vol. 189, no. 3 the american naturalist march 2017

E-Article

Evolution of Thermal Reaction Norms in Seasonally Varying Environments

Priyanga Amarasekare[1,*] **and Christopher Johnson**[2]

1. Department of Ecology and Evolutionary Biology, University of California, Los Angeles, California 90095; 2. Center for Adaptations to a Changing Environment (ACE), Institute of Integrative Biology, ETH Zurich, 8092 Zurich, Switzerland

Submitted October 7, 2015; Accepted October 24, 2016; Electronically published February 1, 2017

Online enhancements: appendixes.

abstract: Thermal reaction norms of ectotherms exhibit a distinctive latitudinal pattern: the temperature at which performance is maximized coincides with the mean habitat temperature in tropical ectotherms but exceeds the mean temperature in temperate ectotherms. We hypothesize, on the basis of Jensen's inequality, that this pattern is driven by latitudinal variation in seasonal temperature fluctuations. We test this hypothesis with an eco-evolutionary model that integrates the quantitative genetics of reaction norm evolution with stage-structured population dynamics, which we parameterize with data from insects. We find that thermal optima of temperate and Mediterranean species evolve to exceed the mean habitat temperature if seasonal fluctuations are strong, while the thermal optimum of tropical species evolves to coincide with the mean habitat temperature if fluctuations are weak. Importantly, ecological dynamics can impose a constraint on reaction norm evolution. Tropical species cannot tolerate an increase in seasonal fluctuations at the high mean habitat temperature it experiences, while the temperate species cannot tolerate a reduction in seasonal fluctuations if the mean temperature is higher. In both cases, stochastic extinction during periods of low abundances precludes adaptation to a novel thermal environment. Our findings suggest a potential directionality in colonization success. Tropical ectotherms, because of their high thermal optima, can successfully colonize temperate habitats, while temperate ectotherms, because of their low optima, are less successful in colonizing tropical habitats.

Keywords: eco-evolutionary dynamics, life-history traits, reaction norms, reproduction temperature variation.

Introduction

Ectotherm life-history traits (fecundity, development, survivorship) typically exhibit unimodal responses to temperature variation (Van der Have and de Jong 1996; Van der Have 2002; Kingsolver 2009; Kingsolver et al. 2011). Such responses are characterized by a temperature at which the trait value is maximized (thermal optimum) and a range over which the organism can respond to temperature (response breadth). A large number of empirical studies (reviewed in Huey and Berrigan 2001; Deutsch et al. 2008; Kingsolver 2009; Dell et al. 2011; Kingsolver et al. 2011; Amarasekare and Savage 2012) show that the qualitative nature of these reaction norms (e.g., Gaussian, left-skewed) is conserved across ectotherm taxa (invertebrates, amphibians, reptiles). This is because the temperature responses of biochemical and physiological processes (e.g., reaction kinetics, enzyme inactivation, hormonal regulation) that underlie these reaction norms are themselves conserved across ectotherm taxa (Van der Have and de Jong 1996; Van der Have 2002; Kingsolver 2009). However, there are quantitative differences, the most prominent of which is the latitudinal variation in the relationship between thermal optima and the mean habitat temperature. Tropical ectotherms exhibit thermal optima for reproduction that are close to the mean habitat temperature, while temperate ectotherms' optima are well above the mean habitat temperature (Deutsch et al. 2008; Tewksbury et al. 2008). Our goal is to elucidate the mechanisms that drive this difference.

As is well known, the response breadth of thermal reaction norms tends to increase with increasing latitude. The standard explanation for this pattern is latitudinal differences in seasonal temperature variation. Temperate ectotherms exhibit a greater response breadth because they experience thermal environments with larger seasonal fluctuations (Gilchrist 1995). We might therefore hypothesize that seasonal temperature variation may also be driving latitudinal variation in thermal optima. However, it is not immediately clear how stronger seasonal fluctuations cause thermal optima to exceed the mean habitat temperature. While previous theory has shown that larger seasonal fluctuations can select for a wider temperature response (Gilchrist 1995) and a lower optimal body temperature (Martin and Huey 2008), there is no theory we know of that investigates how seasonal fluctuations influence latitudinal variation in thermal optima.

