

# Toward a Mechanistic Understanding of Thermal Niche Partitioning

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**ABSTRACT:** We develop a theoretical framework to elucidate the mechanistic basis of thermal niche partitioning in ectotherms. Using a food web module of two consumers competing for a biotic resource, we investigate how temperature effects on species' attack and mortality rates scale up to population-level outcomes of coexistence and exclusion. We find that differences between species in their competitive effects ultimately arise from asymmetries generated by the nonlinear nature of the temperature response of mortality: cold-adapted species and thermal specialists limit themselves more strongly than they limit their warm-adapted and generalist competitors. These asymmetries become greater as seasonal temperature fluctuations increase, generating latitudinal variation in coexistence patterns and priority effects. Characterizing species' thermal niches in terms of mechanistic descriptions of trait responses to temperature allows us to make testable predictions about the population-level outcomes of competition based solely on three fundamental—and easily measurable—quantities: attack rate optima, response breadths, and temperature sensitivity of mortality. We validate our framework by testing its predictions with data from an insect host-parasitoid community. Simply by quantifying the three basic quantities, we predict that priority effects cannot occur in this system, which is borne out by population-level experiments showing that the outcome of competition does not depend on initial conditions. More broadly, our framework can predict the conditions under which exotic invasive species can exclude or coexist with native biota as well as the effects of climate warming on competitive communities across latitudinal gradients.

**Keywords:** coexistence, competition, mutual invasibility, priority effects, temperature variation, thermal niches.

## Introduction

Differences between species in their responses to abiotic variation is a crucial prerequisite for coexistence via tempo-

ral niche partitioning. Because abiotic conditions favorable to a given species are not favorable to its competitors, species experience only weak interspecific competition when they are rare and mostly intraspecific competition when they are abundant. This concentration of intraspecific competition relative to interspecific competition allows stable coexistence (Chesson 2000).

Most previous theory has focused on how temporal niches concentrate intraspecific relative to interspecific competition at the population level (Armstrong and McGehee 1980; Chesson 2000). Few, if any, studies have focused on the mechanisms that cause species to differ in their responses to abiotic variation and how these differences generate temporal patterns of resource exploitation (niches). A mechanistic understanding of temporal niche partitioning begins with the contact point between the environment and the population: the phenotypic attributes (traits) of individual organisms (e.g., birth, mortality, and resource consumption rates). We need to determine how trait responses to abiotic variation collectively affect fitness (per capita growth rate), the metric that translates individual-level processes to population-level outcomes. This is important because the ability of a given species to increase when rare in the presence of a competitor is ultimately determined by the degree to which its trait responses differ from those of the competitor. The more accurately we can assess these individual-level differences, the more correctly we can predict the population-level outcomes of coexistence and competitive exclusion. Here we develop a trait-based mathematical framework to address this issue. We focus on temperature as the axis of abiotic variation, not least because the vast majority of the biodiversity on the planet consists of ectotherms, species whose body temperature depends on the environmental temperature. We use a food web module, two consumers competing for a biotic resource, that constitutes a fundamental building block of most real communities.

Most previous theory on temperature effects on species interactions has focused on pairwise consumer-resource in-

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teractions (Vasseur and McCann 2006; Amarasekare 2015) or tritrophic food chains (Binzer et al. 2012). The studies investigating temperature effects on competition have mostly utilized the phenomenological Lotka-Volterra approach, which does not consider resource population dynamics (Urban et al. 2012). We adopt the mechanistic approach, based on the  $R^*$  rule (Tilman 1982), of modeling consumer species engaged in exploitative competition for a resource species that has its own dynamics. We derive mutual invasibility criteria in terms of trait-level differences between species, which allows us to predict the conditions under which coexistence and exclusion occur based solely on the key parameters of trait responses (e.g., thermal optima and response breadths). We test model predictions with data from a well-studied insect host-parasitoid community.

### Mathematical Framework

We consider the simplest model of a food web: two consumer species engaging in exploitative competition for a biotic resource. The dynamics of such a community are given by

$$\begin{aligned}\frac{dR}{dt} &= (b(T) - d_r(T))R(1 - q(T)R) \\ &\quad - a_1(T)RC_1 - a_2(T)RC_2, \\ \frac{dC_1}{dt} &= e_1a_1(T)RC_1 - d_1(T)C_1, \\ \frac{dC_2}{dt} &= e_2a_2(T)RC_2 - d_2(T)C_2,\end{aligned}\tag{1}$$

where the state variables  $R$ ,  $C_1$ , and  $C_2$  depict, respectively, the abundances of the resource, consumer 1 and consumer 2. All life-history and consumption traits are explicitly temperature dependent. The functions  $b(T)$  and  $d_r(T)$  depict the temperature responses of resource birth and mortality rates, and  $q(T)$  depicts the temperature dependence of resource self-limitation. The functions  $a_i(T)$  and  $d_i(T)$  ( $i = 1, 2$ ) depict the temperature responses of the consumers' attack and mortality rates. The parameter  $e_i$  depicts the conversion efficiency of consumer  $i$ . Conversion efficiencies are typically temperature independent due to the underlying stoichiometric properties (Peters 1983; Custer 2005). In the absence of evidence that conversion efficiency changes systematically with temperature (Uszko et al. 2017), we follow previous studies (Vasseur and McCann 2006; Binzer et al. 2012; Amarasekare 2015; Uszko et al. 2017) in considering it to be temperature independent. We consider the two consumers as exhibiting type I functional responses (i.e., per capita consumption rate increases linearly with resource density). We do so because we want to understand the circumstances under which temperature variation alone can allow consumer

coexistence in the absence of intrinsically driven consumer-resource fluctuations (Armstrong and McGehee 1980) that arise when consumers exhibit type II functional responses (i.e., per capita consumption rate increases with resource density at a decelerating rate; Holling 1959).

We begin our analysis with a mechanistic description of the temperature responses of species' traits. We briefly present the previously known results for consumer coexistence in a constant environment. We derive analytical expressions for mutual invasibility criteria in terms of the characteristics of the thermal regime (mean habitat temperature and the amplitude of seasonal fluctuations) and differences between species' in their responses to the thermal regime. Importantly, we characterize species' differences in terms of the key parameters of their trait responses. As we illustrate below, this approach yields testable predictions about mutual invasibility that are framed entirely in terms of measurable trait parameters.

### Temperature Responses of Species' Traits

In this section, we provide mechanistic descriptions of trait responses that constitute key components of the dynamical model (eq. [1]). A defining feature of ectotherm traits is that they exhibit plastic responses to temperature: when the environmental temperature changes, the trait response changes accordingly. These individual-level phenotypic responses, called reaction norms (Roff 1992), arise from temperature effects on the underlying biochemical processes (e.g., reaction kinetics, hormonal regulation; Johnson and Lewin 1946; Sharpe and DeMichele 1977; Schoolfield et al. 1981; Nijhout 1994; Van der Have and de Jong 1996; Van der Have 2002; Ratkowsky et al. 2005; Kingsolver 2009; Kingsolver et al. 2011). Briefly, temperature effects on biochemical rate processes (e.g., reaction kinetics and enzyme inactivation) give rise to trait responses that are monotonic or left skewed. Mortality and maturation rates exhibit this type of response. Temperature effects on biochemical regulatory processes (e.g., neural and hormonal regulation; Nijhout 1994; Hochachka and Somero 2002; Long and Fee 2008) involve negative feedback; that is, rate processes on the left- and right-hand sides push the system toward an intermediate optimum. These yield trait responses that are unimodal and symmetric (e.g., Gaussian). Reproductive and resource consumption rates exhibit this type of response.

Importantly, the nature of the biochemical-level responses to temperature are conserved across ectotherm taxa (Johnson and Lewin 1946; Sharpe and DeMichele 1977; Schoolfield et al. 1981; Nijhout 1994; Van der Have and de Jong 1996; Van der Have 2002; Ratkowsky et al. 2005), yielding trait responses at the phenotypic level whose qualitative nature (e.g., monotonic, unimodal) is also conserved across taxa. This is confirmed by several large-scale data analyses

(Englund et al. 2011; Kingsolver et al. 2011; Amarasekare and Savage 2012; Dell et al. 2016). This generality allows us to incorporate mechanistically derived temperature response functions, derived from first principles of thermodynamics, into our dynamical model of consumer-resource interactions (eq. [1]), yielding a trait-based framework that applies broadly across ectotherm taxa, habitat, and latitude.

*Temperature Response of Mortality.* Per capita mortality rate of all ectotherms (see references in Gillooly et al. 2002) increases monotonically with temperature according to the Boltzmann-Arrhenius relationship (Van der Have and de Jong 1996; Gillooly et al. 2001, 2002; Savage et al. 2004):

$$d(T) = d_{T_R} e^{A_d(1/T_R - 1/T)}, \quad (2)$$

where  $d$  is the mortality rate at temperature  $T$  (in kelvins),  $d_{T_R}$  is the trait value at a reference temperature (typically 24°–25°C; Sharpe and DeMichele 1977; Schoolfield et al. 1981), and  $A_d$  is the Arrhenius constant, which quantifies how fast the mortality rate increases with temperature.

*Temperature Responses of Birth and Attack Rates.* A large number of studies spanning invertebrates, fish, and lizards show that the per capita birthrate exhibits a symmetric, unimodal response to temperature (e.g., Dreyer and Baumgartner 1996; Carriere and Boivin 1997; Morgan et al. 2001; Dannon et al. 2010; Hou and Weng 2010; Jandricic et al. 2010; Amarasekare and Savage 2012; Dell et al. 2016). A similarly comprehensive data analysis of resource consumption rates in a range of ectothermic taxa (Englund et al. 2011; Amarasekare 2015) show that the per capita attack rate exhibits a qualitatively similar response. Both are well described by a Gaussian function,

$$a(T) = a_{T_{opt}} e^{-(T - T_{opt})^2 / 2s_a^2}, \quad (3)$$

where  $T_{opt}$  is the temperature at which the attack (birth) rate is maximal ( $a_{T_{opt}}$ ) and  $s_a$  depicts the response breadth, the temperature range over which the species can reproduce or exploit resources.

*Temperature Response of Resource Self-Limitation.* Here we describe the temperature response of resource self-limitation ( $q(T)$ ). The consumer species limit themselves indirectly through their effects on resource abundance, the strength of which, as we show below, is determined by the temperature responses of their attack and mortality rates. Temperature effects on resource self-limitation can be monotonic or unimodal (Savage et al. 2004; Amarasekare and Coutinho 2014; Amarasekare 2015). When the strength of competition increases with increasing temperature, as is the case when increasing activity levels increase the per individual demand for resources,  $q(T)$  is given by the

Boltzmann-Arrhenius relationship (eq. [2]). When competition is strongest at temperatures optimal for reproduction, as is the case when the demand for resources is most intense during periods of peak reproductive activity (Amarasekare and Coutinho 2014; Amarasekare 2015),  $q(T)$  is given by a Gaussian function (eq. [3]).

Having provided mechanistic descriptions of trait responses to temperature, we can now proceed to derive the criteria for mutual invasibility, that is, the conditions under which each consumer species can increase from initially small numbers when its competitor is at equilibrium with the resource. Starting with the well-known results for a constant thermal environment ( $R^*$  rule), we proceed to derive mutual invasibility criteria for seasonally varying environments.

