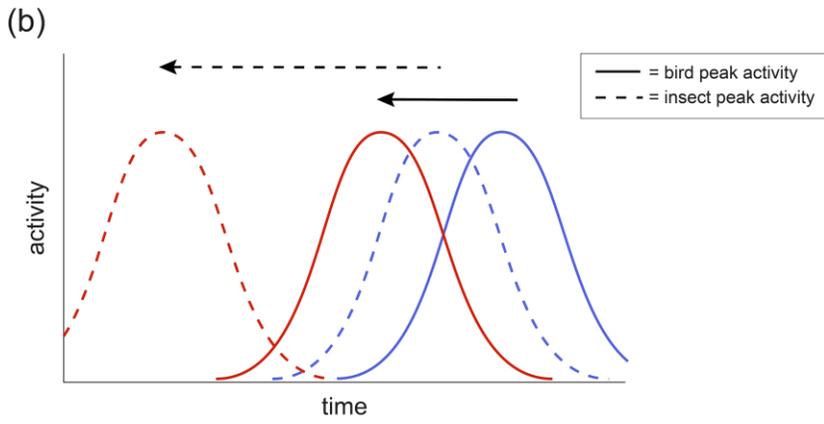
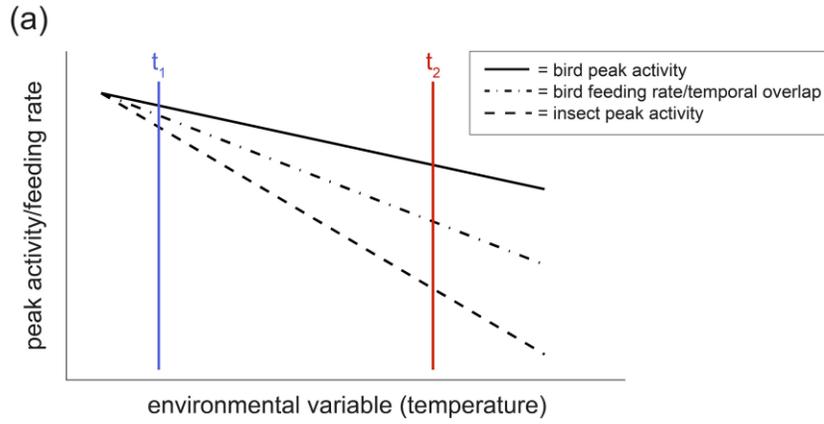
785 **Figure 1**



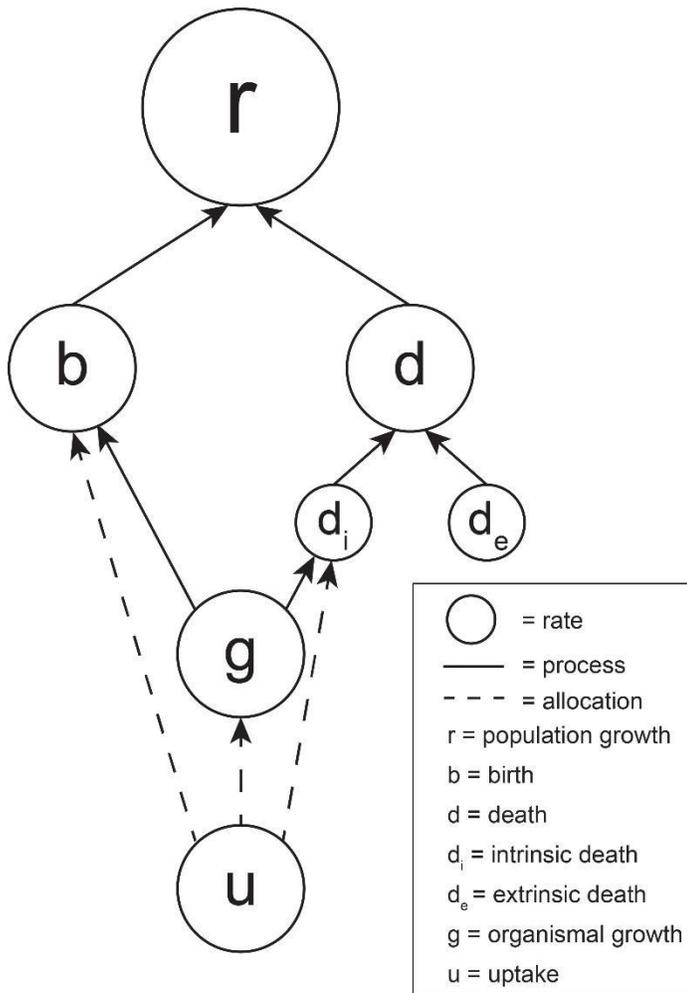
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Figure 2