---

* Corresponding author; e-mail: amarasek@ucla.edu.

Am. Nat. 2017. Vol. 189, pp. E000–E000.
DOI: 10.1086/690293

We address this question with a theoretical framework that integrates quantitative genetic models of reaction norm evolution with stage-structured models of population dynamics. The distinctive feature of this framework is that it incorporates mechanistic descriptions of life-history trait responses to temperature, derived from first principles of thermodynamics, into population models that realistically depict the complex life cycles characteristic of multicellular ectotherms. We incorporate both density-dependent population regulation and extinction at low abundances due to demographic stochasticity. It is, to our knowledge, the first time that these biological features have been incorporated into a model of reaction norm evolution.

Mathematical Framework

Overview

Our analysis involves two main parts. The first part involves developing a hypothesis for why the difference between a species' thermal optimum and the mean habitat temperature increases with increasing latitude. As pointed out above, thermal reaction norms of ectotherms are nonlinear functions of temperature. This allows us to use a mathematical property of nonlinear functions (Jensen's inequality; Jensen 1906) to develop our hypothesis. The second part of our analysis involves developing an eco-evolutionary model to test the predictions of this hypothesis. This part involves the following steps. First, we derive an expression for the mean reaction norm using standard quantitative genetics. Second, we specify the ecological dynamics, taking into account the stage structure (e.g., eggs, juveniles, adults) that is characteristic of ectotherm life cycles. Third, we integrate the quantitative genetic and ecological components into a dynamical model of eco-evolutionary dynamics, from which we derive an expression for the mean fitness of the population. Fourth, we incorporate mechanistic descriptions of how temperature affects ectotherm life-history traits (fecundity, development, mortality) into the full eco-evolutionary model. In the final step, we parameterize the model with data on ectotherm species from different latitudes (tropical, Mediterranean, temperate) to investigate how thermal reaction norms evolve in seasonally varying environments.

Hypothesis Based on Jensen's Inequality

Jensen's inequality is a property of nonlinear mathematical functions. Specifically, if f is a nonlinear function of the variable x with mean $\bar{x}$, $f(\bar{x}) \neq \overline{f(x)}$. When the function is concave down (e.g., unimodal), $f(\bar{x}) > \overline{f(x)}$ and vice versa (Ruel and Ayers 1997). To give a concrete (and familiar) example, logistic population growth is a concave-down function of population size, that is,

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right).$$

The growth rate (dN/dt) is zero when $N = 0$ and $N = K$ and attains a maximum ($rK/4$) at the mean population size ($\bar{N} = K/2$). Therefore, when N is less than or greater than $K/2$,

$$\frac{dN}{dt} < \frac{rK}{4},$$

and the mean population growth over all population sizes ($\overline{dN/dt}$) is less than the population growth at the mean population size ($d\bar{N}/dt$). For instance, if $r = 1$ and $K = 1$,

$$\overline{\frac{dN}{dt}} = \int_0^K rN\left(1 - \frac{N}{K}\right)\mathrm{d}N = \frac{rK^2}{6} = 0.167$$

$$\text{while } \frac{d\bar{N}}{dt} = 0.25.$$

Jensen's inequality is important for understanding how reaction norms evolve in thermally variable environments. Temperature effects on biochemical processes (e.g., reaction kinetics, hormonal regulation) dictate that the thermal reaction norms of life-history traits (fecundity, development, survivorship) be unimodal functions of temperature, that is, the trait value increases with temperature to a maximum and declines as temperature increases further (Van der Have and de Jong 1996; Huey and Berrigan 2001; Van der Have 2002; Frazier et al. 2006; Kingsolver 2009; Kingsolver et al. 2011; Amarasekare and Savage 2012). Since unimodal functions are concave down, performance at the mean habitat temperature should exceed the average performance over the temperature range experienced. How, then, would the optimum evolve to exceed the mean habitat temperature?

