

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

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## **Abstract**

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

## Introduction

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

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

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

We focus on asymmetric climate change effects for two principal reasons. First, at the population level, the ultimate response to climate change that we are often most interested in is whether and to what extent a population might grow or decline with climate change. In general, barring changes in immigration or emigration, changes in population abundances must reflect non-zero population growth rates (i.e. birth rates minus death rates). A change to, say, a negative growth rate from a positive one with a change in the environment implies that birth and death rates have changed with the environment in a manner such that the death rate now exceeds the birth rate. Thus, this fundamental asymmetry is central to understanding population changes in response to climate change, as well as all other dynamic changes in population abundance.

Second, there exists a large and growing list of asymmetric climate change effects that have been identified both within and among species. For example, studies have identified asymmetric effects of temperature among different rates within species (Huey & Kingsolver 2019; Bozinovic *et al.* 2020; Wang *et al.* 2020; Jørgensen *et al.* 2022), in consumer-resource interactions (Dell *et al.* 2014; Gilbert *et al.* 2014; Bideault *et al.* 2021; Gibert *et al.* 2022; Álvarez-Codesal *et al.* 2023), and in host-parasite systems (Mordecai *et al.* 2013, 2019; Cohen *et al.* 2017; Taylor *et al.* 2019; Kirk *et al.* 2022). Although the ubiquity of asymmetric climate change effects is becoming clear, we currently lack a cohesive framework with which to conceptualize how these asymmetries are likely to fit together and interact to ultimately produce changes in populations.

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

### **Clarifying Asymmetries and Mismatches**

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

Asymmetry in the context of climate change responses is currently widely used in two contexts. First, asymmetry is used to describe when two or more rates have different thermal sensitivities (e.g. Gibert *et al.* 2022). Second, asymmetry is also used to describe the case where the thermal performance curves of two species are not equivalent (also referred to by some

authors as mismatch; e.g. Cohen *et al.* 2017). We believe that these definitions are inadequate when the goal is to understand how a process of interest is likely to change with climate due to changes in component processes or rates. Therefore, our definition focuses not on whether the components change in the same manner or not with climate change, but whether the changes in the components with climate change subsequently alter a process of interest (Box 1). This is because it is possible that the components change with the environment proportionally in exactly the same way and generate effects on a rate of interest (Figure 1a), and for the components to change with the environment in different ways and generate no effect on a process of interest (Figure 1b). Crucially, it is how these components specifically combine that determine whether their changes generate an asymmetric effect on a focal process. Furthermore, we think that asymmetry is a more appropriate term for this situation than mismatch. We view the term mismatch as implying that there must be some optimum constituting a ‘match’, with a ‘mismatch’ describing when this optimum is not occurring (Cushing & Dickson 1977; Cushing 1990). This definition fits the case where mismatch is used in the climate change literature to describe when some interaction process was ‘matched’ at some point in time, but climate change has led to the development of a discrepancy (e.g. phenological mismatches). However, we believe that using mismatch to describe, for example, differences in thermal performance curves among species, generates confusion because: 1) it conflates multiple usages of the word mismatch, 2) what would often be a ‘match’ in terms of an optimum for one species is likely to be a ‘mismatch’ for the other species if they interact antagonistically, and 3) the optimal situation for one species (aka a ‘match’) may often be to be ‘mismatched’ in terms of, say, thermal optima (Smith & Amarasekare 2018; Casas Goncalves & Amarasekare 2021). If differences lead to downstream effects, we believe referring to this as an ‘asymmetry’ or ‘asymmetric effect’

provides a better term and forces one to specify, for example, exactly how differences in thermal performance are related to a focal process of interest.

Last, we note mismatches, such as phenological mismatches, may arise due to asymmetric climate change effects and can generate additional asymmetries in the framework we introduce below. For example, peak activity rates of predators and prey, such as birds and insects, may show differential responses to temperature generating a phenological mismatch (Reed *et al.* 2013; Damien & Tougeron 2019; Figure 1c). This phenological mismatch could then alter bird feeding rates through the asymmetric effects of peak activity changes in birds and insects on the abundance of insects experienced by the birds. Lowered feeding rates, in turn, may lead to asymmetric effects between birth and death rates in bird or insect populations thus generating yet another asymmetry (see below).

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

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

Our framework starts with the recognition that the most concerning *species*' responses to climate change generally come in the form of changes in population size through the population growth rate ( $r$ ). Thus, we focus on the population growth rate. All factors that feed into population growth within our framework are also rates. By definition, in a closed population, changes in growth rates are driven by changes in the demographic rates of births ( $b$ ) and deaths ( $d$ ). Thus, a **demographic asymmetry** arises when birth and death rates respond to some aspect of climate change (e.g., temperature) in a non-compensatory way. Demographic asymmetries form the top-level asymmetry and all other asymmetries must feed into the demographic asymmetry to affect population change.

Changes in birth rates arise through two general pathways. First, resource uptake ( $u$ ; of any form from light to prey) generates energy and biosynthetic metabolites that are allocated to reproduction, organismal growth, and maintenance (dashed lines in Figure 2). The allocation of resources to reproduction is a principal driver of birth rates, given variation in life history that determines offspring size, fecundity, and reproductive effort. Indirectly, birth rates at the population level are also determined by the timing of maturation based on development rate. Thus, organismal growth ( $g$ ) feeds into the rate of births at the population level by influencing the number of adults.

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

This minimal model represents a single species and can be broken into life stages if needed. It can also be connected to other species via connecting rates, such as the predator functional response, which, for example, would link the uptake rate,  $u$ , for the predator and the extrinsic death rate,  $d_e$ , for the prey (see Interspecific Asymmetries). Species interactions can connect two or more models in a variety of ways, depending on whether the interaction alters mortality, resource uptake, or allocation of resources. For example, a vector borne pathogen may be connected to both the vector and the host through the rate at which the vector bites hosts.

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

### **Intraspecific Asymmetries**

Within the rate-hierarchy framework, asymmetries affecting population growth rate can arise at multiple levels of biological organization. At the highest level are demographic asymmetries that directly change population growth rates (and therefore also mean fitness; Lande 1982). A **demographic asymmetry** arises when there is non-compensatory responses of birth or death rates to climate change. Population growth will be promoted when birth rates increase faster with climate change than death rates, while population declines will result when death rates increase faster with climate change than birth rates. Given the nonlinearity or unimodality of some climate change responses such as many thermal functions, population growth may increase or decrease with changes in climate. A commonly assumed form of the demographic asymmetry comes from Amarasekare and Savage (2012), in which birth rates are a unimodal function of temperature and death rates are an exponentially increasing function of temperature (Fig 3a). The

difference between these two functions generates the canonical left-skewed population growth rate thermal performance curve ( TPC; Ratkowsky *et al.* 1982, 1983; Amarasekare & Savage 2012) and a demographic asymmetry through the non-compensatory effects of temperature on the birth and death rates..