791 **Figure 3**



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Figure 4

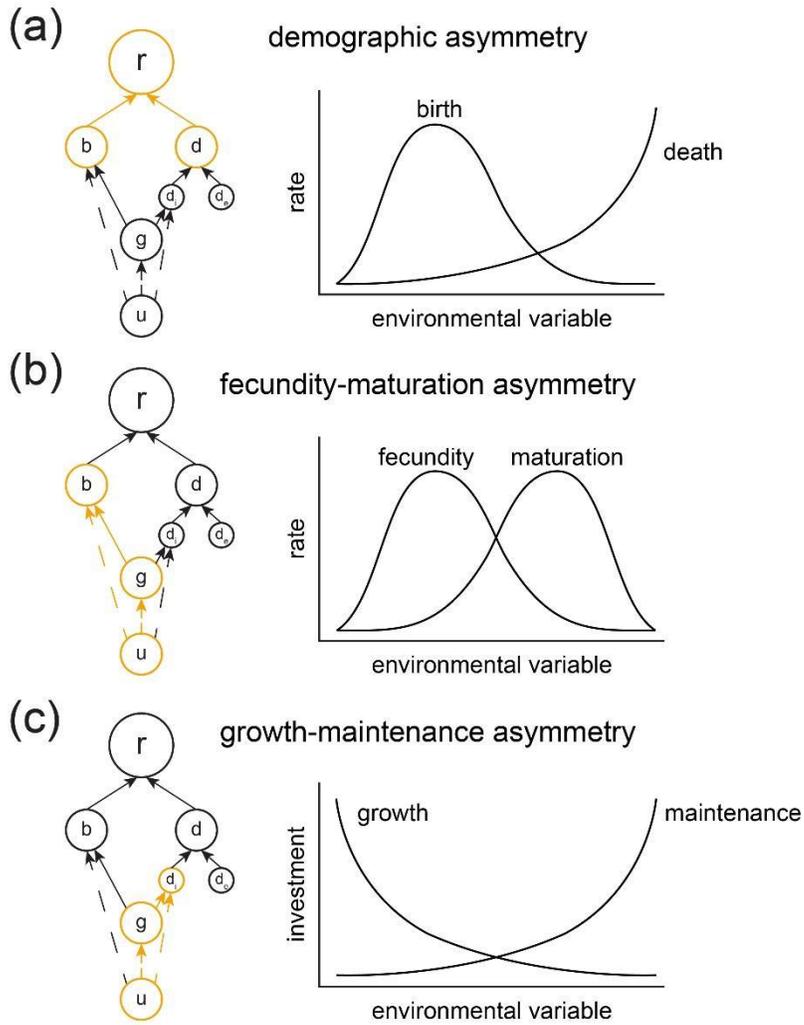
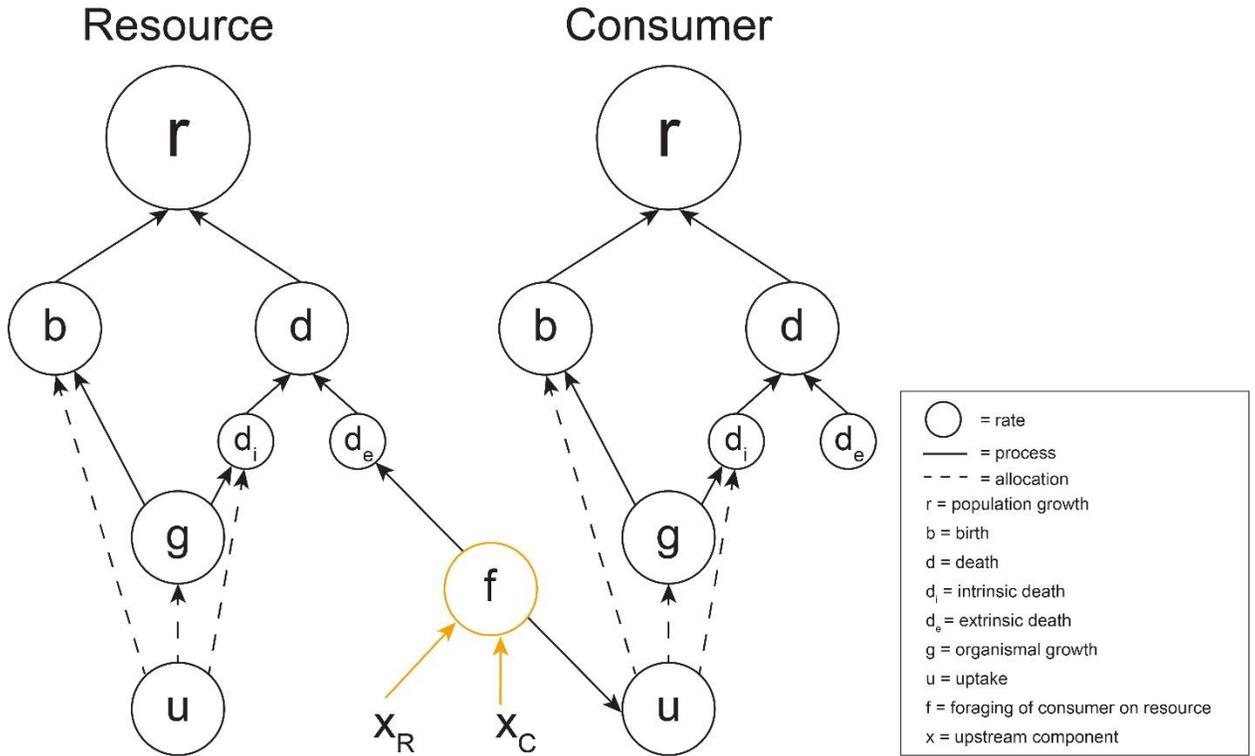