We focus on the temperature response of reproduction, as it is a major component of fitness. Data from a large number of ectotherms spanning different taxa, habitats, and latitudes (e.g., Dreyer and Baumgartner 1996; Carriere and Boivin 1997; Morgan et al. 2001; Zamani et al. 2006; Parajulee 2006; Jandricic et al. 2010; Hou and Weng 2010; Dannon et al. 2010; Dell et al. 2011; Amarasekare and Savage 2012) show that the temperature response of per capita fecundity (number of offspring per female) is symmetric unimodal (fig. 1) and well described by a Gaussian function:

$$b(T) = b_{T_{\text{opt}}} e^{-\frac{(T - T_{\text{opt}_b})^2}{2s_b^2}}, \tag{1}$$

where T_{opt_b} is the temperature (K) at which fecundity is maximal ($b_{T_{\text{opt}}}$), and s_b depicts the temperature range over which fecundity deviates from the optimum.

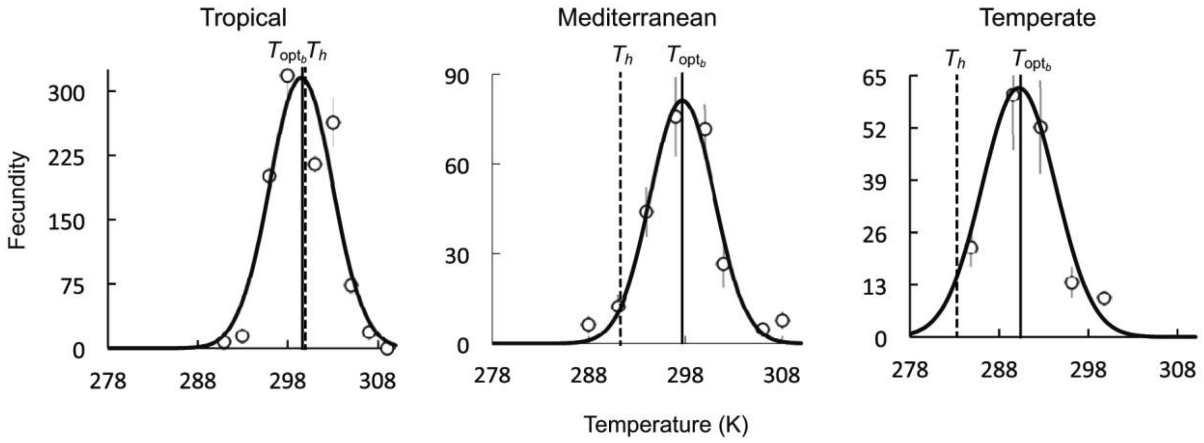

Figure 1: Temperature responses of fecundity for tropical, Mediterranean, and temperate insect species. Open circles are data from temperature experiments, and the solid curve is the fit to a Gaussian function (eq. [1]). In all panels, T_{h} is the mean habitat temperature, and T_{opt_b} is the optimum temperature at which fecundity is maximized. Parameter values are given in table B1, appendix B.

Consider an ectotherm species experiencing a constant thermal environment characterized by $\bar{T}$. The temperature response of its per capita fecundity is given by

$$b(\bar{T}) = b_{T_{\text{opt}}} e^{-\frac{(\bar{T}-T_{\text{opt}_b})^2}{2s_b^2}}. \tag{2}$$

Because $b(T)$ is a concave-down function, $b(\bar{T})$ is maximized (i.e., $b(\bar{T}) = b_{T_{\text{opt}}}$) when $T_{\text{opt}_b} = \bar{T}$. Hence, the organism will maximize its fitness when the temperature at which fecundity is maximal coincides with the habitat temperature.

Now consider the same organism, with maximum fecundity $b_{T_{\text{opt}_{\bar{T}}}}$ and $T_{\text{opt}_b} = \bar{T}$, in a seasonal environment with fluctuations of amplitude A_T around the mean temperature $\bar{T}$. Its temperature response of fecundity is given by

$$b(T(t)) = b_{T_{\text{opt}_{\bar{T}}}} e^{-\frac{(T(t)-\bar{T})^2}{2s_b^2}}, \tag{3}$$

where seasonal temperature variation ($T(t)$) is given by $\bar{T} - A_T\omega t$, with $\omega = \cos(2\pi/t_m)$ (or $-\sin(2\pi/t_m)$) and $t_m = 365$ days.