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

A **fecundity-maturation asymmetry** arises due to changes in the birth rate driven by non-compensatory changes in the upstream rates of resource allocation to reproduction and maturation (Fig 3b). This asymmetry can be seen through the lens of an expression describing how the birth rate is generated:

$$b = AF = A \frac{ur}{c}.$$

The total birth rate ( $b$ ) is the product of the number of mature adults  $A$  and the fecundity of individuals  $F$ . The number of mature adults in the population depends on the organismal growth rate ( $g$ ) (or inversely, maturation time). Faster development and shorter maturation times resulting from increases in resource acquisitions ( $u$ ) and allocations to growth ( $g$ ) will lead to a

subsequent increase in the number of reproducing adults, so one of the upstream contributors to  $b$  passes through growth to a change in  $A$ . Fecundity ( $F$ ) is determined by a combination of factors including resource allocations to reproduction ( $u_r$ ) and the costs per offspring ( $c$ ), following a typical Smith-Fretwell quantity-quality trade-off (Smith & Fretwell 1974). Thus, the other upstream contributor to  $b$  is straight from the uptake rate given the fraction of  $u$  allocated to reproduction. Given that the cost per offspring could also be climate-dependent, there are at least three ways in which birth rates change due to asymmetric effect of the upstream component rates.

A common example of potential maturation-fecundity asymmetries in ectotherms is the relationship between temperature, size at maturity, and fecundity. At cooler temperatures, ectotherms tend to grow slower, reach maturity at a larger size, and due to their larger size produce a larger number of eggs (Atkinson 1994; Roff 2001). Thus, birth rates may change with temperature because of the simultaneous changes in  $A$  and  $F$ . Whether or not these changes lead to a decrease in birth rates with temperature can be complex, depending on, for example, whether the relationship between size and fecundity itself is temperature dependent (Arendt 2011). In general, maturation-fecundity asymmetries could be difficult to detect if changes in maturation and fecundity counterbalance each other and only result in a demographic and life history shift in the population.

A **growth-maintenance asymmetry** arises due to changes in the death rate driven by non-compensatory changes in the growth rate ( $g$ ) and the rate of allocation to maintenance (Fig 3c). As with the fecundity-maturation asymmetry, the rate of allocation of resources to maintenance ( $u_m$ ) influences the likelihood of survival in concert with the rate of growth and

maturation that sets expected lifespan by setting the age and size at maturation. This asymmetry can be seen through the lens of an expression that clarifies how survival is generated:

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

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

For example, across ectothermic taxa, increases in environmental temperatures drive elevated maintenance metabolic rates, up to a point, influencing the cost of maintenance ( $c_m$ ), and correspondingly necessitate higher rates of resource allocation requirements for maintenance ( $u_m$ ). If not compensated for by changes in the uptake rate ( $u$ ), increasing metabolic rates will result in concurrent decreases in resource allocation to organismal growth ( $u_g$ ). Huey and Kingsolver (2019) proposed the “metabolic meltdown hypothesis” which, suggests that growth-maintenance asymmetries will frequently arise, given direct negative effects of climate change on resource and nutrient availability or indirectly by negative effects of higher temperatures on locomotion and foraging rates. This hypothesis is supported by empirical studies demonstrating combined negative effects of temperatures and resource availability on organismal and population growth rates (Brett *et al.* 1969; Thomas *et al.* 2017).

### **Interspecific Asymmetries**

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

#### *Predator-prey interactions*

Feeding rates connect predators and prey as they determine the uptake rate of the predator and influence the extrinsic death rate of the prey. We define a **predator-prey asymmetry** as the case when the foraging rate changes with climate due to the non-compensatory effects of upstream factors related to both the predator/consumer ( $x_c$ ) and prey/resource ( $x_r$ ) that respond to climate (Figure 4). As predation events depend on movement and encounters between predator and prey, the detection of prey by the predator, and the successful attack by the predator (Jeschke *et al.* 2002; DeLong 2021; Wootton *et al.* 2023), there are many ways in which climate change may alter the emergent foraging rate.

One of the earliest recognized drivers of climate change asymmetries are **phenological mismatches**. Predators and prey must be in the same area at the same time for predation to occur, and environmental factors like temperature may influence the likelihood of this co-occurrence, especially in highly seasonal habitats (Damien & Tougeron 2019). In a classic case

of phenological mismatch, differential changes in the timing of breeding activity of insectivorous Great tits (*Parus major*) and their caterpillar prey affects foraging rates of the birds (Reed *et al.* 2013). The migration of Great tits is triggered by daylength and temperature, but caterpillar phenology advances more quickly with warming than egg laying phenology of the birds (Reed *et al.* 2013; Burgess *et al.* 2018), resulting in reduced availability of prey during peak resource demand for the birds. As foraging rates depend on prey availability through the functional response, this disparity in timing lowers the foraging rates (a change in  $x_r$ ) and can also generate a demographic asymmetry for the birds by reducing reproductive rates and/or increasing death rates due to resource shortage. As phenological changes are widely documented with climate change, this may be a common source of climate change asymmetries.

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

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

(Aljetlawi *et al.* 2004; Pawar *et al.* 2012; Dell *et al.* 2014). A movement asymmetry may arise when predator foraging rates change due to the predator and prey having different thermal sensitivities of movement (i.e., upstream changes in  $x_c$  and  $x_r$ ; Dell *et al.* 2014). Such movement sensitivities to climate change may be due to differences in average searching velocities of predator relative to prey, but also may be caused by changes in activity patterns or attack or escape speeds. For example, Öhlund *et al.* (2015) showed how an asymmetry in the relationships

between temperature, pike attack speeds, and trout escape speeds generated an overall temperature dependence of attack rates of pike on trout. A specific form of the movement asymmetry can be caused by differences in thermy among predators and prey (Gibert *et al.* 2022), in which one species is an endotherm while the other is an ectotherm. In this scenario, the endotherm would show minimal change in searching velocity while the ectotherm would have a greater thermal sensitivity, creating a change in encounter rates that alters the foraging rate and potentially leads to a demographic asymmetry for both species.