#### *Consumer Coexistence in the Absence of Temperature Variation*

When consumer species exhibit linear (type I) functional responses, the  $R^*$  rule operates and the species that can maintain itself at a lower resource level excludes the other (see app. A for details; apps. A–G are available online). Dependence of species' traits on temperature does not alter this outcome if the thermal environment is constant; that is, there are no fluctuations around the mean habitat temperature.

#### *Consumer Coexistence in the Presence of Temperature Variation*

Previous theory tells us that consumers that cannot coexist in a constant environment can do so in a variable environment, provided they are sufficiently different in their responses to temporal environmental variation (Armstrong and McGehee 1980; Chesson 2000). However, determining whether species' responses are sufficiently different requires that we understand how they differ in the first place. This requires understanding how temperature affects the traits of individual organisms. Our novel contribution is to elucidate how the population-level differences between species, which are expressed in terms of their per capita growth rates (fitness), arise from differences in their trait responses. This mechanistic representation allows us to predict the population-level outcomes of competition based solely on species' trait differences.

#### *General Criteria for Mutual Invasibility*

We derive mutual invasibility criteria in a seasonally varying environment when species' traits are explicit functions of temperature (as described above). Each consumer spe-

cies can increase when rare if its per capita growth rate, when averaged over the year, is positive; that is,

$$\frac{1}{\tau} \frac{dC_i}{dt} \frac{1}{C_i} = \frac{1}{\tau} \int_0^\tau e_i a_i(T(t)) \overline{R_{C_j}} - d_i(T(t)) dt > 0, \quad (4)$$

$$i, j = 1, 2, \quad i \neq j,$$

where  $T(t)$  denotes the seasonal temperature regime experienced by the community,  $\tau = 365$  days, and  $\overline{R_{C_j}}$  is the average resource abundance set by consumer  $j$  (equivalent to  $R^*$  in a constant thermal environment; app. A).

Importantly, because each consumer's growth rate is a linear function of its abundance (i.e.,  $dC_i/dt$  is linear in  $C_i$ ),

$$\overline{R_{C_j}} = \frac{d_j(T(t))}{e_j a_j(T(t))},$$

provided the community experiences a predictably varying thermal environment (e.g., mean annual temperature and the amplitude of seasonal fluctuations remain approximately constant over time) in which consumer abundances return to their original values after a period of 1 year (app. A).

Now we can specify the mutual invasibility criteria in terms of the  $R^*$  rule in a temporally varying environment:

$$\frac{1}{\tau} \int_0^\tau e_i a_i(T(t)) \frac{d_j(T(t))}{e_j a_j(T(t))} - d_i(T(t)) dt > 0, \quad (5)$$

which, after some rearrangement (see app. B for a detailed derivation), gives us

$$\frac{\int_0^\tau [e_i a_i(T(t)) / e_j a_j(T(t))] d_j(T(t)) dt}{\int_0^\tau d_i(T(t)) dt} > 1. \quad (6)$$

The next step is to separate terms that are temperature independent and move them to the right-hand side. To do this, let

$$d'_i(T) = \frac{d_i(T)}{d_{i_{T_{\text{opt}}}}}$$

and

$$a'_i(T) = \frac{a_i(T)}{a_{i_{T_{\text{opt}}}}}.$$

Then,

$$\frac{\int_0^\tau a'_i(T(t)) [d'_j(T(t)) / a'_j(T(t))] dt}{\int_0^\tau d'_i(T(t)) dt} > \frac{e_j a_{j_{T_{\text{opt}}}} d_{i_{T_{\text{opt}}}}}{d_{j_{T_{\text{opt}}}} e_i a_{i_{T_{\text{opt}}}}}. \quad (7)$$

Let

$$\frac{d_{i_{T_{\text{opt}}}}}{e_i a_{i_{T_{\text{opt}}}}} = R_{i_{T_{\text{opt}}}} \quad (i = 1, 2),$$

where  $R_{i_{T_{\text{opt}}}}$  is the equilibrium resource abundance set by consumer species  $i$  ( $i = 1, 2$ ) at its physiologically optimal

temperature. Now we can restate mutual invasibility criteria as

$$\frac{\int_0^\tau a'_i(T(t)) [d'_j(T(t)) / a'_j(T(t))] dt}{\int_0^\tau d'_i(T(t)) dt} > \frac{R_{i_{T_{\text{opt}}}}}{R_{j_{T_{\text{opt}}}}}. \quad (8)$$

Equation (8) specifies the invasion criterion for a given consumer species. We can combine the criteria for the two species to obtain a single inequality,

$$\frac{\int_0^\tau d'_2(T(t)) dt}{\int_0^\tau a'_2(T(t)) [d'_1(T(t)) / a'_1(T(t))] dt} < \frac{R_{1_{T_{\text{opt}}}}}{R_{2_{T_{\text{opt}}}}} \quad (9)$$

$$< \frac{\int_0^\tau a'_1(T(t)) [d'_2(T(t)) / a'_2(T(t))] dt}{\int_0^\tau d'_1(T(t)) dt},$$

which provides the sufficient condition for mutual invasibility.

In order for the inequality in equation (9) to hold, the leftmost expression has to be less than the rightmost expression. This gives us the necessary condition for mutual invasibility:

$$\frac{\int_0^\tau d'_2(T(t)) dt}{\int_0^\tau a'_2(T(t)) [d'_1(T(t)) / a'_1(T(t))] dt} < \frac{\int_0^\tau a'_1(T(t)) [d'_2(T(t)) / a'_2(T(t))] dt}{\int_0^\tau d'_1(T(t)) dt}, \quad (10)$$

which can be rearranged to give

$$\left( \frac{\int_0^\tau d'_1(T(t)) dt}{\int_0^\tau a'_2(T(t)) [d'_1(T(t)) / a'_1(T(t))] dt} \right) \left( \frac{\int_0^\tau d'_2(T(t)) dt}{\int_0^\tau a'_1(T(t)) [d'_2(T(t)) / a'_2(T(t))] dt} \right) < 1. \quad (11)$$

Mutual invasibility requires that both necessary and sufficient conditions be satisfied, which occurs when species limit themselves more than they limit their competitors. When the necessary condition is satisfied but the sufficient condition is not, we get competitive dominance; that is, the superior competitor excludes the inferior competitor. When the necessary condition is not satisfied, we get priority effects; that is, species limit themselves less than they limit their competitors and the outcome of competition depends on initial abundances.

Note that equation (11) is equivalent to the necessary condition for mutual invasibility in the Lotka-Volterra framework:

$$\left( \frac{\alpha_{21}}{\alpha_{11}} \right) \left( \frac{\alpha_{12}}{\alpha_{22}} \right) < 1,$$

with

$$\frac{1}{\int_0^\tau d'_i(T(t)) dt}$$



being equivalent to  $\alpha_{ii}$  and

$$\frac{1}{\int_0^T a'_j(T(t)) [a'_i(T(t)) / d'_i(T(t))] dt}$$

being equivalent to  $\alpha_{ji}$  ( $i, j = 1, 2, i \neq j$ ). Note that intraspecific competition strength ( $\alpha_{ii}$ ) is inversely proportional to the species' temperature-dependent mortality rate, while interspecific competition strength ( $\alpha_{ij}$ ) is inversely proportional to the species' resource acquisition ability (its time-varying attack rate  $a'_j(T(t))$ ) weighted by the time-varying resource availability set by its competitor

$$R^*_i(T(t)) = \frac{d'_i(T(t))}{a'_i(T(t))}.$$

(Recall that conversion efficiency is temperature independent.) We explore these connections in more detail below.

#### *From Trait-Level Responses to Species-Level Differences*

Equation (11) tells us that mutual invasibility depends on species' attack and mortality responses to temperature. As noted above, these responses are described by mechanistically derived functions whose parameters have clear biological meaning. This allows us to characterize species' responses to temperature variation in terms of these trait response parameters: attack rate optima, response breadth, and temperature sensitivity of mortality. We can then predict the degree to which consumer species should differ in these parameters, such that each species is able to maintain a positive per capita growth rate when it is rare and its competitor is abundant. To this end, we identify certain fundamental properties of trait responses that generate asymmetries between species in their population-level responses to the joint effects of temperature and competition.

As noted above, interspecific competition strength experienced by a given species is inversely proportional to the resource availability set by its competitor, that is, the competitor's temperature-dependent  $R^*$ . The larger a species'  $R^*$ , the weaker is its competitive effect on other species. The temperature dependence of  $R^*$  is determined by the interaction between the temperature response of the mortality rate, which is exponential, and that of the attack rate, which is unimodal. If  $R^*(T)$  were driven solely by the attack rate response, it should be U-shaped with a minimum at the species' attack rate optimum (i.e., resource availability is lowest, and interspecific competition is strongest, at this temperature; fig. 1). However, a species'  $R^*(T)$  depends also on its mortality response. The exponential nature of the mortality response generates an asymmetry in  $R^*(T)$  such that it becomes J-shaped (fig. 1). This is because the attack rate declines once temperatures increase above the optimum, while the mortality rate keeps increasing. Hence, attack and mortality rates act synergistically to decrease interspecific com-