The average fecundity over the year is given by

$$\overline{b(T(t))} = \frac{b_{T_{\text{opt}_{\bar{T}}}}}{t_m}\int_0^{t_m} e^{-\frac{(A_T\omega t)^2}{2s_b^2}}\,\mathrm{d}t. \tag{4}$$

Since seasonal temperature variation is nonnegative (i.e., $A_T\omega t > 0$ always),

$$e^{-\frac{(A_T\omega t)^2}{2s_b^2}} < 1$$

and $\overline{b(T(t))} < b(\bar{T})$. This means that an organism whose maximum fecundity occurs at the mean habitat temperature will have a lower fitness in a seasonal environment compared with a constant environment. Natural selection will therefore favor the evolution of a higher maximum fecundity ($b_{T_{\text{opt}_s}}$) in a seasonal environment. Importantly, if selection drives maximum fecundity to exceed that attained in a constant environment (i.e., $b_{T_{\text{opt}_s}} > b_{T_{\text{opt}_{\bar{T}}}}$), the thermal optimum will no longer coincide with the mean habitat temperature (i.e., $T_{\text{opt}_b} \neq \bar{T}$). Given empirical evidence that maximum performance is greater at higher temperatures (Savage et al. 2004; Frazier et al. 2006), $b_{T_{\text{opt}_s}} > b_{T_{\text{opt}_{\bar{T}}}}$ means that $T_{\text{opt}_b} > \bar{T}$.

On the basis of the argument given above, if natural selection leads to adaptations that maximize fitness in a given thermal environment, fecundity of ectotherms experiencing seasonally varying thermal environments should be maximized at a temperature (T_{opt_b}) that exceeds the mean habitat temperature. The greater the amplitude of seasonal fluctuations, the greater should be the difference between the physiologically optimal temperature and the mean habitat temperature.

This hypothesis leads to two predictions. If the amplitude of seasonal fluctuations is what drives the relationship between thermal optima and the mean habitat temperature, then (i) thermal optima of temperate ectotherms should not evolve to exceed the mean habitat temperature if the amplitude of seasonal fluctuations decreased while the mean temperature stayed the same and (ii) thermal optima of tropical ectotherms should not evolve to coincide with the mean habitat temperature if the amplitude of seasonal fluctuations increased while the mean temperature stayed the same.

The manipulations of the seasonal environment required to test these predictions are difficult to implement in a field or laboratory setting. They are, however, relatively easy to implement in a mathematical model. Importantly, because temperature fluctuations, through their effects on life-history traits, influence both selection and population dynamics, such a model needs to incorporate both ecological and evolutionary dynamics. This brings us to the second part of our analysis.

Model of Eco-Evolutionary Dynamics

We develop an eco-evolutionary model that integrates quantitative genetics of reaction norm evolution with ecological dynamics. We consider maximum fecundity ($b_{T_{\mathrm{opt}}}$) to be the trait that natural selection acts on. Energetic constraints impose a trade-off between maximum fecundity and response breadth such that response breadth evolves as a correlated trait. This combination of selection and constraints drives the evolution of the reaction norm. Evolution occurs against the backdrop of ecological dynamics characterized by stage-structure and density-dependent population regulation, with the possibility of stochastic extinction when populations go through periods of low abundances.

We begin by developing a quantitative genetic expression for the thermal reaction norm for fecundity, which we then incorporate into a stage-structured model of ecological dynamics.