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

### *Host-parasite interaction*

For a host-parasite interaction, the connection between species may or may not involve a connecting rate, and, given the diversity of types of host-parasite interactions, hosts and parasites may be connected in a variety of ways. For any kind of parasite that primarily draws off resources of the host (e.g., tick, tapeworm, etc.), the connection between the rate hierarchy of the host and the parasite would be directly through the two uptake rates (Figure 5). That is, the parasite gathers resources out of the host's resource stream, impacting the host's available resources. We thus draw an arrow toward the host's uptake rate from the parasite's uptake rate. The host's realized uptake rate, then, is generated by the interacting effects of their own resource gathering activity and the parasite's resource extracting behavior. In this way, an **uptake rate asymmetry** can arise due to the non-compensatory effects of host and parasite foraging. If warming, for example, increases the rate of resource uptake of a parasite more quickly than that of its host, there would be a net decline in the realized uptake rate of the host. This change in uptake rate would cascade up to host demography and also potentially feedback to alter the demography of the parasite. Further, a transfer of resources from host to parasite might be disproportionate or not depending on whether the fraction of resources passing through the gut varies with resource flow. A parasite that has an uptake rate that saturates with increasing flow through would have a different proportional effect on host resource assimilation, and emergence of an asymmetry would depend on whether or not host uptake rate was altered by climate change. Additionally, parasite induced anorexia or hyperphagy in its host (Hite & Cressler 2019; Hite *et al.* 2020) could also mediate an uptake rate asymmetry.

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

immune responses (Figure 5). As parasite pathogenicity and host immune responses can both be dependent on the environment (Wright & Cooper 1981; Thomas & Blanford 2003), environmental changes could lead to asymmetries that alter the death rate of the host. In sub-lethal infections, the presence of the endoparasite could necessitate increased host allocations to immune function, leading to fecundity-maturation or growth-maintenance asymmetries. In particular, all of these processes could be temperature dependent if the host's decision to tolerate or fight the endoparasite depends on temperature, or if the host is an ectotherm making uptake, allocation, and demographic processes temperature dependent.

For ectoparasites that are vectors (e.g. mosquitos), the additional player (vectored pathogen) generates new possible avenues of asymmetries (Figure 6). Here the biting rate would serve as a connecting rate between the host, pathogen, and vector. This is an expansion of the uptake rate asymmetry, as some form of 'biting' would be involved in any such host-parasite interaction. Thus, the biting rate could cause a demographic asymmetry by increasing reproduction of the vector, decreasing reproduction of the host, and increasing death rate of the host caused by pathogen transmission, and altering the states (susceptible or infected with pathogen carried by the vector) of individuals in the host population. . The biting rate is also a critical connecting rate determining the net reproductive rate ( $R_0$ ) of vectored pathogens themselves. A seminal study by Mordecai et al. (2013) makes clear how  $R_0$  is dependent on numerous upstream rates (e.g., vector development rate and competence), creating a wide range of potential asymmetries. As most of these upstream rates are dependent on climate, including temperature,  $R_0$  is temperature dependent as well (Mordecai *et al.* 2013, 2019).

### **Mutualistic interactions**

As for host-parasite and consumer-resource interactions, we can incorporate mutualistic interactions into the framework through a connecting rate or by connecting rates directly between the mutualists. How the players in the mutualism are connected is dependent on how the mutualism operates. For example, plants and their pollinators can be connected through a visitation rate that links the birth rate of the plant to the uptake rate of the pollinator (often through pollen or nectar consumption for the pollinator; Figure 7). This visitation rate is a downstream rate that could be affected by upstream features of the pollinator ( $x_{po}$ ) and the plant ( $x_{pl}$ ), such as pollinator energy demands or plant attractiveness. A protective mutualism, such as ant-acacia mutualisms, also might have a mutualism connecting rate that links uptake for the ants from resources provided by the acacia to the extrinsic death rate or uptake rate of the acacias as the ants prevent defoliation (Janzen 1966). Endosymbiotic mutualists may have similar or more complex relationships between connecting rates than other mutualisms. For example, the protist *Paramecium bursaria* hosts an algal *Zoochlorella* symbiont. The paramecium in this interaction receives sugars provided from algal photosynthesis while the paramecium both provides protection and nutrients for the algae (Karakashian 1963; Brown & Nielsen 1974). Thus, this system might be described by a mutualism connecting rate that links the uptake rate of the paramecium and the uptake rate and extrinsic death rate of the algae.

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

dependent. Given that mutualistic interactions generally involve connections to rates such as uptake rates and extrinsic death rates, the temperature dependence of mutualisms generated by asymmetric responses can potentially lead to changes that could scale up to a demographic asymmetry and population growth or decline. For example, in an experimental plant-pollinator system, increasing temperatures led to fewer flowers per plant and lower nectar volume, but higher nectar concentration (de Manincor *et al.* 2023). However, the net asymmetric effect of these changes with temperatures led to reduced visitation rates and shorter bee handling times with negative consequences for flower seed set under warmer conditions (de Manincor *et al.* 2023).

Under some circumstances, asymmetric climate change effects on mutualisms may shift these interactions along the so-called mutualism-parasitism continuum (Bronstein 1994; Johnson *et al.* 1997). For example, in the aforementioned *Paramecium bursaria-Zoochlorella* system, at high temperatures ‘ghost’ *Paramecium* without algal symbionts have higher fitness than *Paramecium* that contain *Zoochlorella* symbionts (Salsbery & DeLong 2018). A potential explanation for this is that the paramecia are mixotrophs that receive energy from both their algal symbionts and through bacterivory. At higher temperatures, bacterivory may lead to greater fitness for *Paramecium* without symbionts relative to those with symbionts because the energy gained from the algae at high temperatures is less than the potential energy that could be gained from bacteria. This is because the space within a cell is finite, generating a trade-off between allocating that space to algae or food vacuoles. In this case, changes in the relative potential benefits of bacterivory and photosynthates from the algae with temperature generate an asymmetric effect on uptake rates that switches the presence of algae from beneficial to detrimental. Given the potential for the costs and benefits of symbioses to be environmentally

dependent (Bronstein 1994; Johnson *et al.* 1997; Hoeksema & Bruna 2015; Cruz *et al.* 2023), asymmetric climate change effects may play a particularly important role in moving host-symbiont relationships along the mutualism-parasitism continuum.