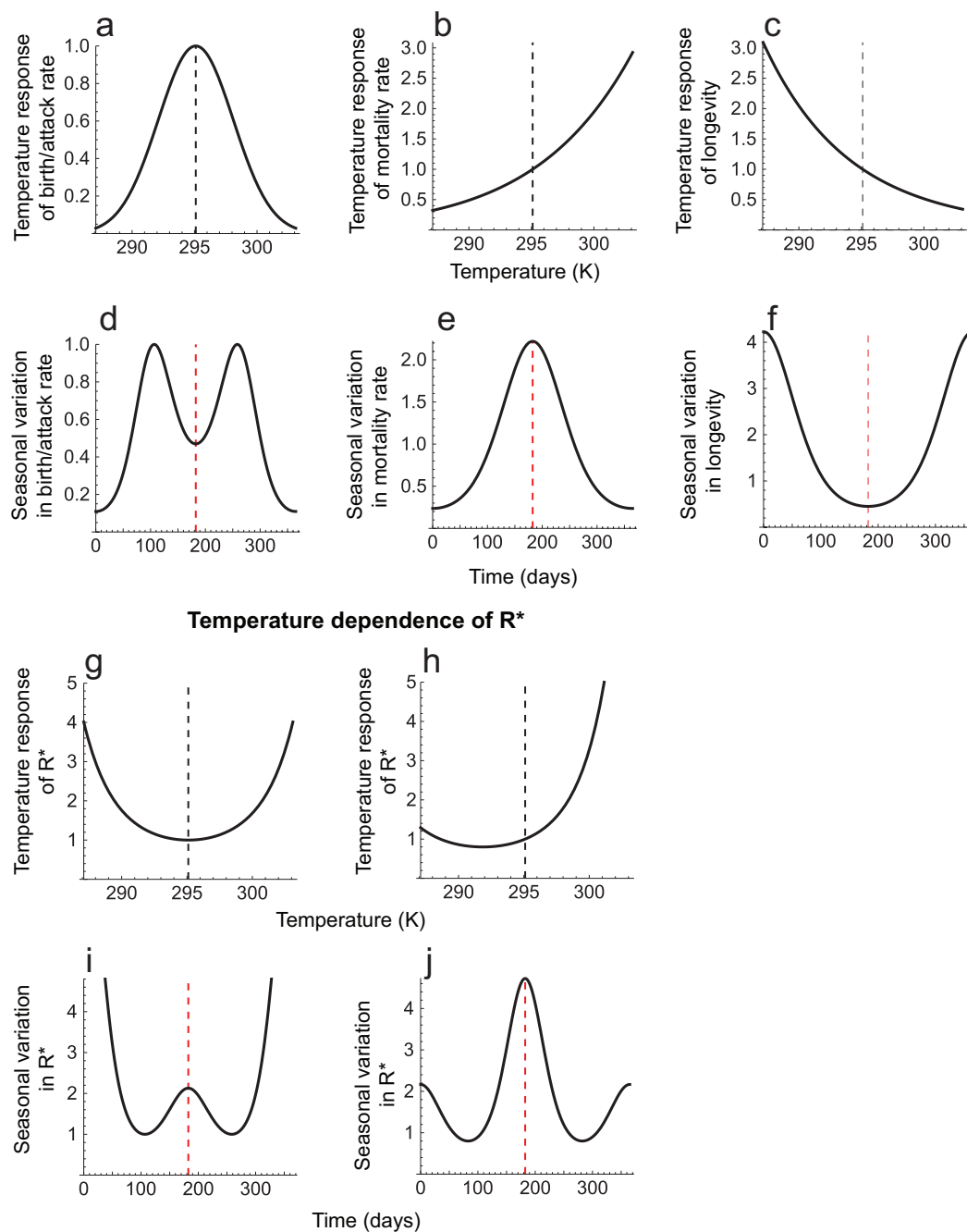
petition with increasing temperature. The attack rate also declines once temperatures decrease below the optimum, but now mortality also decreases. Hence, attack and mortality rates act antagonistically, with the decreasing attack rate decreasing interspecific competition, while the decreasing mortality rate increases it. Therefore, the decrease in interspecific competition strength is greater at temperatures above the attack rate optimum than at temperatures below it. The crucial consequence is that interspecific competition strength depends on the nature of thermal adaptation. Cold-adapted species are active at lower temperatures and have lower thermal optima than warm-adapted species; thermal specialists are active over a narrower temperature range than thermal generalists. The fact that the temperature response of  $R^*$  is concave-up (fig. 1) necessarily means that cold-adapted species and thermal specialists experience lower average resource availability than warm-adapted species and thermal generalists. This leads to the first asymmetry between species: cold-adapted species experience stronger competition from warm-adapted species, as do thermal specialists from thermal generalists.

As also noted in the previous section, self-limitation strength is inversely proportional to the consumer species' temperature-dependent mortality rate. This means that self-limitation depends on the average mortality experienced during the species' activity period (i.e., the temperature range within which it exploits the resource, given by the breadth of the attack response). Average mortality, in turn, depends on the nature of thermal adaptation. The fact that the temperature response of mortality is concave-up (fig. 1) means that cold-adapted species (lower thermal optima) and thermal specialists (lower response breadth) experience lower average mortality than warm-adapted species and thermal generalists. This leads to the second asymmetry between species: cold-adapted species experience stronger self-limitation than warm-adapted species, as do thermal specialists than thermal generalists. With these asymmetries in mind, we now proceed to express mutual invasibility criteria in terms of the parameters of attack and mortality responses.

#### *Mutual Invasibility Criteria in Terms of Trait Differences between Species*

Our goal is to develop trait-based predictions about mutual invasibility that apply to ectotherms inhabiting any latitude. To this end, we express thermal optima and response breadths in terms of the latitudinal relationships these parameters exhibit or can potentially exhibit based on evolutionary considerations. It is widely observed that thermal optima of ectotherm species inhabiting higher latitudes exceed the mean habitat temperature, while those of species inhabiting lower latitudes coincide with the mean habitat temperature (Deutsch et al. 2008; Tewksbury et al. 2008).

### Temperature dependence of life history and consumption traits



**Figure 1:** Temperature responses of birth, attack, and mortality rates and their effect on  $R^*$  values. *a*, Resource birthrate and consumers' attack rate, both of which exhibit symmetric unimodal temperature responses. *b*, Mortality rate, which increases exponentially with temperature. *c*, Longevity, which decreases exponentially with temperature. In *a*–*c*, the dashed vertical line denotes the birth/attack rate optima and the reference temperature for mortality/longevity. Panels *d*–*f* depict how these trait responses change as a function of seasonal temperature variation (with mean  $M_T$  and amplitude  $A_T$ ), with the dashed vertical line denoting the maximum habitat temperature ( $M_T + A_T$ ). Panel *g* depicts  $R^*(T)$  when mortality is temperature insensitive ( $A_d = 0$ ), and panel *h* depicts  $R^*(T)$  when mortality is temperature sensitive ( $A_d > 0$ ). The fourth row depicts how  $R^*(T)$  changes over time as a function of seasonal variation when mortality is temperature insensitive (*i*) and when it is temperature sensitive (*j*). Note that when  $R^*(T)$  is determined solely by the attack response, it is higher (and interspecific competition is lower) at lower temperatures and is the lowest (interspecific competition is the strongest) during favorable times of the year for a given species. In contrast, when  $R^*(T)$  is driven by both attack and mortality responses, it is the highest (interspecific competition is the weakest) during the warmest time of the year.

This is exactly the pattern we would expect if seasonal temperature variation is the main selective factor driving the evolution of thermal reaction norms: higher-amplitude seasonal fluctuations at higher latitudes favor individuals whose trait responses have greater breadth. A greater response breadth necessarily means a thermal optimum that exceeds the mean habitat temperature (Amarasekare and Johnson 2017).

Without loss of generality, consider consumer 1 to be the resident species adapted to the ambient thermal environment at a given latitude. We want to know how different an incoming species (consumer 2) would have to be in its attack and mortality responses, given that its ability to increase when rare depends on both the new thermal regime and competition from the resident species.

Let seasonal temperature variation be depicted by the sinusoidal function  $T(t) = M_T - A_T S(t)$ , where  $M_T$  is the mean habitat temperature,  $A_T$  is the amplitude of seasonal fluctuations ( $A_T = (T_{\max} - T_{\min})/2$ ), and  $S(t) = \cos(2\pi t/\tau)$  (or  $-\sin(2\pi t/\tau)$ ;  $\tau = 365$  days). The resident species' attack and mortality response parameters will depend on the latitude it inhabits. We can express the latitudinal relationship between consumer 1's attack rate optimum and the mean habitat temperature as  $T_{\text{opt}_1} = M_T + n(A_T)A_T$ , where  $n(A_T)$  depicts the slope of the relationship between  $T_{\text{opt}_1} - M_T$  (deviation of the attack rate optimum from the mean temperature) and  $A_T$  (amplitude of seasonal fluctuations). We expect a similar relationship between consumer 1's reference temperature ( $T_{R_1}$ ) and latitude; that is,  $T_{R_1} = M_T + g(A_T)A_T$ . When these relationships are linear, the slope is  $n$  (or  $g$ ); when it is nonlinear, the slope is a function of  $A_T$ . For example, if the deviation between the optimum temperature and the mean habitat temperature ( $T_{\text{opt}_1} - M_T$ ) increases with the amplitude of seasonal fluctuations ( $A_T$ ) at a decelerating rate and saturates to a maximum,

$$n(A_T) = \frac{nA_T}{A_0 + A_T},$$

where  $A_0$  is the amplitude of fluctuations at which  $n(A_T) = n/2$ .

We can express the relationship between response breadth and latitude as  $s_{a_i} = m(A_T)A_T$ , where  $m(A_T)$  depicts the nonlinearity in the relationship between response breadth and the amplitude of seasonal fluctuations. Note that we use the amplitude of seasonal fluctuations as a proxy for latitude because it is not the latitude per se that matters in terms of temperature effects on species' traits but the seasonal temperature regime associated with that latitude. Arrhenius constants are thermodynamically constrained to be within a narrow range of values (typically 5,000–12,000, with an average of 6,700; Dell et al. 2016). We do not, therefore, consider latitudinal variation in the thermal sensitivity of mortality.

Now consider an incoming species, consumer 2, whose persistence depends on adapting to both the new thermal regime as well as competition from species 1. We would expect consumer species 2 to deviate from the latitudinal relationships in the following manner:  $T_{\text{opt}_2} = M_T + (n(A_T) \pm x)A_T$  and  $s_{a_2} = \nu s_{a_1} = \nu m(A_T)A_T$ . In biological terms, this means that consumer 2's thermal optimum deviates (positively or negatively) from the latitudinal relationship by an amount  $x$ , and its response breadth by an amount  $\nu$  ( $\nu > 0$ ). We express differences between species in their temperature response of mortality in a similar manner:  $T_{R_2} = M_T + (g(A_T) \pm y)A_T$  and  $A_{d_2} = pA_{d_1}$  ( $p > 0$ ). We assume, for reasons of analytical tractability, that  $g = n$ .

By substituting these relationships into equations (9) and (11) and doing some algebra (app. B), we arrive at the following mechanistic descriptions of the mutual invasibility criteria.

The necessary condition for mutual invasibility is given by

$$\left( \frac{\int_0^\tau e^{-[A_{d_1}/M_T - A_T S(t)]} dt}{\int_0^\tau e^{-AS(t)(S(t)+2n) - DS(t) - [A_{d_1}/M_T - A_T S(t)]} dt} \right) \left( \frac{\int_0^\tau e^{-[pA_{d_1}/M_T - A_T S(t)]} dt}{\int_0^\tau e^{AS(t)(S(t)+2n) + DS(t) - [pA_{d_1}/M_T - A_T S(t)]} dt} \right) < 1 \quad (12)$$

and the sufficient condition by

$$\frac{\int_0^\tau e^{-pB_2[S(t)+n+x/M_T - A_T S(t)]} dt}{\int_0^\tau e^{-A(S(t)+2n)^2 - D(S(t)+2n+[x/2]) - B_1[S(t)+n/M_T - A_T S(t)]} dt} < \frac{R_{1T_{\text{opt}}}}{R_{2T_{\text{opt}}}} < \frac{\int_0^\tau e^{A(S(t)+2n)^2 + D(S(t)+2n+[x/2]) - pB_2[S(t)+2n/M_T - A_T S(t)]} dt}{\int_0^\tau e^{-B_1[S(t)+2n+x/M_T - A_T S(t)]} dt}, \quad (13)$$

where

$$A = \frac{1 - \nu^2}{2m^2\nu^2},$$

$$B_1 = \frac{A_{d_1}A_T}{M_T + nA_T},$$

$$B_2 = \frac{A_{d_1}A_T}{M_T + (n+x)A_T},$$

$$C = \frac{x}{m^2}, \quad D = \frac{C}{\nu^2},$$

$$R_{1T_{\text{opt}}} = \frac{d_{1T_{\text{R}}}}{e_1 a_{1T_{\text{opt}}}},$$

and

$$R_{2T_{\text{opt}}} = \frac{d_{2T_{\text{R}}}}{e_2 a_{2T_{\text{opt}}}}.$$

In deriving equations (12) and (13), we have assumed the simplest possible relationship for latitudinal variation in thermal optima and response breadths; that is,  $T_{\text{opt}_2} = M_T + (n \pm x)A_T$  and  $s_{a_2} = \nu s_{a_1} = \nu m(A_T)A_T$ . Nonlinear lati-

tudinal relationships do not qualitatively alter our findings (see below).