Thermal Reaction Norm for Fecundity. Let maximum fecundity ($b_{T_{\mathrm{opt}}}$) be driven by a quantitative trait x, which is subject to stabilizing selection and has a polygenic basis, that is, it is controlled additively by a number of loci (Falconer and McKay 1996; Lynch and Walsh 1998). The trait x is normally distributed and has a probability density function (PDF) of

$$p(x,\bar{x}) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{(x-\bar{x})^2}{2\sigma^2}}, \tag{5}$$

where $\bar{x}$ is the trait mean and σ^2 is the variance. The latter consists of an additive genetic component (σ_{G}^2) and an environmental component (σ_{E}^2; Falconer and McKay 1996; Lynch and Walsh 1998). As a first step in investigating reaction norm evolution from an eco-evolutionary perspective, we focus on the evolution of the mean trait $\bar{x}$ and consider σ^2 to remain constant.

Maximum fecundity ($b_{T_{\mathrm{opt}}}$) peaks at an optimal trait value $x = \mu$ and declines as the trait value deviates from the optimum. This relationship can be characterized by a Gaussian function:

$$b_{T_{\mathrm{opt}}}(x) = \beta e^{-\frac{(x-\mu)^2}{2\gamma^2}}, \tag{6}$$

where β is the maximum value of $b_{T_{\mathrm{opt}}}$ and γ depicts the variability in $b_{T_{\mathrm{opt}}}$ when x deviates from μ.

One might expect energetic or other constraints to generate a trade-off between $b_{T_{\mathrm{opt}}}$ and s_b, that is, an increase in maximum fecundity comes at the cost of a reduction in the temperature range over which the organism can reproduce. We can quantify this negative correlation between $b_{T_{\mathrm{opt}}}$ and s_b by considering the area under the reaction norm curve (K) to be constant, that is,

$$K = \frac{\beta\sqrt{2\pi}}{\sqrt{1/s_{\max}^2}},$$

where $s_{\max}$ is the maximum response breath that can be achieved given biochemical and physiological constraints in a given thermal environment. A trade-off between $b_{T_{\mathrm{opt}}}$ and s_b means that as $b_{T_{\mathrm{opt}}}$ evolves, s_b evolves as a correlated trait.

We can write down the thermal reaction norm for fecundity for an individual organism as

$$b(T,x) = b_{T_{\mathrm{opt}}}(x) e^{-\frac{\left(T-T_{\mathrm{opt}_b}\left(b_{T_{\mathrm{opt}}}(x)\right)\right)^2}{2s_b\left(b_{T_{\mathrm{opt}}}(x)\right)^2}}, \tag{7}$$

where $T_{\mathrm{opt}_b}(b_{T_{\mathrm{opt}}}(x))$ is the temperature at which $b(T,x) = b_{T_{\mathrm{opt}}}(x)$ and

$$s_b\left(b_{T_{\mathrm{opt}}}(x)\right) = \frac{K}{b_{T_{\mathrm{opt}}}(x)\sqrt{2\pi}}.$$

The average value of $b_{T_{\mathrm{opt}}}(x)$ is obtained by integrating over all possible values of x, that is,

$$\begin{aligned} \bar{b}_{T_{\mathrm{opt}}}(\bar{x}) &= \int_{-\infty}^{+\infty} b_{T_{\mathrm{opt}}}(x) p(x,\bar{x}) \mathrm{d}x \\ &= \frac{\beta\gamma}{\sqrt{\sigma^2+\gamma^2}} e^{-\frac{(\bar{x}-\mu)^2}{2(\sigma^2+\gamma^2)}}, \end{aligned} \tag{8}$$

which yields the following mean reaction norm for the population:

$$\bar{b}(T,\bar{x}) = \bar{b}_{T_{\mathrm{opt}}}(\bar{x}) e^{-\frac{\left(T-T_{\mathrm{opt}_{\bar{b}}}\left(\bar{b}_{T_{\mathrm{opt}}}(\bar{x})\right)\right)^2}{2s_b\left(\bar{b}_{T_{\mathrm{opt}}}(\bar{x})\right)^2}}. \tag{9}$$