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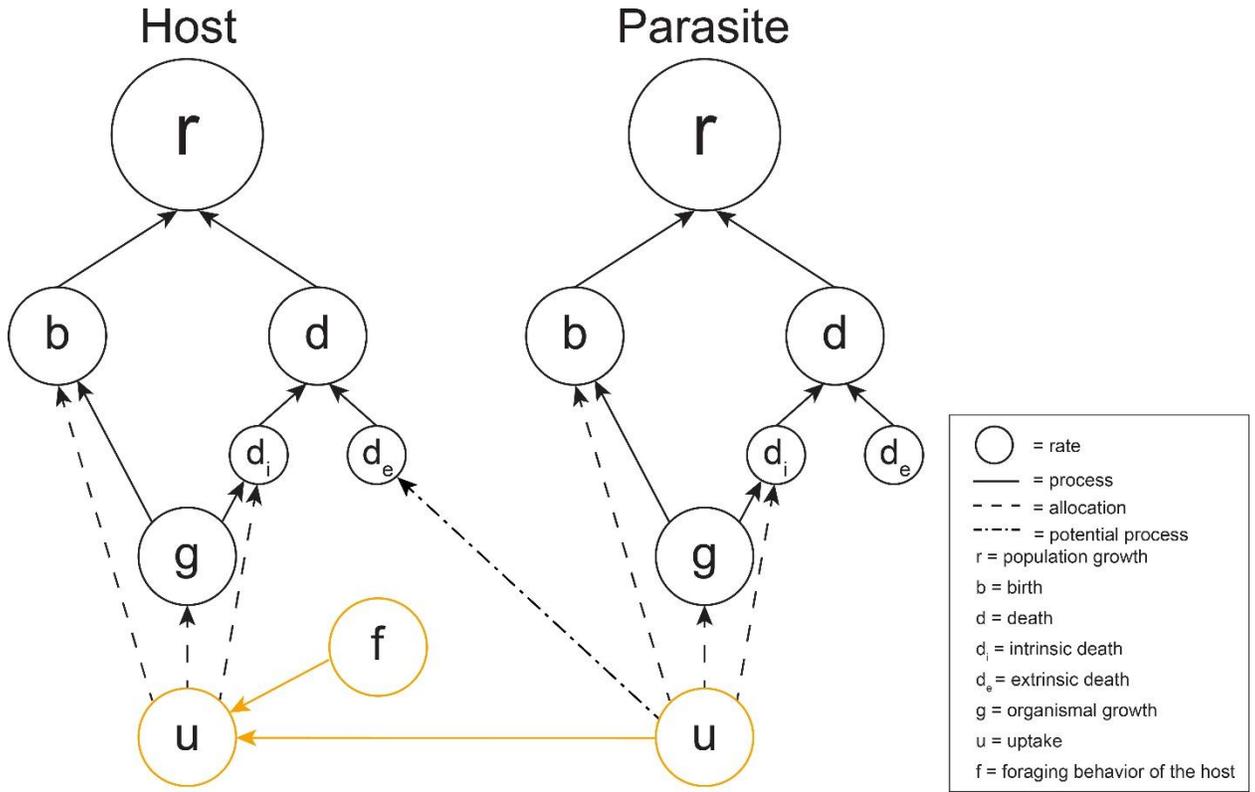