As noted above, the necessary condition is equivalent to that for mutual invasibility in the Lotka-Volterra framework:

$$\left(\frac{\alpha_{21}}{\alpha_{11}}\right)\left(\frac{\alpha_{12}}{\alpha_{22}}\right) < 1,$$

with

$$\alpha_{11} = \frac{1}{\int_0^T e^{-[A_{d1}/M_T - A_T S(t)]} dt}, \quad \alpha_{22} = \frac{1}{\int_0^T e^{-[pA_{d1}/M_T - A_T S(t)]} dt},$$

$$\alpha_{21} = \frac{1}{\int_0^T e^{-AS(t)(S(t)+2n)-DS(t)-[A_{d1}/M_T - A_T S(t)]} dt},$$

and

$$\alpha_{12} = \frac{1}{\int_0^T e^{AS(t)(S(t)+2n)+DS(t)-[pA_{d1}/M_T - A_T S(t)]} dt}.$$

The intraspecific competitive effect is inversely proportional to the species' temperature-dependent mortality; its strength is determined by the thermal sensitivity of mortality (as depicted by the Arrhenius constant  $A_d$ ) and the seasonal temperature regime at a given latitude ( $M_T$ ,  $A_T$ ). The interspecific competitive effect is determined by the species' temperature-dependent attack rate weighted by its competitor's temperature-dependent  $R^*$ ; its strength depends on (i) species' differences in temperature sensitivity of mortality ( $p$ ), attack rate optima ( $x$ ), and response breadth ( $v$ ); (ii) latitudinal variation in thermal optima and response breadth ( $n$  and  $m$ , respectively); and (iii) the seasonal temperature regime ( $M_T$ ,  $A_T$ ). The key point is that our trait-based approach allows us to derive mutual invasibility criteria in terms of parameters characterizing the abiotic (thermal) environment ( $n$ ,  $m$ ,  $M_T$ ,  $A_T$ ) and species' differences in attack and mortality responses to temperature ( $x$ ,  $v$ , and  $p$ ).

### Model Analysis

We begin with a general analysis to predict the degree to which competing species should differ in their thermal optima ( $x$ ), response breadth ( $v$ ), and temperature sensitivity of mortality ( $p$ ) for coexistence to occur and how these differences change with latitudinal variation in the seasonal temperature regime. We test the coexistence predictions with data from a naturally occurring insect community: the harlequin bug (*Murgantia histrionica*) and its two egg parasitoids (*Trissolcus murgantiae* and *Ooencyrtus johnsonii*; see app. C for details on the biology).

Both analyses focus on mutual invasibility, a necessary condition for coexistence. The sufficient condition involves demonstrating the stability of the coexistence equilibrium. Because the nonautonomous nature of the system precludes an analytical stability analysis, we investigate stability through numerical analyses of the full model (eq. [1]). Specifically,

we numerically integrate the system of equations until the transient dynamics have run their course and the system achieves a stationary state (i.e., intra-annual fluctuations in abundance that repeat themselves with a period of 1 year). We quantify stability by investigating the sensitivity of this steady state to initial conditions. If the stationary state observed in the numerical integration corresponds to a stable equilibrium, all initial conditions should converge to this attractor.

## Results

### General Analysis

Equations (12) and (13) depict the most general case in which consumer species differ in their thermal optima ( $T_{opt}$ ), response breadth ( $s_d$ ), and temperature sensitivity of mortality ( $A_d$ ). By adjusting the various metrics, we can elucidate the role that attack and mortality responses, and any interactions thereof, play in consumer coexistence.

*Species Differ Only in Temperature Response of Mortality.* When species differ only in their temperature response of mortality ( $p \neq 1$ ,  $x = 0$ ,  $v = 1$ ), the necessary condition simplifies to

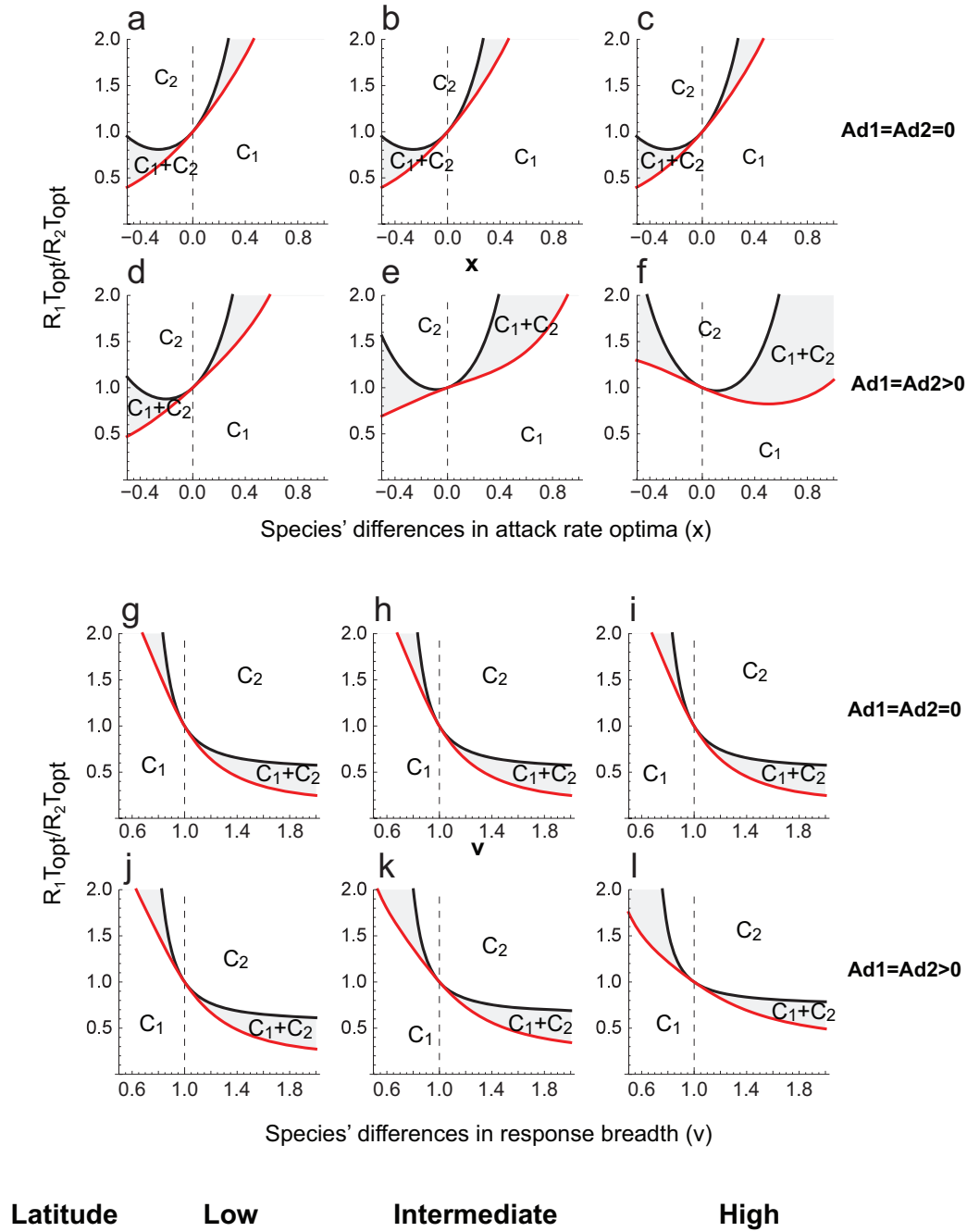
$$\left(\frac{\int_0^T e^{-[A_{d1}/M_T - A_T S(t)]} dt}{\int_0^T e^{-[A_{d1}/M_T - A_T S(t)]} dt}\right)\left(\frac{\int_0^T e^{-[pA_{d1}/M_T - A_T S(t)]} dt}{\int_0^T e^{-[pA_{d1}/M_T - A_T S(t)]} dt}\right) < 1. \quad (14)$$

Note that intra- and interspecific competitive effects are equal in magnitude, making the left-hand side evaluate to 1. Hence, the above inequality can never be satisfied. In biological terms, when species differ solely in their temperature sensitivity of mortality, mutual invasibility is not possible because there is no temporal separation in resource use. Chesson (2000) has previously noted that mortality differences alone are insufficient for coexistence. The novel insight of our trait-based approach, explained in the sections that follow, is that while the temperature response of mortality cannot in itself allow mutual invasibility, the nature of its nonlinearity is crucial in generating asymmetries between species that allow them to partition thermal niches.

*Species Differ in One Aspect of Attack Rate Response: Mortality Is Temperature Insensitive.* The key results are that (i) species need differ in only one aspect of their attack response for mutual invasibility to occur, (ii) conditions for mutual invasibility are invariant with latitude, and (iii) the only possible outcomes are coexistence or competitive exclusion; that is, priority effects are not possible. Below we show how these results come about.

We first show that mutual invasibility is possible when species differ in only one aspect of their attack rate response (fig. 2). Consider first, the necessary condition for mutual





**Figure 2:** Sufficient condition for mutual invasibility (eq. [13]) as a function of the difference in attack rate optima ( $x$ ) when consumer species have the same response breadths ( $v = 1$ ;  $a-f$ ) and of the difference in response breadth ( $v$ ) when consumer species have the same attack rate optima ( $x = 0$ ;  $g-l$ ). Panels  $a-c$  and  $g-i$  depict the two cases when neither consumer species' mortality rate is sensitive to temperature, and panels  $d-f$  and  $j-l$  depict the two when mortality rate is temperature sensitive but consumer species do not differ in their thermal sensitivity of mortality ( $p = 1$ ). In each panel, the black and red curves correspond, respectively, to the invasion thresholds, that is, the maximum value of  $R_{1_{\text{Topt}}}/R_{2_{\text{Topt}}}$ , below which the resident species (consumer 1) can invade, and the minimum value of  $R_{1_{\text{Topt}}}/R_{2_{\text{Topt}}}$ , above which the incoming species (consumer 2) can invade. Consumer 2 is excluded in the region marked  $C_1$ , and consumer 1 is excluded in the region marked  $C_2$ . Mutual invasibility occurs in the shaded region marked  $C_1 + C_2$ . Note that consumer 1's invasion threshold is a U-shaped function of  $x$ , while consumer 2's is monotonic increasing/decreasing in  $x$  (fig. 2d-2f). As the amplitude of seasonal fluctuations ( $A_T$ ) increases, the minimum of the resident species' invasion threshold (i.e., the minimum of  $R_{1_{\text{Topt}}}/R_{2_{\text{Topt}}}$  at which it can invade when rare) shifts from negative ( $x < 0$ ) to positive ( $x > 0$ ), while the invading species' invasion threshold changes from monotonic increasing in  $x$  to monotonic decreasing. This leads to a qualitative change in the patterns of mutual invasibility as  $A_T$  increases (cf.  $a-c$  with  $d-f$ ). When species differ only in their response breadth, both species' invasion thresholds are monotonic decreasing functions of  $v$  ( $j-l$ ). As  $A_T$  increases, consumer 1's invasibility decreases and consumer 2's invasibility increases as the latter's response breadth increases (cf.  $g-i$  with  $j-l$ ). In all panels, the slopes of the latitudinal relationships are  $n = 0.6$  and  $m = 0.6$ . Temperature regimes for the different latitudes are low:  $M_T = 300$  K,  $A_T = 2$ ; intermediate:  $M_T = 290$  K,  $A_T = 6$ ; high:  $M_T = 282$ ,  $A_T = 12$ . Parameter values for  $p = 1$  are  $A_{d_1} = A_{d_2} = 7,000$ .