### **Asymmetries and Indirect Interactions**

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

### **Asymmetries, Communities, and Ecosystems**

Until now, we have focused our discussion of asymmetries around effects of climate change that impact the demographics and the growth or decline of populations. For communities and ecosystems composed of these species, however, asymmetric effects of climate change on species growth rates can propagate to yet another level to cause **community** or **ecosystem**

**asymmetries.** These asymmetries occur when there are non-compensatory changes among the constituent species that shape community- or ecosystem-level rates or properties are themselves functions of the rates of change of constituent species in response to climate change that are non-compensatory (Figure 8). Defining community and ecosystem asymmetries allows us to apply our framework to potentially inform predictions about consequences of species-specific changes for aggregate responses across species and ecosystem functioning. As the biodiversity-ecosystem functioning and climate change literature have made clear, species contributions to ecosystem functioning are rarely equal (Huston 1997; Tilman *et al.* 1997), and climate change impacts on species within a community are likely to vary dictating the cases of climate change ‘winners’ and ‘losers’ (Kimball *et al.* 2010; Somero 2010; Sorte *et al.* 2013; Clucas *et al.* 2014). Therefore, barring a compensatory mechanism such as the portfolio effect in which interspecific diversity in responses buffers community properties from change due to averaging across species (Doak *et al.* 1998; Tilman *et al.* 1998), asymmetric effects of climate change on community and ecosystem-level properties such as ecosystem functioning are likely to be common.

### **Conclusions and Future Prospects**

Here we provide a framework for understanding how asymmetric responses to climate change in rates within and among species combine to impact populations, communities, and ecosystems. Although most of the examples we used throughout have focused on asymmetric responses to mean temperatures, we believe that this framework is equally applicable to asymmetric responses in other variables likely to be affected by climate change. For example, in a study of Sonoran Desert plant community change over 25 years, Kimball *et al.* (2010) showed how later winter rains in colder conditions alter germination rates across annual plants leading to community change. For each plant species, their germination response to the timing of

precipitation could be viewed as altering birth rates and causing demographic asymmetries that led to declines or increases in population growth. Our focus on temperature is largely a reflection of the fact that this has been the most widely studied component of climate change, particularly with regard to asymmetries. Expanding research to include asymmetric responses to a greater number of changing climatic features, including the variance of those features (Vasseur *et al.* 2014; IPCC 2021), will provide a more holistic view of how climate change is likely to influence populations.

One caution about directly interpreting how an asymmetry at one level influences population growth or decline that is made apparent by the framework is that there is the potential that an asymmetry at one level can be canceled out by another rate response to climate change. For example, using data across 35 species of birds, McLean *et al.* (2016) showed that warmer temperatures were associated with earlier lay dates and earlier lay dates were associated with higher reproductive rates. However, despite these changes suggesting higher reproduction rates with higher temperatures, they found no relationship between temperature and population growth, suggesting that some negative effect of temperature must be compensating for the increase in reproduction (McLean *et al.* 2016). We believe that the framework herein may be particularly useful in helping to identify where compensating asymmetric effects might occur and therefore provide target rates to be measured to determine whether a particular asymmetry is likely to scale to influence the population. Another possible way in which asymmetries could be canceled is through feedbacks that are not currently incorporated into the minimal rate hierarchy model. For example, consider a predator-prey asymmetry in which climate change increases the predator feeding rate, increases prey extrinsic mortality, and decreases the prey population growth rate and density. As predator feeding rates are increasing functions of prey densities,

lower prey densities could feedback to lower predator feeding rates or could lead to reduced density dependence in the prey which could alter birth or death rates. Although this increases the complexity of understanding asymmetric climate change impacts, applying the framework to think through these possibilities makes clear where these feedbacks might emerge, how they might ultimately affect population growth rates, and facilitates the identification of rates researchers should focus on measuring to understand the population effects of asymmetric climate change responses.

One impetus for the development of the framework herein was that there is often a disconnect in the literature between climate change responses used to infer asymmetries and their effects on systems and the climate change response itself. For example, given the ubiquity of thermal performance curves, differences among species in thermal performance are often used to suggest the existence of asymmetries that will impact the system (Cohen *et al.* 2017; Gsell *et al.* 2023; Meehan & Lindo 2023). Yet, applying the framework here, it becomes clear that the relevance of differences in thermal performance curves for asymmetries is dependent on what metric of performance is being compared among species, where in the rate hierarchy the asymmetry of interest occurs, and how ‘performance’ translates to the downstream rate of interest. For example, in seeking to explain the temperature dependence of chytrid prevalence in frogs, Cohen *et al.* (2017) performed an experiment comparing frog preferred temperatures, chytrid growth rates in culture, and chytrid growth rates on frogs. Although chytrid growth rates on frogs are indeed likely to be a determinant of prevalence, applying the framework here to this problem would suggest that the temperature dependence of several other processes should also be considered, such as the susceptibility of the frogs to infection, chytrid spore survival, etc. If the temperature dependence of all of these processes are well-correlated, these extra

considerations may not be necessary, but, in general, this will be an assumption that requires testing. As another example, a commonly measured potential climate change response in the literature is the relationship between sprint speed and temperature (Hertz *et al.* 1983; Berkum 1988), which is often taken to be correlated with overall organismal performance. However, in our framework, sprint speed is likely to be a low-level rate on the hierarchy that could, for example, alter feeding rates depending on how sprint speeds, predator attack or prey escape rates, and their relationships with temperature combine (Öhlund *et al.* 2015). However, taking into account all of the other possible temperature responses in the rate hierarchy, it becomes clear that sprint speed responses need not be directly correlated with the overall relationship between temperature and population growth (fitness) at the highest level of the hierarchy. Overall, we hope that this framework can help identify what rates are the important ones to measure for a particular process of interest and for making inference on how or if those rates are likely to scale to bring about population changes.

Throughout, we also have assumed that the climate change responses that generate asymmetries and their potential impacts are constant. However, if individuals differ in their climate responses, this creates the opportunity for natural selection that could cause the evolution of responses and lead to an eco-evolutionary feedback, which then alters the asymmetry and its likely consequences. This also highlights the potential role that plasticity may play in moderating the effects of climate change response asymmetries. As mentioned above, feedback effects from asymmetric climate change responses could alter the environments to elicit feedback or phenotypic plasticity that counteract or generate new asymmetries. Such changes are likely to depend on the specifics of systems (e.g. is there heritable variation in a particular climate change response involved in an asymmetry?), but studies focusing on these processes will provide

important information on how organisms might adapt to the consequences of climate change response asymmetries and climate change more generally.