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Figure 6



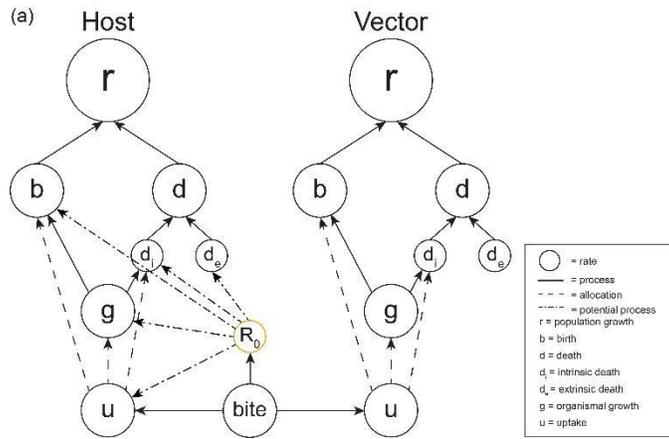
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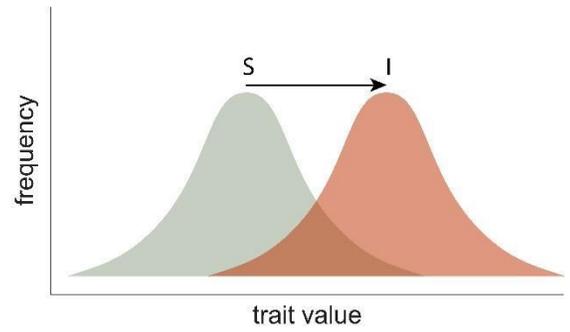
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Figure 7



(b)