invasibility when species differ in their attack rate optima ( $x \neq 0$ ) but not response breadth ( $v = 1$ ):

$$\left( \frac{\tau}{\int_0^\tau e^{-(x/m^2)S(t)} dt} \right) \left( \frac{\tau}{\int_0^\tau e^{(x/m^2)S(t)} dt} \right) < 1. \quad (15)$$

Note that when mortality is insensitive to temperature ( $A_d = 0$ ), asymmetries between species in intra- and inter-specific competition vanish. Now, both species experience the same intraspecific competition strength  $\alpha_{ii} = \tau$ . Their  $R^*$  values depend only on their attack rate responses (i.e.,  $R_i^*(T) = 1/a_i(T)$ ,  $i = 1, 2$ ) and therefore become U-shaped, rather than J-shaped, functions of temperature (fig. 1). Hence, interspecific competition strength becomes

$$\alpha_{ji} = \frac{1}{\int_0^\tau [a_j'(T(t))/a_i'(T(t))] dt} = \frac{1}{\int_0^\tau e^{\pm(x/m^2)S(t)} dt}.$$

Let consumer  $i$  ( $i = 1, 2$ ) have a lower attack rate optimum than consumer  $j$ ; that is, it is more cold adapted. During the cooler periods of the year when consumer  $i$ 's attack rate is high, consumer  $j$ 's attack rate is low and its  $R^*$  is high. Therefore, competition from consumer  $j$  is low when the thermal environment is favorable to consumer  $i$ , and vice versa, making

$$\frac{\alpha_{ji}}{\alpha_{ii}} \ll 1 \quad (i, j = 1, 2; \quad i \neq j)$$

and satisfying the mutual invasibility criteria (fig. 2a–2c).

Now let us consider the necessary condition for mutual invasibility when consumer species exhibit the same thermal optima ( $x = 0$ ) but differ in response breadth ( $v \neq 1$ ):

$$\left( \frac{\tau}{\int_0^\tau e^{-(1-v^2/2m^2v^2)S(t)(S(t)+2n)} dt} \right) \left( \frac{\tau}{\int_0^\tau e^{(1-v^2/2m^2v^2)S(t)(S(t)+2n)} dt} \right) < 1. \quad (16)$$

Let consumer  $i$  have a wider response breadth than consumer  $j$ ; that is, it is a thermal generalist. Since the generalist is active over a wider temperature range than the specialist, it experiences higher resource availability, on average, than the specialist. This means that the generalist experiences weaker interspecific competition from the specialist than vice versa. Since both species experience the same intraspecific competition strength  $\tau$ , it follows that the specialist limits itself much more strongly than it limits the generalist; that is,

$$\frac{\alpha_{ij}}{\alpha_{jj}} \ll \frac{\alpha_{ji}}{\alpha_{ii}}.$$

This difference is sufficient to cause the left-hand side of equation (16) to become less than 1. Mutual invasibility is possible once the sufficient condition, which consists of temperature-independent quantities, is satisfied (fig. 2g–2i).

Next we show that when mortality is insensitive to temperature, conditions for mutual invasibility are invariant

with latitude. Specifically, when  $A_d = 0$ , the sufficient condition for mutual invasibility is independent of the amplitude of seasonal fluctuations ( $A_T$ ):

$$\frac{\tau}{\int_0^\tau e^{-A(S(t)+2n)^2 - D(S(t)+2n+[x/2])} dt} < \frac{R_{1T_{opt}}}{R_{2T_{opt}}} \quad (17)$$

$$< \frac{\int_0^\tau e^{A(S(t)+2n)^2 + D(S(t)+2n+[x/2])} dt}{\tau},$$

where

$$A = \frac{1-v^2}{2m^2v^2},$$

$$D = \frac{x}{v^2m^2},$$

$$R_{1T_{opt}} = \frac{d_{1T_{opt}}}{e_1 a_{1T_{opt}}},$$

and

$$R_{2T_{opt}} = \frac{d_{2T_{opt}}}{e_2 a_{2T_{opt}}}.$$

Therefore, thermal limits to similarity in terms of attack rate optima and/or response breadth are invariant with latitude. That is, given a resident consumer species optimally adapted to its thermal environment, with its attack rate optimum and response breadth determined by the latitudinal relationships specified above, an incoming competitor has to differ by a minimum amount  $x$  (when species differ in their attack rate optima) and/or  $v$  (when species differ in response breadth) to be able to increase when rare, regardless of whether the thermal regime is tropical or temperate.

Our third result is that when mortality is temperature insensitive, the only possible outcomes are coexistence or competitive dominance. We illustrate this mathematically for the case when species differ only in their attack rate optima ( $x \neq 0$ ,  $v = 1$ ). By integrating the denominators of the necessary condition (eq. [15]), we get

$$\left( \frac{1}{I_0[x/m^2]} \right) \left( \frac{1}{I_0[x/m^2]} \right) < 1, \quad (18)$$

where  $I_0[x/m^2]$  is the modified Bessel function of the first kind (Watson 1995). By definition,  $I_0[0] = 1$  and  $I_0[y] > 1$  for all nonzero  $y$ . Recall that  $x$  represents the difference between species' attack rate optima, which can be negative or positive, and  $m$  is a positive constant that determines the slope of the latitudinal relationship in response breadth. Therefore, the denominators in equation (18) exceed the respective numerators, and the necessary condition is always satisfied. A similar argument applies when species differ only in their response breadths. Priority effects do not arise in this case because when species differ only in their attack rate optima or response breadth, it is not possible for both species to limit their competitor more than they limit themselves.

*Species Differ in One Aspect of Attack Rate Response: Mortality Is Temperature Sensitive.* This case yields two key results. First, we see strong latitudinal differences in coexistence and competitive dominance, even when species do not differ in their temperature sensitivity of mortality ( $p = 1$ ). Second, when species do differ ( $p \neq 1$ ), we observe priority effects, the incidence of which increases with increasing seasonal fluctuations.

The crucial point is that when mortality is temperature sensitive, asymmetries between species in their intra- and interspecific competitive effects come into play. The exponential nature of the mortality response leads to stronger intra- and interspecific competition at lower temperatures. This means that species that are cold adapted (i.e., with lower thermal optima) or thermal specialists (i.e., narrower response breadth) both limit themselves more strongly and experience stronger competition from species that are warm adapted (higher thermal optima) or thermal generalists (wider response breadth). At the same time, species that are warm adapted or thermal generalists both limit themselves weakly and experience weaker competition from species that are favored during the colder months of the year. Whether mutual invasibility occurs or priority effects emerge depends, therefore, on the degree to which species that are warm adapted or are thermal generalists can limit themselves relative to how much they limit their competitors.

We begin by explaining how mutual invasibility occurs, and why priority effects do not occur, when species differ in only one aspect of their attack rate response and have identical mortality responses. We then explain how the above asymmetry between species' competitive effects lead to latitudinal patterns in mutual invasibility. We end this section with an explanation of how species' differences in attack and mortality responses generate priority effects and any latitudinal variation thereof.

*Species have identical mortality responses.* Consider first the case when species differ in their attack rate optima ( $x \neq 0$ ) but not response breadth ( $v = 1$ ) and have identical mortality responses ( $p = 1$ ). Now the necessary condition simplifies to

$$\left( \frac{\int_0^T e^{-[A_{di}/M_T - A_T S(t)]} dt}{\int_0^T e^{-CS(t) - [A_{di}/M_T - A_T S(t)]} dt} \right) \left( \frac{\int_0^T e^{-[A_{ji}/M_T - A_T S(t)]} dt}{\int_0^T e^{CS(t) - [A_{ji}/M_T - A_T S(t)]} dt} \right) < 1. \quad (19)$$

Since species do not differ in their temperature sensitivity of mortality, self-limitation strength is the same for both species; that is,

$$\alpha_{ii} = \frac{1}{\int_0^T e^{-[A_{di}/M_T - A_T S(t)]} dt}.$$

However, the exponential mortality response combined with the difference in thermal optima generates species' dif-

ferences in the self-limitation strength they actually experience. To see this, let consumer  $i$  have a lower attack rate optimum ( $x > 0$ ); that is, it is more cold adapted than consumer  $j$ . Because mortality is lower at lower temperatures, consumer  $i$  experiences strong intraspecific competition during the favorable (colder) periods of the year. At the same time, it experiences relatively weak competition from consumer  $j$ . This is because although consumer  $j$ 's mortality is low at lower temperatures, its attack rate is also low. Hence it has a high  $R^*$  at low temperatures. Consumer  $i$ 's high attack rate at lower temperatures further lowers consumer  $i$ 's competitive effect on consumer  $j$ ; that is,

$$\alpha_{ij} = \frac{1}{\int_0^T a_i(T(t))R_j^* dt} = \frac{1}{\int_0^T e^{(x/m^2)S(t) - [A_{di}/M_T - A_T S(t)]} dt}$$

becomes low.

The fact that the two species differ in their attack rate optima means that the competitive effect of consumer  $i$  on consumer  $j$ , ( $\alpha_{ji} = 1/\int_0^T a_j(T(t))R_i^* dt = 1/\int_0^T e^{-(x/m^2)S(t) - [A_{ji}/M_T - A_T S(t)]} dt$ ), is also low. This is because consumer  $i$ 's mortality is high and attack rate is low at high temperatures, causing its  $R^*$  value to become very high. Since consumer  $j$ 's attack rate is high at high temperatures, competitive effect of consumer  $i$  on consumer  $j$  becomes very low. However, higher mortality at higher temperatures means that consumer  $j$ 's self-limitation is not as strong during the favorable (warmer) periods of the year. We therefore have the situation where consumer  $i$  limits itself much more strongly than it limits consumer  $j$  ( $\alpha_{ji}/\alpha_{ii} \ll 1$ ). Consumer  $j$ , in contrast, cannot limit itself as strongly as consumer  $i$  during favorable (warmer) times of the year. At the same time, consumer  $j$ 's low mortality at low temperatures means a lower  $R^*$  and stronger interspecific competition on consumer  $i$ . This, combined with the fact that consumer  $i$ 's attack rate is high at low temperatures, can cause the competitive effect of consumer  $j$  on consumer  $i$  to become high. The net outcome is that consumer  $j$  can limit consumer  $i$  more strongly than it limits itself ( $\alpha_{ij}/\alpha_{jj} > 1$ ), particularly when species' differences in attack rate optima is low (i.e.,  $x \rightarrow 0$ ). For the necessary condition to be satisfied, therefore, the amount by which intraspecific competition exceeds interspecific competition in the cold-adapted species (consumer  $i$ ) has to be greater than the amount by which interspecific competition exceeds intraspecific competition in the warm-adapted species (consumer  $j$ ); that is,  $\alpha_{ji}/\alpha_{ii} < 1$  by a greater amount than  $\alpha_{ij}/\alpha_{jj} > 1$ . Importantly, it is the exponential nature of the mortality response that makes this possible: the increase in mortality with temperature is disproportionately greater at higher temperatures than at lower temperatures (fig. 1). This means that the increase in consumer  $i$ 's  $R^*$ —and hence the reduction in its competitive effect on consumer  $j$ —is greater than the de-

crease in consumer  $j$ 's  $R^*$ —and hence the increase in its competitive effect on consumer  $i$ .