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

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# Figures

## Figure 1

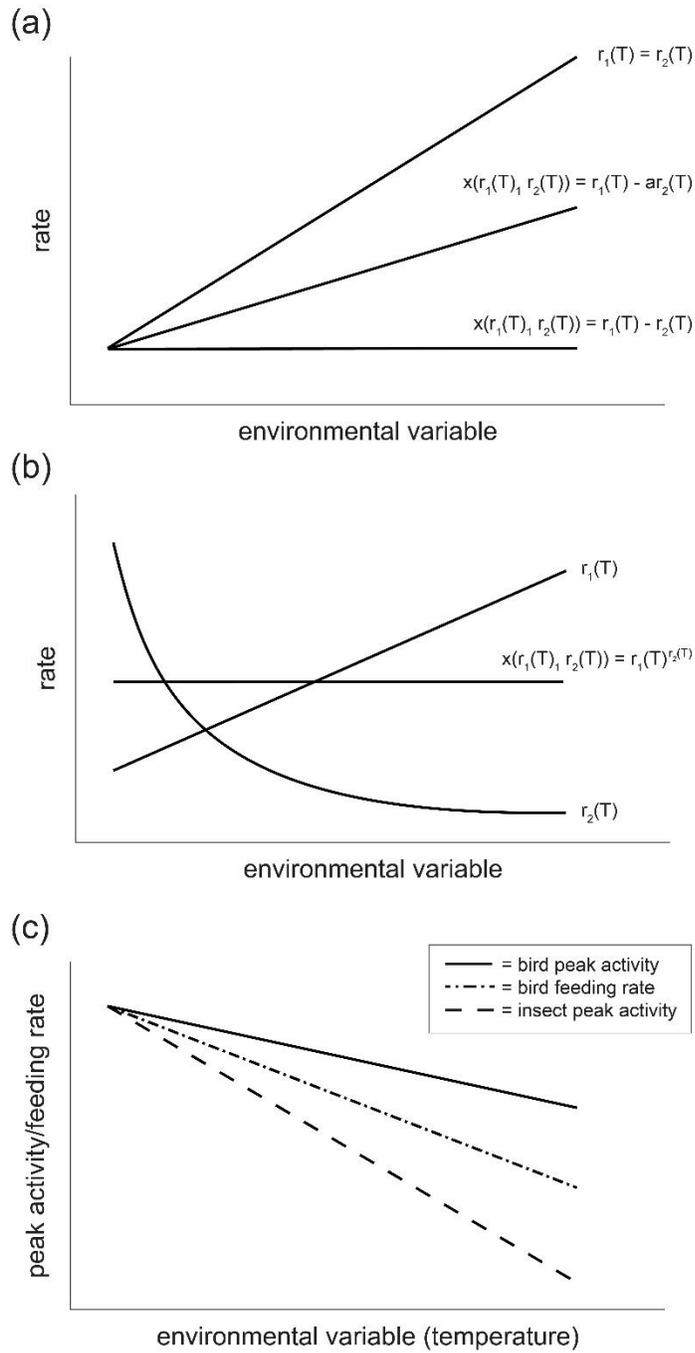
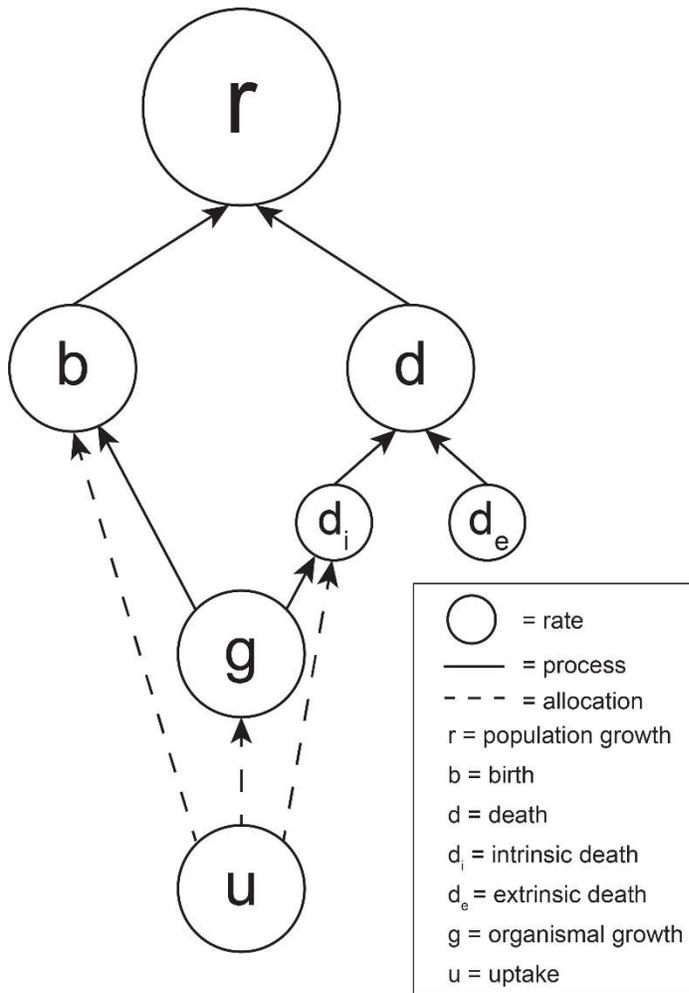