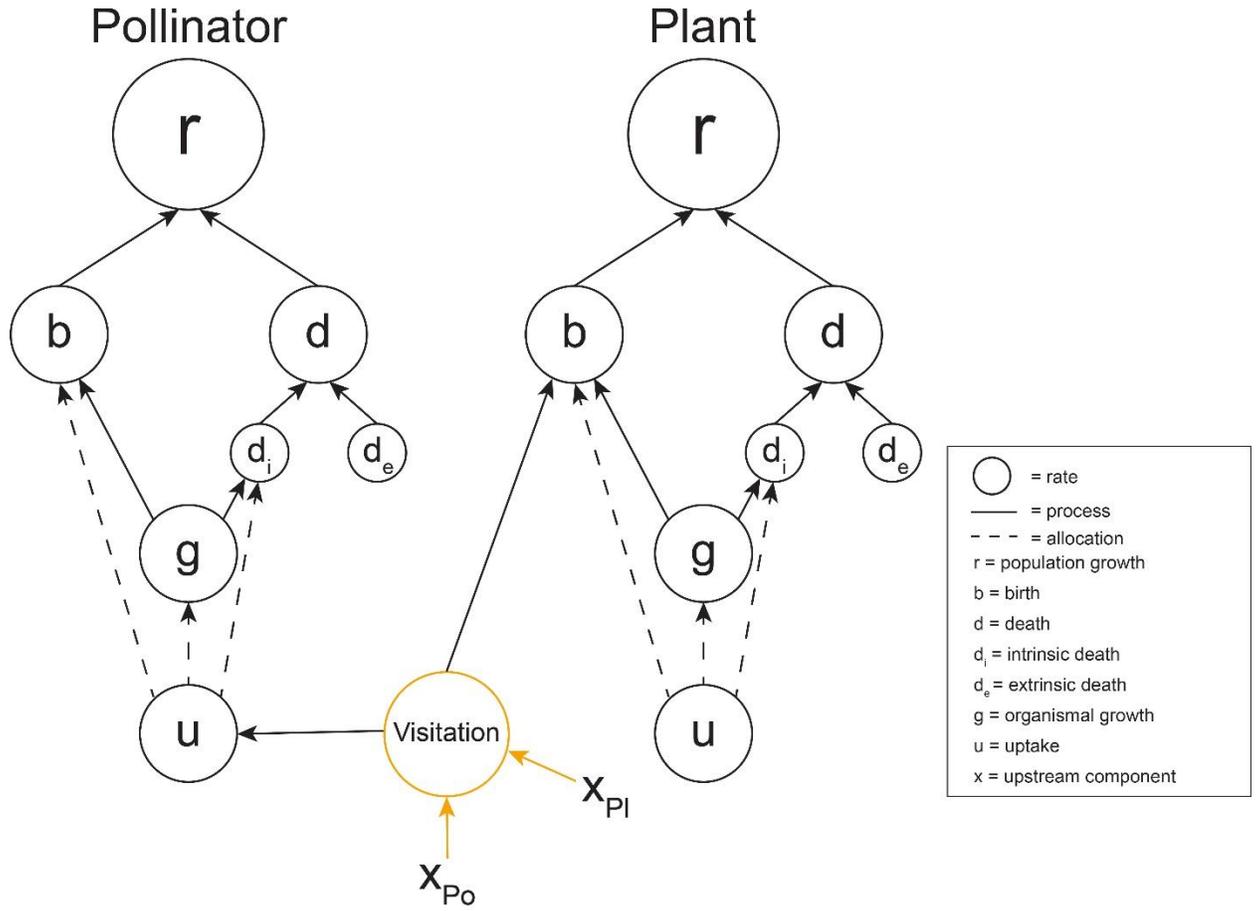
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Figure 8

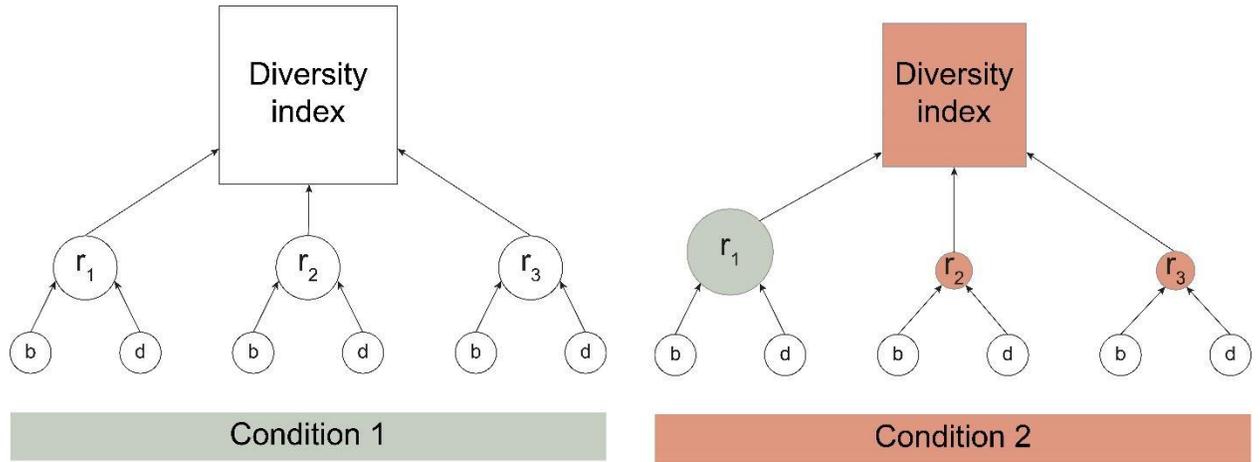


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Figure 9



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815

816 **Figure Legends**

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

823

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

828

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

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

840

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

849

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

855

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

861

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

868

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

873

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

881

882

883 **Text Boxes**

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

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

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

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