In summary, when species differ in their attack rate optima and have identical mortality responses, the necessary condition is always satisfied and priority effects do not arise. Coexistence occurs if the sufficient condition is satisfied; competitive dominance occurs otherwise. Importantly, these outcomes ensue because intraspecific competition is much stronger than interspecific competition in the species with the lower attack rate optimum, a direct result of the nonlinear mortality response.

Now consider the case when consumers differ in their response breadth ( $v \neq 1$ ) but not attack rate optima ( $x = 0$ ) and have identical mortality responses ( $p = 1$ ). The necessary condition simplifies to

$$\left( \frac{\int_0^T e^{-[A_{di}/M_T - A_T S(t)]} dt}{\int_0^T e^{-[(1-v)^2/2m^2v^2]S(t)(S(t)+2n) - [A_{di}/M_T - A_T S(t)]} dt} \right) \left( \frac{\int_0^T e^{-[A_{di}/M_T - A_T S(t)]} dt}{\int_0^T e^{-[(1-v)^2/2m^2v^2]S(t)(S(t)+2n) - [A_{di}/M_T - A_T S(t)]} dt} \right) < 1. \quad (20)$$

Although species do not differ in their temperature sensitivity of mortality, the exponential nature of the mortality response leads to species' differences in self-limitation strength. Let consumer  $i$  have the greater response breadth; that is, it is a thermal generalist compared to consumer  $j$ . Consumer  $j$  (the specialist) is active during the favorable time of the year for both species, during which the increase in mortality with temperature is relatively small. Therefore, the specialist experiences fairly strong intraspecific competition. At the same time, since its average attack rate is lower than that of the generalist's, the specialist's time-averaged  $R^*$  value exceeds that of the generalist; that is, the specialist exerts weaker competition on the generalist than vice versa. The generalist, because of its greater response breadth, is active at temperatures both below and above the optimal range. It therefore experiences a variable mortality response. The exponential nature of the mortality response means that the increase in mortality at higher temperature exceeds the decrease at lower temperatures, resulting in the generalist experiencing higher average mortality and weaker self-limitation than the specialist. The net result is that the generalist limits itself less than it limits the specialist, that is,  $\alpha_{ji}/\alpha_{ij} > 1$ , while the specialist limits itself more strongly than it limits the generalist, that is,  $\alpha_{ij}/\alpha_{ji} \ll 1$ . As in the previous case, nonlinearity in the mortality response ensures that the increase in the specialist's (consumer  $j$ )  $R^*$ —and hence the reduction in its competitive effect on the generalist (consumer  $i$ )—is greater than the decrease in the generalist's (consumer  $i$ )  $R^*$ —and hence the increase in its competitive effect on the specialist (consumer  $j$ ).

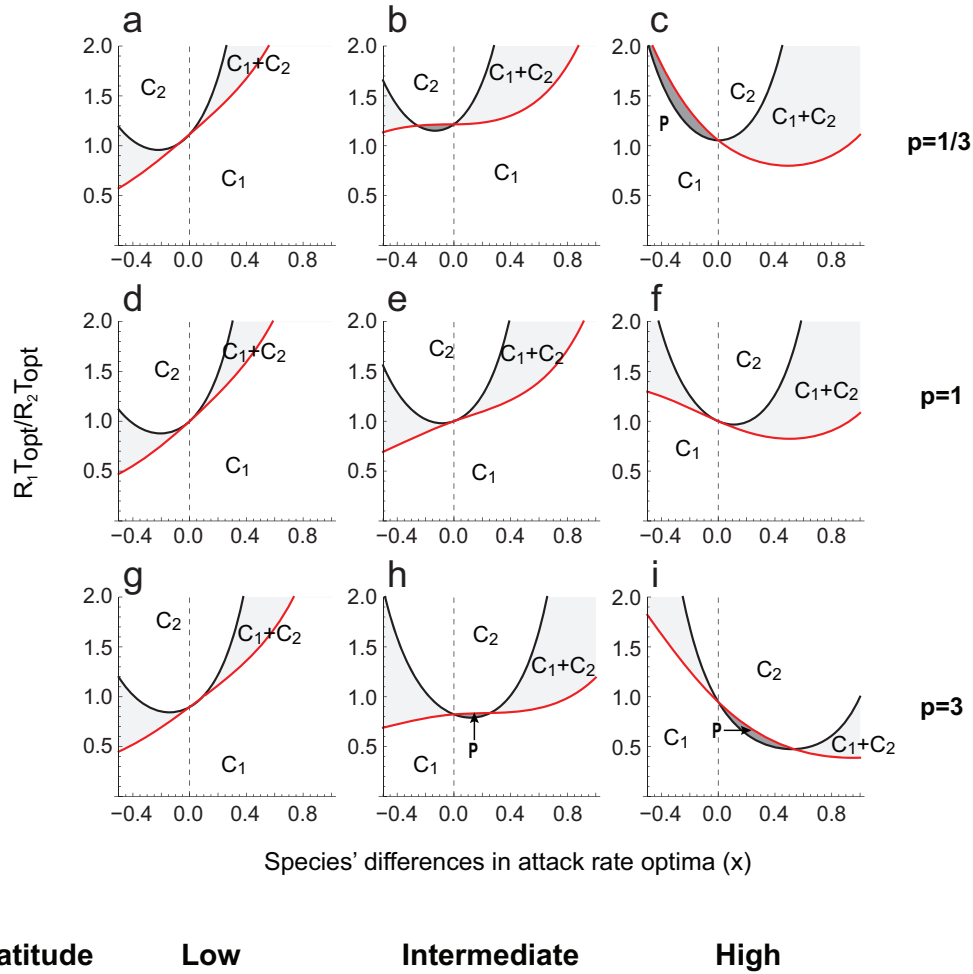
These outcomes ensue because the exponential mortality response ensures that intraspecific competition is much stronger than interspecific competition in the thermal specialist.

In summary, when species differ in one aspect of their attack rate response and have identical mortality responses, mutual invasibility is possible because of greater intraspecific than interspecific competition in the cold-adapted species when species differ only in their thermal optima and in the thermal specialist when species differ only in their response breadth.

The key insight is that species' differences in their competitive responses generate latitudinal patterns in mutual invasibility (fig. 2). To see this, consider first the case when species differ only in their attack rate optima (fig. 2a–2f). When the amplitude of seasonal fluctuations ( $A_T$ ) is small, the incoming species (consumer 2) can more easily increase when rare when its attack rate optimum ( $T_{opt_2}$ ) is closer to the mean habitat temperature ( $M_T$ ) than that of the resident (consumer 1); that is,  $x < 0$ . This is because, when fluctuations are small, the invader's fitness (per capita growth rate) is maximized when  $T_{opt_2}$  is close to  $M_T$ . Hence, its invasibility decreases as  $x$  increases. In contrast, when  $A_T$  is large, the invader can more easily increase when rare when its attack rate optimum is farther away from the mean habitat temperature ( $x > 0$ ). This is because the larger the fluctuations, the greater is the average mortality (due to the exponential nature of its mortality response) experienced by the resident. Therefore, a higher attack rate optimum allows the invader to capitalize on the favorable (warmer) periods of the year during which interspecific competition is weak due to the high mortality experienced by the resident species. As a result, the invading species' ability to increase when rare increases as  $x$  increases (fig. 2; app. D). Of note, latitudinal patterns are stronger when species differ in their attack rate optima ( $x$ ) rather than response breadth ( $v$ ; cf. fig. 2d–2f with fig. 2j–2l). This is because  $x$  induces greater nonlinearity in the mutual invasibility criteria compared to  $v$ . Confirmation of this is seen by inspecting the mutual invasibility conditions (eqq. [12], [13]); when  $x = 0$ , the nonlinearity all but disappears.

*Species differ in their mortality response.* When species differ in their temperature sensitivity of mortality ( $p \neq 1$ ), priority effects become possible. Importantly, their emergence depends on the degree to which warm-adapted species and thermal generalists can limit themselves relative to how much they limit their competitors.

With this in mind, consider the case when species differ in their attack rate optima but not response breadth plus they differ in their temperature sensitivity of mortality. Consumer  $i$  is cold adapted (lower attack rate optimum), while consumer  $j$  is warm adapted (higher thermal optimum). Mutual invasibility is possible if the species with the higher attack rate optimum experiences lower temperature sensitivity of mortality; that is, there is a trade-off between mortality and attack rate efficiency (fig. 3). The argument is as follows. The cold-



**Figure 3:** Sufficient condition for mutual invasibility as a function of  $x$  when consumer species have the same response breadths ( $v = 1$ ) but have different attack rate optima ( $x \neq 0$ ) and thermal sensitivity of mortality ( $a-c$ ,  $p > 1$ ;  $g-i$ ,  $p < 1$ ). As in figure 1, the black and red lines correspond, respectively, to the  $R_{1_{\text{Topt}}}/R_{2_{\text{Topt}}}$  value below and above which consumers 1 and 2 can invade. Mutual invasibility occurs in the shaded region marked  $C_1 + C_2$ , and priority effects occur in the region marked  $P$ . Parameter values are  $A_{d_i} = 15,000$  when  $p = 1/3$  and  $A_{d_i} = 5,000$  when  $p = 3$ . Other parameter values are as in figure 2.

adapted species experiences greater temperature sensitivity of mortality ( $A_{d_i} > A_{d_i}$ ). A steeper mortality response means very low mortality at lower temperatures (and stronger self-limitation). It also means very high mortality at high temperatures. This, combined with its low attack rate at high temperatures increases the cold-adapted species  $R^*$ , causing its competitive effect on the warm-adapted species to be weaker than when species do not differ in their temperature sensitivity of mortality. Thus, a lower attack rate optimum combined with greater temperature sensitivity of mortality causes the cold-adapted species to limit itself much more strongly than it limits the warm-adapted species as compared to when species exhibit the same temperature sensitivity of mortality. At the same time, a shallower mortality response in the warm-adapted species means stronger intraspecific com-

petition during the favorable (warmer) months of the year. It also means higher mortality at lower temperatures, which, combined with its low attack rate, increases the warm-adapted species'  $R^*$  and decreases its competitive effect on the cold-adapted species. Thus, a higher attack rate optimum combined with lower temperature sensitivity of mortality causes the warm-adapted species to limit itself more, and to limit its competitor less, than when both species experience the same temperature sensitivity of mortality. In sum, a trade-off between mortality and attack rate efficiency ensures that the necessary condition for mutual invasibility is always, and easily, met. Priority effects are not possible.

The flip side of the above argument shows that priority effects can occur when the warm-adapted species experiences greater temperature sensitivity of mortality ( $A_{d_i} > A_{d_i}$ ). The



warm-adapted species has a low attack rate at low temperatures, but the steeper mortality response means very low mortality at low temperatures. This translates to a smaller  $R^*$  and stronger competition on the cold-adapted species. However, a steeper mortality response also means very high mortality at high temperatures, making for weak self-limitation during the favorable (warmer) months of the year. Hence, the warm-adapted species limits its competitor much more than it limits itself compared to when species do not differ in their temperature sensitivity of mortality. At the same time, the shallower mortality response of the cold-adapted species means that it experiences lower longevity and, hence, weaker intraspecific competition during the favorable (colder) periods of the year. A shallower slope also means lower mortality at higher temperatures, which lowers the cold-adapted species'  $R^*$  and increases its competitive effect on the warm-adapted species. Hence, the cold-adapted species limits itself less, and its competitor more, than when both species experience the same temperature sensitivity of mortality. Taken together, these differences in species' competitive effects can cause the necessary condition for mutual invasibility to fail, leading to a priority effect (fig. 3).