Figure 2



**Figure 3**

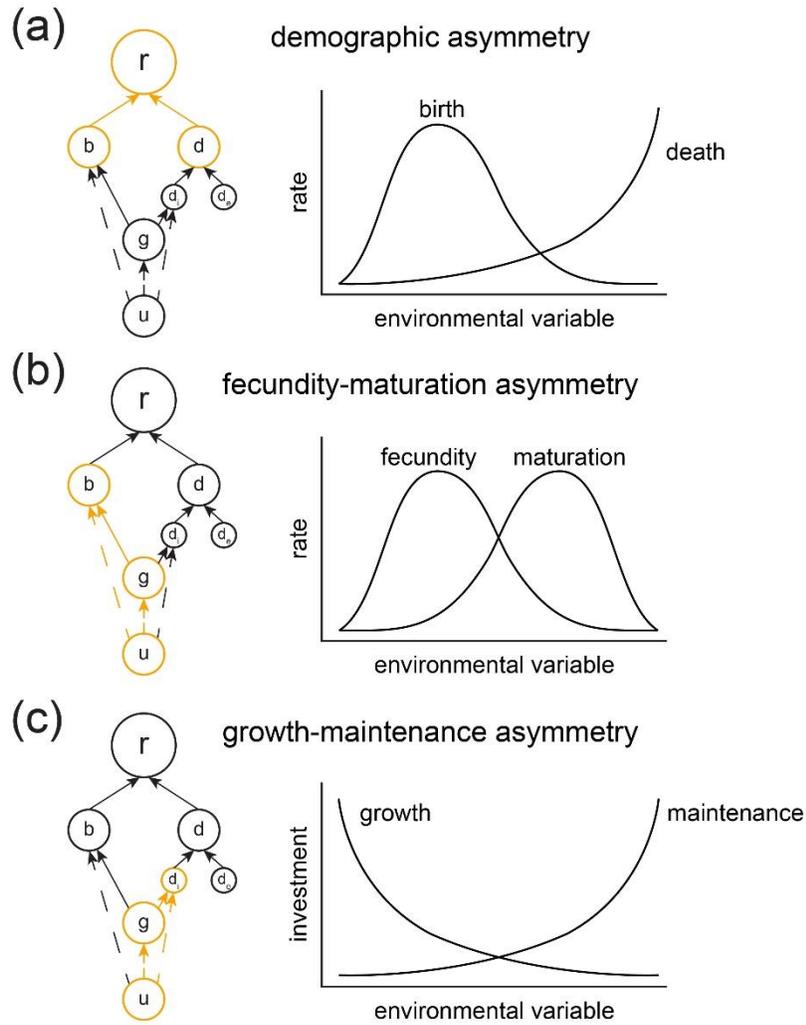


Figure 4

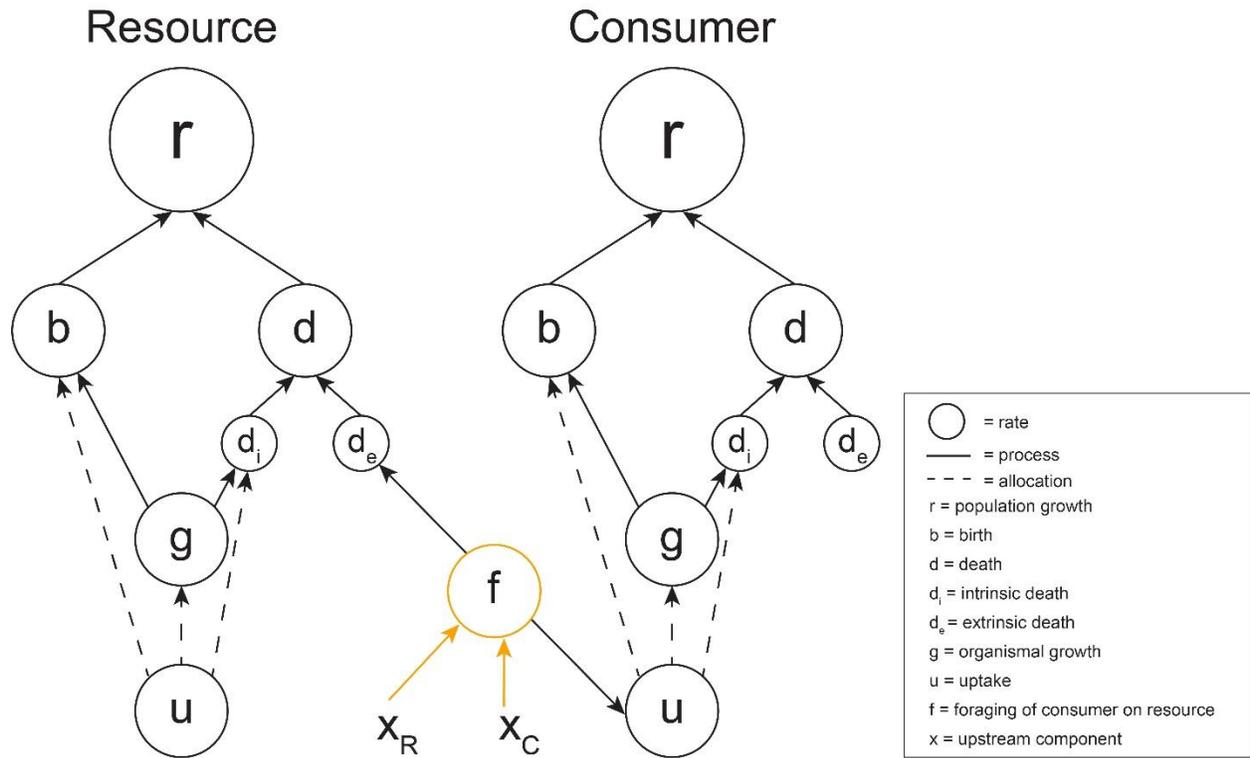
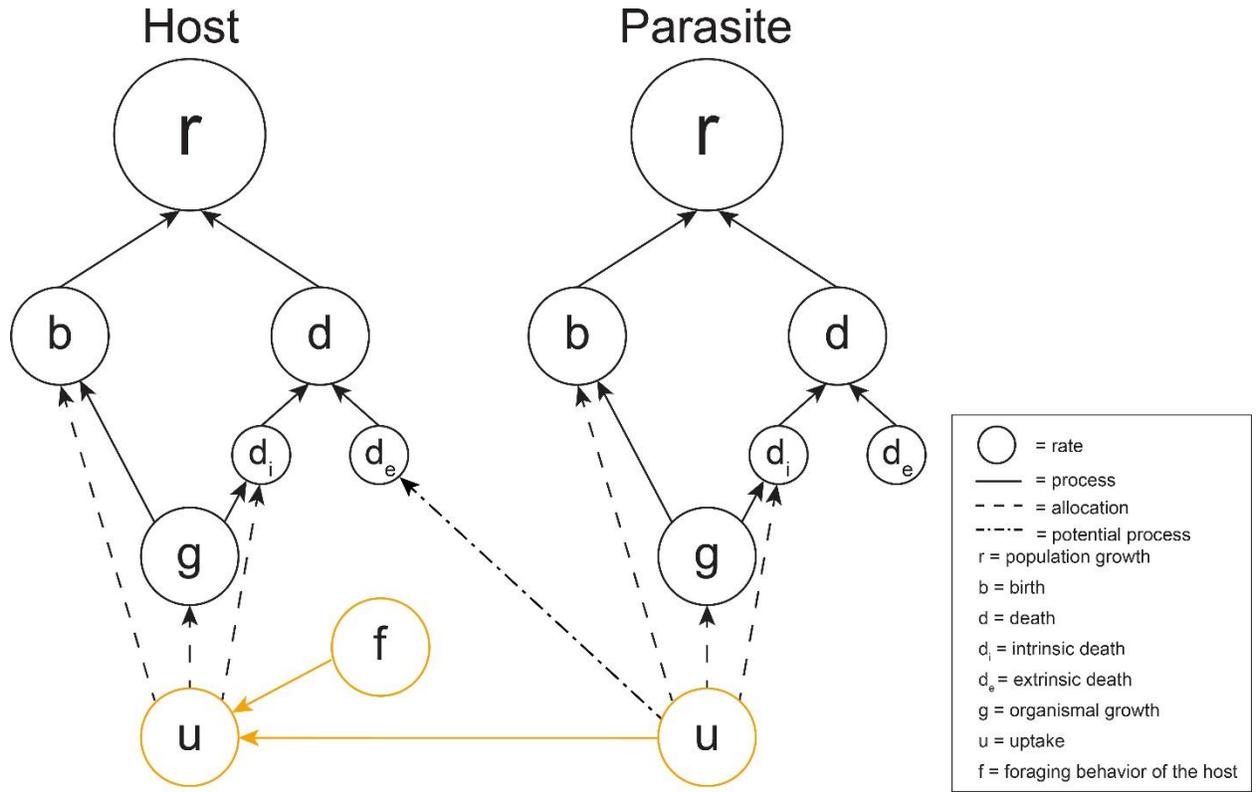