When species differ in their response breadth, mutual invasibility is possible when the thermal generalist exhibits greater temperature sensitivity of mortality and priority effects arise when it exhibits lower temperature sensitivity. Which outcome ensues depends on the asymmetry between species in their competitive effects. When the thermal generalist exhibits greater temperature sensitivity of mortality, it limits itself more and its competitor less than when both species experience the same temperature sensitivity of mortality. Similarly, when the specialist experiences lower temperature sensitivity of mortality, it limits itself more and its competitor less than when both species experience the same temperature sensitivity of mortality. Hence, a trade-off between mortality and response breadth ensures that the necessary condition for mutual invasibility is always met. Priority effects arise when we have the opposite case: the thermal generalist experiences lower temperature sensitivity of mortality and the thermal specialist, higher sensitivity (fig. 4). Notably, we see a greater incidence of priority effects at higher latitudes because the higher-amplitude seasonal fluctuations mean that species experience more nonlinear mortality responses and, hence, greater asymmetry in their competitive responses.

*Species Differ in Attack Rate Optima and Response Breadth: Mortality Is Temperature Sensitive.* When consumer species exhibit a trade-off between mortality and attack rate efficiency, priority effects are possible if the species with the lower attack rate optimum and greater temperature sensitivity of mortality also exhibits a lower response breadth. In the absence of such a trade-off, priority effects are possible regardless of which species has the greater response breadth (figs. F1, F2; app. F;

figs. A1, B1, C1–C3, D1, E1, F1, F2, G1, G2 are available online). When species exhibit a trade-off between mortality and response breadth, priority effects are possible only if the species with the greater response breadth and greater temperature sensitivity of mortality has a lower attack rate optimum ( $x \gg 0$ ). Otherwise, priority effects are possible regardless of which species has the greater attack rate optimum (figs. F1, F2; app. F).

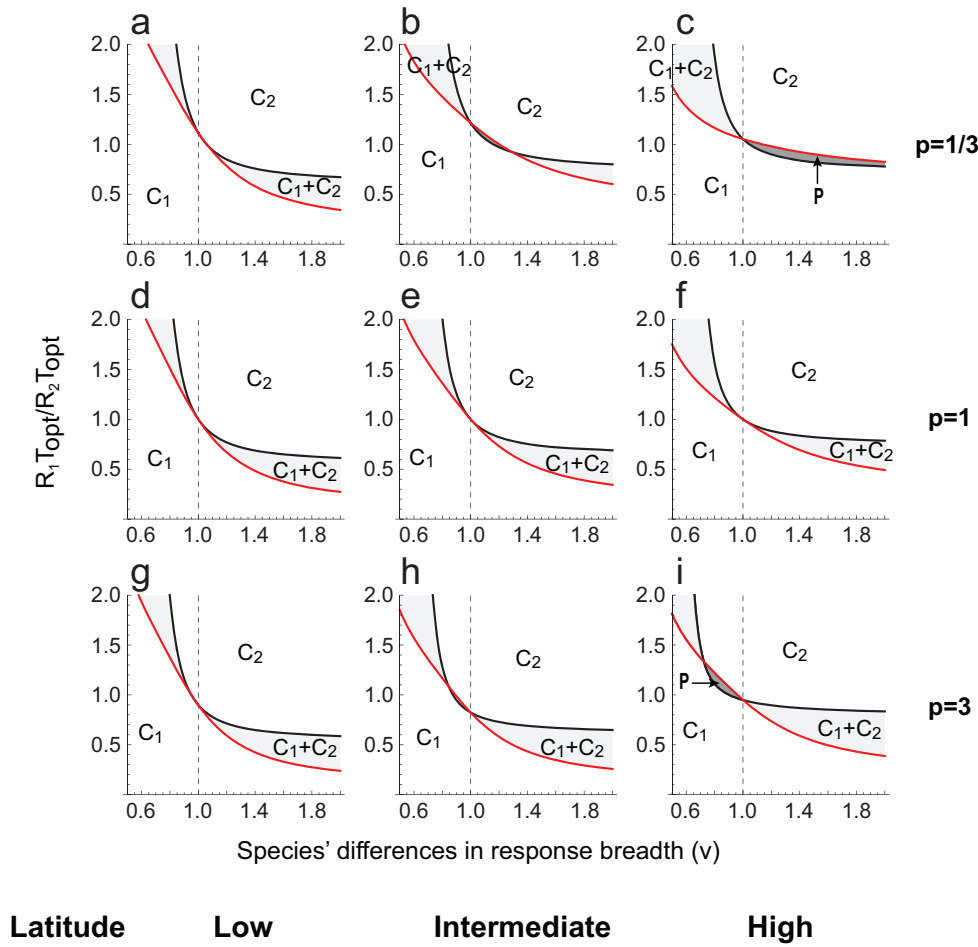
Numerical analyses show that in all of the above cases, when mutual invasibility is possible, the three-species community settles into a steady state characterized by interannual fluctuations of constant amplitude (fig. B1; app. B). Our main findings are also robust to potential nonlinearities in the latitudinal relationships of attack rate optima and response breadth (figs. G1, G2; app. G).

#### *Case Study: Parasitoids of the Harlequin Bug*

Our trait-based framework allows us to predict the outcome of competitive interactions based solely on differences between consumer species in the parameters of their attack and mortality rate responses. These predictions can be tested by using experimental or observational data on population-level abundance patterns. Here we illustrate this approach with a well-studied insect host-parasitoid community.

We know from previous work that the two parasitoids (*Trissolcus murgantiae* and *Ooencyrtus johnsonii*) engage in exploitative competition for a common resource (eggs of the harlequin bug). Here we ask whether they can potentially coexist based solely on differences in their attack and mortality responses to temperature and in the absence of other biological factors (e.g., resource heterogeneity, interference competition, differential nonlinearity in functional responses). We use existing data on the temperature responses of attack and mortality rates (app. C) to quantify the three quantities that encapsulate species' differences in trait responses:  $x$ ,  $v$ , and  $p$ .

The parasitoids have similar response breadths ( $v = 0.98$ ) but differ in attack rate optima ( $x = 1.04$ ) and temperature sensitivity of mortality ( $p = 0.82$ ). Importantly, the species with the lower attack rate optimum *Trissolcus* exhibits greater temperature sensitivity of mortality. Based on this trade-off, we predict that the necessary condition for mutual invasibility should be satisfied and that priority effects should not be possible. When we parameterize the necessary condition (eq. [12]) using the above values of  $x$ ,  $v$ , and  $p$ , we find that it is indeed satisfied. We also find that the observed differences in attack rate optima and temperature sensitivity of mortality nearly satisfy the sufficient condition (eq. [13]; fig. 5). When we calculate the range of possible  $R_{T_{opt}}$  ratios (the right-hand side of the sufficient condition; eq. [13]) given the variability associated with each parameter estimate (see app. C for details), we find that coexistence is possible, although exclusion of *Trissolcus* is the norm (figs. C2, C3; app. C).



**Figure 4:** Sufficient condition for mutual invasibility as a function of  $v$  when consumer species have the same attack rate optima ( $x = 0$ ) but differ in their response breadth ( $v \neq 1$ ) and thermal sensitivity of mortality ( $a-c$ ,  $p > 1$ ;  $g-i$ ,  $p < 1$ ). Mutual invasibility occurs in the shaded region marked  $C_1 + C_2$ , and priority effects occur in the region marked  $P$ . Parameter values are  $A_{d_i} = 15,000$  when  $p = 1/3$  and  $A_{d_i} = 5,000$  when  $p = 3$ . Other parameter values are as in figure 1.

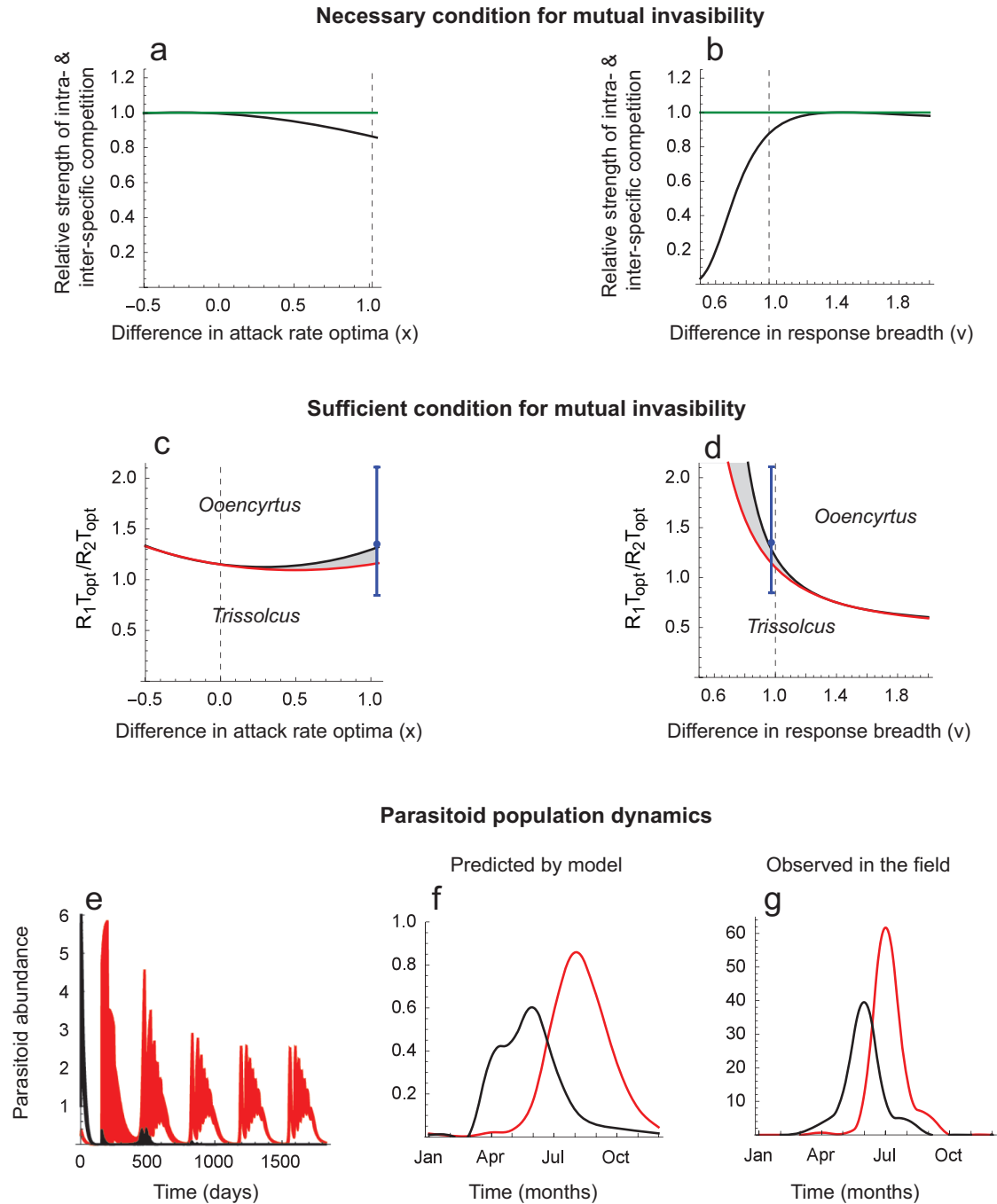
The validity of the results based on mutual invasibility are confirmed by an analysis of the full dynamical model (eq. [1]). When the model is parameterized with the mean values of the temperature response parameters estimated from the data, exclusion of *Trissolcus* is the sole outcome, regardless of the species' initial abundances (fig. 5). No priority effects are observed. When the model is parameterized with values within the range of observed variability in the data that satisfy the sufficient condition for mutual invasibility, it yields a seasonal abundance pattern qualitatively similar to that observed in the field (fig. 5).

### Discussion

Theory tells us that temporal niche partitioning can occur when species differ sufficiently in their responses to abiotic

variation (Chesson 2000). To determine whether species differ sufficiently, we have to know how they differ in the first place. Addressing this issue requires starting at the contact point between the environment and the population—traits of individual organisms—and scaling up from trait responses to population/community patterns. The framework we present here is an attempt to fill this gap in our knowledge.

The novel insight to emerge from our framework is that species' differences at the population level ultimately arise from asymmetries in their competitive effects generated by the nonlinear temperature response of mortality. Importantly, these differences manifest even when species do not differ in their mortality response. It is well established, through both theory and data, that the per capita mortality rate of all ectotherms increases exponentially with temperature, according to the Boltzmann-Arrhenius relationship for reaction kinetics



**Figure 5:** Necessary (*a, b*) and sufficient (*c, d*) conditions for mutual invasibility and population dynamics (*e–g*) for the two parasitoid species of the harlequin bug. In panels *a* and *b*, the solid black curve depicts the left-hand side of the necessary condition (eq. [12]) and the horizontal green line depicts the right-hand side of the necessary condition, which is equal to 1. The dashed vertical lines depict, respectively, the species' differences in attack rate optima ( $x = 1.01$ ; *a*) and response breadth ( $v = 0.98$ ; *b*). The left-hand side of the necessary condition is less than 1 for the parasitoids, thus satisfying the necessary condition. In panels *c* and *d*, the Y-axis depicts the ratio  $R_{1T_{opt}}/R_{2T_{opt}}$ , and the black and red curves depict, respectively, the invasion thresholds (eq. [13]) for *Trissolcus* and *Ooencyrtus* as a function of differences in  $x$  (*c*) and  $v$  (*d*). Above the black line, *Trissolcus* is excluded; below the red line, *Ooencyrtus* is excluded. Coexistence occurs in the gray region. In each panel, the blue circle depicts the ratio of  $R_{T_{opt}}$  values for the two species at their respective temperature optima (i.e.,  $R_{1T_{opt}}/R_{2T_{opt}} = 1.35$ ). The error bars constitute the range of  $R_{T_{opt}}$  ratios computed using the standard errors associated with each parameter estimate. Note that the errors bars are asymmetrical because the parameters affecting the ratio act multiplicatively rather than additively (app. C). *e*, The outcome of the dynamical model of the three-species interaction (eq. [1]), parameterized with the mean values of the parameter estimates, for varying initial abundances of *Trissolcus* (fig. C2 depicts the model outcome for different levels of initial abundances of *Ooencyrtus*; app. C). *f*, The model outcome when parameter values within the range of observed variability allow parasitoid coexistence (app. C). *g*, The seasonal abundance pattern of the two parasitoids observed in the field. Note that the model output is depicted as monthly averages to match the field data.

(Van der Have and de Jong 1996; Gillooly et al. 2001, 2002; Savage et al. 2004). Our findings, therefore, apply to all ectotherm taxa inhabiting thermally variable environments.

Our approach of characterizing species' per capita growth rates in terms of mechanistic descriptions of trait responses to temperature reveals that the exponential nature of the mortality response causes self-limitation strength to decrease with increasing temperature. This leads to the first asymmetry between competing species: cold-adapted species and thermal specialists experience stronger intraspecific competition than warm-adapted species and thermal generalists. Our approach also reveals that the exponential nature of the mortality response translates into lower  $R^*$  values and stronger interspecific competition at temperatures below a species' attack rate optimum compared to temperatures above it. This leads to the second asymmetry between species: cold-adapted species and thermal specialists exert weaker competition on, and experience stronger competition from, warm-adapted species and thermal generalists.

The crucial consequence of these two asymmetries is that coexistence hinges on whether the amount by which cold-adapted species (and thermal specialists) limit themselves more than they limit warm-adapted species (and thermal generalists) exceeds the amount by which warm-adapted species (and thermal generalists) limit cold-adapted species (and thermal specialists) more than they limit themselves (i.e.,  $\alpha_{ii} - \alpha_{ji} > \alpha_{ij} - \alpha_{jj}$ ,  $i = 1, 2$ ,  $i \neq j$ ). If self-limitation strength  $\alpha_{ii}$  in the cold-adapted species (or thermal specialist) exceeds its competitive effect  $\alpha_{ij}$  on the warm-adapted species (or thermal generalist) by an amount sufficient to overcome the deficit between intra- and interspecific competitive strengths in the warm-adapted species (thermal generalist; i.e.,  $\alpha_{ij} > \alpha_{jj}$ ), coexistence is possible. Coexistence is more likely if species exhibit trade-offs between mortality and attack efficiency/response breadth such that species with lower attack rate optima (i.e., those that are thus more cold-adapted) or narrower response breadths (i.e., those that are thus more thermally specialized) experience greater temperature sensitivity of mortality. When priority effects occur, it is because the warm-adapted species or thermal generalists exhibit greater temperature sensitivity of mortality, thus causing their competitive effect on the cold-adapted species or thermal specialists to greatly exceed their ability to limit themselves during the favorable months of the year.

It is this fundamental result—asymmetry between species in their competitive responses, driven by the nonlinear temperature response of mortality—that generates latitudinal patterns of coexistence and priority effects. The reason why we see qualitative changes in coexistence patterns and greater incidence of priority effects at higher latitudes is because the larger seasonal fluctuations at higher latitudes means that species experience a more nonlinear mortality response and, hence, greater asymmetry in their competitive responses.

Priority effects driven by species' responses to temperature variation are unlikely to be observed in the tropics because seasonal fluctuations are so small that tropical ectotherms effectively experience linear mortality responses.

A particular strength of our framework is that we can make testable predictions about the population-level outcome of competition based solely on species' differences in attack and mortality responses. In fact, we can distill these differences to three fundamental quantities: attack rate optima, response breadths, and temperature sensitivities of mortality, which is all we need to make predictions that can be tested at the population level. For instance, if species differ in their attack rate responses but have similar mortality responses, we know that priority effects cannot occur and that coexistence is possible if species with lower attack rate optima or narrower response breadths limit themselves more than they limit competitors with higher attack rate optima or wider response breadths. We also know that if species differ in their temperature sensitivity of mortality, coexistence requires a trade-off between mortality and attack rate efficiency/response breadth. It follows, therefore, that priority effects can arise when species differ in their temperature sensitivity of mortality but do not exhibit such trade-offs.

We test the predictions of our framework with data from a well-studied host-parasitoid system. Simply by quantifying the three basic quantities ( $x$ ,  $v$ , and  $p$ ), we predict that priority effects are not possible in this community. This prediction is borne out by two independent population-level analyses. First, a fully dynamical model, parameterized with trait response data, shows that long-term outcomes are independent of initial conditions. Second, population-level experiments in the lab and field show that competition between the two parasitoid species has a strongly deterministic outcome with no dependence on initial conditions (Kidd and Amarasekare 2012). Because the species with the lower attack rate optimum exhibits greater temperature sensitivity of mortality, we predicted that the necessary condition for mutual invasibility should be met. Quantifying the three quantities using laboratory data showed that the necessary condition was indeed satisfied and that the sufficient condition could be met given the observed level of individual variability in trait responses.

An additional strength of our framework is its generality. Not only can we predict the outcome of competition for consumers inhabiting a particular latitude, but by incorporating latitudinal relationships in how trait responses change with seasonal fluctuations, we can generalize our framework to competitive communities of ectotherms inhabiting any latitude. This generality allows us to test broader hypotheses about whether coexistence becomes more or less likely as one goes from the tropics to the tundra and whether thermal limits to similarity increase or decrease with increasing latitude.

Our approach is sufficiently flexible to address questions about competition starting at either the trait level or the population level. When coexistence is observed in the field with

a potential for thermal niche partitioning, our approach allows researchers to test this potential by quantifying species' differences using just three metrics. Our approach is equally amenable to predicting the population-level outcome based on trait responses. This is particularly important in predicting the impact of exotic invasive species on native biota. When an exotic species is at an early stage of invasion, knowing whether it will exclude or coexist with native species is crucial in implementing appropriate control strategies. One can use trait response data to predict whether an exotic species is likely to successfully establish in a particular geographic location and habitat type and use latitudinal relationships such as the ones used here to predict the geographic range over which an exotic species can exclude native species as opposed to coexisting with native species and eventually becoming naturalized.

Our framework can also predict the effects of climate warming on competitive interactions. By characterizing species' trait responses in terms of deviations in thermal optima from the mean habitat temperature and elucidating the outcome of competition when these deviations are positive versus negative (i.e., an incoming species' attack rate optimum is closer to or farther away from the mean habitat temperature), we provide a mechanistic basis for predicting how an increase in the mean temperature will influence competitive communities. For example, a higher mean should favor higher attack rate optima in the tropics and lower optima in the temperate zone. Perhaps most important, our framework can predict the effects of temperature extremes on competitive interactions. There is increasing evidence that warming will amplify such extremes (IPCC 2014), making it imperative that we be able to predict how species respond to such changes. Given the importance that species' mortality responses play in coexistence, we predict that species' differences in temperature sensitivity of mortality will be crucial in determining which species can survive the combined onslaught of climate warming and resource competition and which species cannot. We further predict that a combination of features—the deviation of the attack rate optima from the mean habitat temperature and the temperature sensitivity of mortality—will collectively determine the fate of competitive communities in the face of warming. Given that the qualitative nature of trait responses to temperature are conserved across ectotherm taxa and their parameters are thermodynamically constrained to lie within a narrow range of values, predictions about climate warming on competing species, especially the impact of invasive species on native biota, could be made using trait response data even from distantly related species.

Our framework investigates how different an incoming consumer species' trait responses have to be to invade a resident community in which both resource and consumer species are adapted to the ambient thermal environment. (This scenario directly captures the case of exotic species that in-

vade novel habitats to which they are not adapted.) In doing so we focus on the ecological differences, that is, differences that species exhibit on short timescales in the absence of any evolutionary feedback. A complete understanding of this problem requires analyzing the evolutionary divergence between competing species in response to the dual selection pressures of temperature and competition. This will be the subject of a future article.

In conclusion, the framework we have developed allows us to predict the population-level outcomes of competitive interactions based on the fundamental characteristics of ectotherm species' thermal niches that are easily empirically measured. Its generality and flexibility makes it amenable to both empirical testing and further theoretical analyses. The mechanistic understanding of species' thermal niche partitioning we have achieved here not only yields conceptual insights about species coexistence in variable environments but also provides a basis for addressing important environmental issues such as climate change and invasive species.

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