Figure 5



**Figure 6**

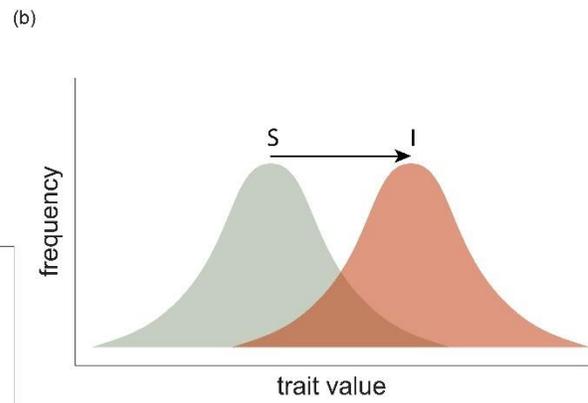
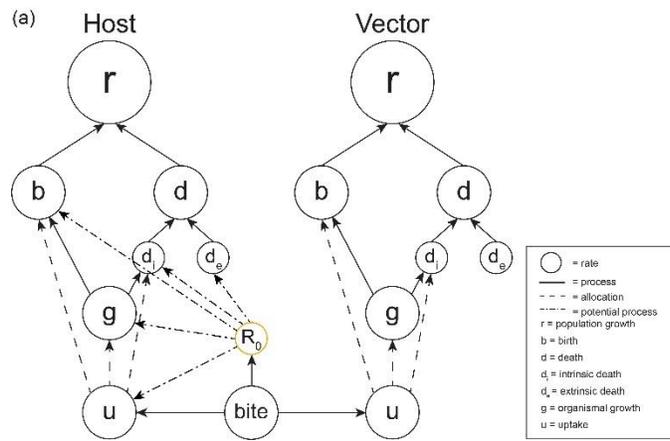
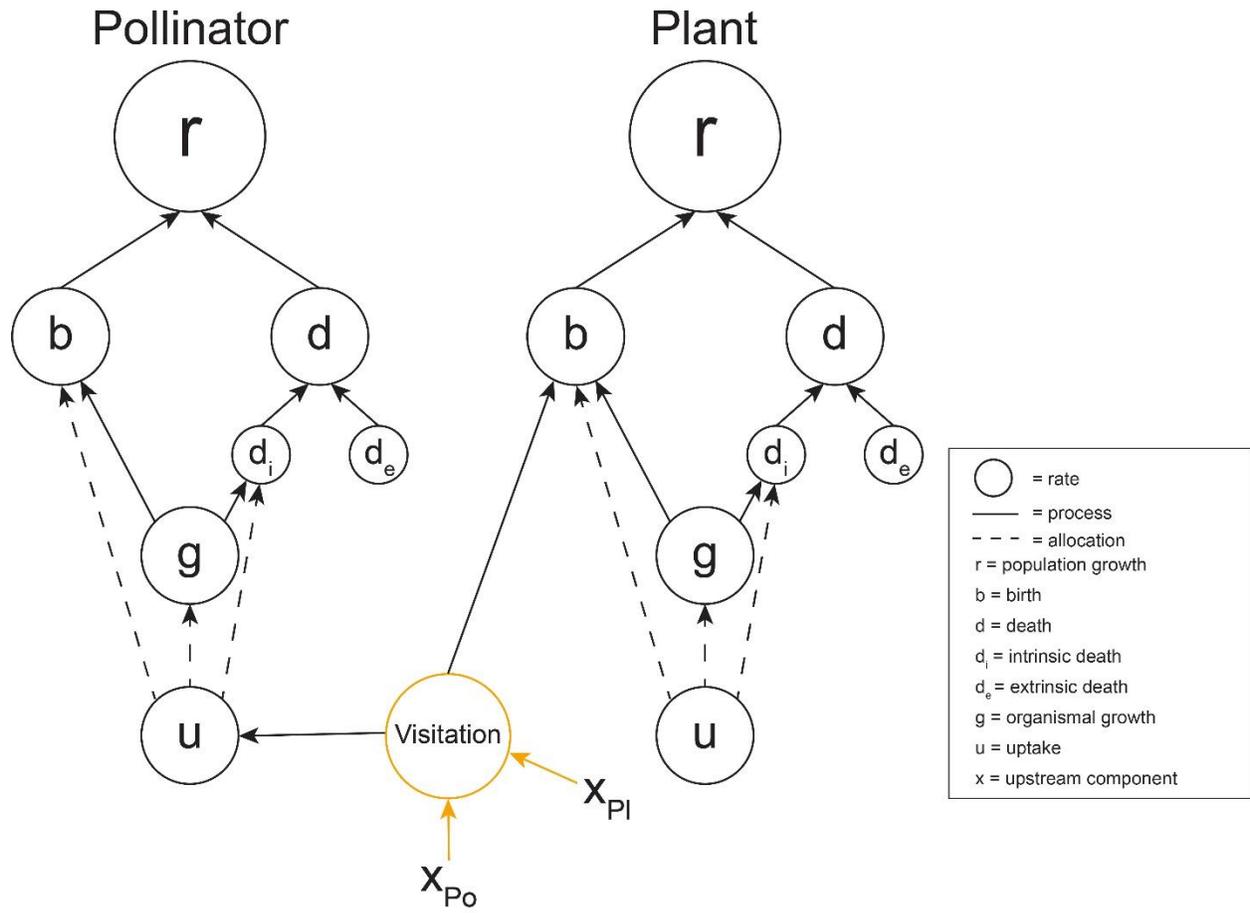
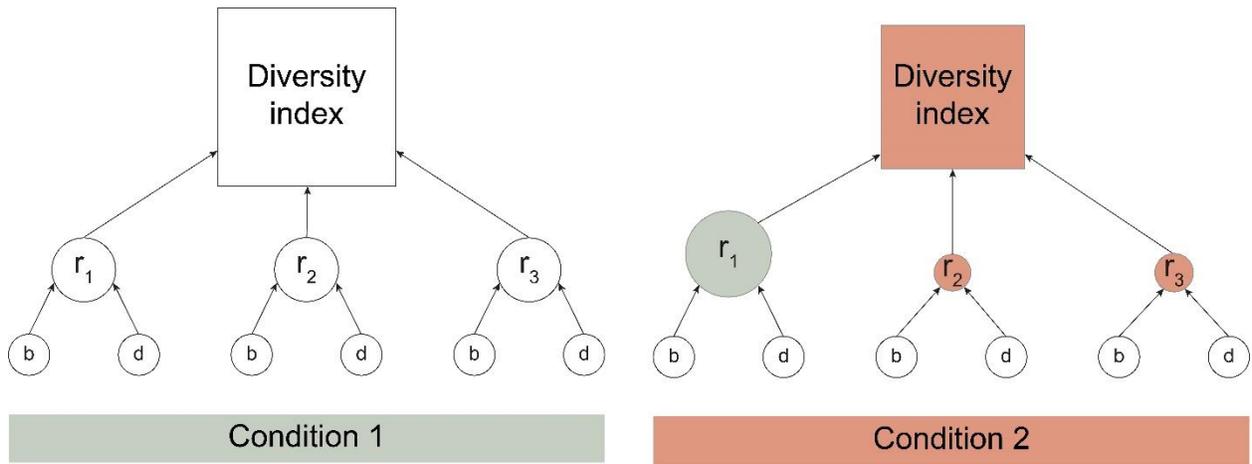


Figure 7



**Figure 8**



## Figure Legends

**Figure 1.** Conceptual representations of asymmetries. We define asymmetric effects of climate change as changes in a focal rate due to changes in the effects of components determining that rate with climate change. This is because components ( $r_i$ 's) can change in same manner with an environmental variable such as temperature ( $T$ ) and, yet, may or may not have an effect on the focal rate ( $x$ ) depending on how they combine to determine  $x$  (a). Components can also change in different ways and yet have no effect on the focal rate (b). Climate mismatches, such as phenotypic mismatches, can also lead to asymmetric effects. For example, changes in the timing of bird and insect peak activity with temperature can generate an asymmetric effect on the abundance of insects experienced by birds leading to decreased bird feeding rates (c).

**Figure 2.** A single-species depiction of our framework for understanding asymmetric responses to climate change and their impacts on populations. Each circle represents a rate, and arrows between circles show how rates influence one another. Solid lines represent direct determinations of rates and dashed lines represent allocations of resources to different rates. The top rate  $\mathbf{r}$  is the rate of change of the focal population (population growth rate). This is determined by the birth rate  $\mathbf{b}$  and the death rate  $\mathbf{d}$ . The birth rate is determined by average organismal growth rates in the population ( $\mathbf{g}$ ) and energy allocation to reproduction  $\mathbf{b}$  from resource uptake rates  $\mathbf{u}$ . Death rates are determined by both intrinsic death rates  $\mathbf{d}_i$  and extrinsic death rates  $\mathbf{d}_e$ . Intrinsic death rates are determined by average organismal growth rates in the population and allocation of energy from resource uptake. Last, organismal growth rates  $\mathbf{g}$  are determined by allocation of energy from resource uptake.

**Figure 3.** A graphical depiction of demographic (a), fecundity-maturation (b), and growth-maintenance (c) intra-specific asymmetries. Upstream rates directly contributing to each asymmetry within our hierarchy are highlighted in yellow. Demographic asymmetries are the highest level asymmetry and are characterized by non-compensatory changes in birth (*b*) and death (*d*) rates in response to environmental change. Fecundity-maturation and growth-maintenance asymmetries occur at the lower levels of our framework and arise due to resource allocation trade-offs between organismal growth and either reproduction or maintenance as climate changes and relationships between organismal growth and birth or death rates.

**Figure 4.** The rate hierarchies of a resource (R) and consumer (C) are connected by the foraging rate (f). The foraging rate connects the uptake rate of the consumer and the extrinsic death rate of the resource. Varied asymmetric climate change effects can alter the foraging rate which can lead to cascading effects up the resource and consumer rate hierarchies to influence their population growth rates.

**Figure 5.** Example of a host-parasite interaction in which the rate hierarchy of the parasite is connected to the host rate hierarchy through its uptake rate reducing the uptake rate of the host. Asymmetric effects of climate change on host and parasite uptake rates could potentially filter up the rate hierarchies to alter population growth. Some parasites also may have direct effects on the extrinsic death rate, for example, through the development of toxins or direct mortality of cells.

**Figure 6.** Example rate hierarchies for a host and vector of a pathogen. The uptake rates of the host and vector are connected via the biting rate of the vector. This biting rate is also connected

to the  $R_0$  of the pathogen (the basic reproduction number). In turn,  $R_0$  alters the proportion of the population that is infected by the pathogen and potentially a variety of different rates in the population depending how infection shifts rates between infected and non-infected individuals (b).

**Figure 7.** Example of a plant-pollinator interaction in which the visitation rate of the pollinator to flowers connects the uptake rate of the pollinator to the birth rate of the plant. Asymmetric climate change effects on visitation rates thus can alter pollinator uptake rates and plant birth rates potentially cascading up to have demographic consequences.

**Figure 8. Demographic asymmetries among species within communities can lead to community and ecosystem asymmetries.** As climate change alters environmental conditions (Condition 1 to Condition 2), demographic asymmetries within species can lead to changes in population growth rates among species comprising a community. Community- or ecosystem-level attributes that are dependent on contributions from component species, such as diversity indices, may then experience asymmetric climate change effects due to among-species shifts.

## Text Boxes

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

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

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

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