The temperature at which $\bar{b}_{T_{\mathrm{opt}}}(\bar{x})$ is achieved is calculated by solving

$$\bar{b}_{T_{\mathrm{opt}}}(\bar{x}) = \beta e^{-\frac{\left(T_{\mathrm{opt}_{\bar{b}}}\left(\bar{b}_{T_{\mathrm{opt}}}(\bar{x})\right)-T_{\mathrm{opt}_\beta}\right)^2}{2s_b\left(\bar{b}_{T_{\mathrm{opt}}}(\bar{x})\right)^2}} \tag{10}$$

for $T_{\mathrm{opt}_{\bar{b}}}(\bar{b}_{T_{\mathrm{opt}}}(\bar{x}))$. Since equation (10) is nonlinear in $T_{\mathrm{opt}_{\bar{b}}}(\bar{b}_{T_{\mathrm{opt}}}(\bar{x}))$ (i.e., it appears as a squared term when one expands eq. [10]), we use the quadratic formula to solve it. This yields

$$T_{\mathrm{opt}_{\bar{b}}}\left(\bar{b}_{T_{\mathrm{opt}}}(\bar{x})\right) = T_{\mathrm{opt}_\beta} - \sqrt{2}\sqrt{-s_b\left(\bar{b}_{T_{\mathrm{opt}}}(\bar{x})\right)^2 \ln\frac{\bar{b}_{T_{\mathrm{opt}}}(\bar{x})}{\beta}}, \tag{11}$$

where T_{opt_β} is the temperature at which β is achieved. Note that $b_{T_{\mathrm{opt}}}(\bar{x})$ changes as the trait x evolves, and hence $T_{\mathrm{opt}_{\bar{b}}}(\bar{b}_{T_{\mathrm{opt}}}(\bar{x}))$ also changes over time. We want to know the conditions under which $b_{T_{\mathrm{opt}}}(\bar{x})$ evolves toward β, as a result of which $T_{\mathrm{opt}_b}(\bar{b}_{T_{\mathrm{opt}}}(\bar{x}))$ approaches T_{opt_β}.

Having derived an explicit expression for the thermal reaction norm using principles of quantitative genetics, the next step is to specify the ecological dynamics.

Ecological Dynamics. We consider the simplest depiction of an ectotherm life cycle, a population of juveniles and adults:

$$\begin{aligned}\frac{dJ}{dt} &= b(T,x)Ae^{-q_b(T)A} - m_{\mathrm{J}}(T)J - J(d_{\mathrm{J}}(T) + q_{d_{\mathrm{J}}}(T)J),\\ \frac{dA}{dt} &= m_{\mathrm{J}}(T)J - A(d_{\mathrm{A}}(T) + q_{d_{\mathrm{A}}}(T)A),\end{aligned} \tag{12}$$

where the variables J and A represent, respectively, the abundances of juveniles and adults. Recruitment to the juvenile stage occurs via adult reproduction ($b(T,x)Ae^{-q_b(T)A}$), and losses occur via the maturation of juveniles into the adult stage ($m_{\mathrm{J}}(T)J$) and juvenile mortality ($d_{\mathrm{J}}(T)J(1 + q_{d_{\mathrm{J}}}(T)J)$). Recruitment to the adult stage occurs via juvenile maturation ($m_{\mathrm{J}}(T)J$) and losses, through adult mortality ($d_{\mathrm{A}}(T)A(1 + q_{d_{\mathrm{A}}}(T)A)$). The functions $m_{\mathrm{J}}(T)$, $d_{\mathrm{J}}(T)$, and $d_{\mathrm{A}}(T)$ denote, respectively, the temperature responses of the per capita juvenile maturation rate, the juvenile mortality rate, and the adult mortality rate in the absence of density-dependent population regulation, and the functions $e^{-q_b(T)A}$, $q_{d_{\mathrm{J}}}(T)J$, and $q_{d_{\mathrm{A}}}(T)A$ depict, respectively, the temperature responses of density-dependent fecundity, juvenile mortality, and adult mortality. Function definitions are given in the sections below on the temperature responses of life-history traits and competition.

Eco-Evolutionary Dynamics. The feedback between ecological dynamics and reaction norm evolution is mediated by the mean fitness of the population ($\bar{W}$). To derive an equation for mean fitness, we start with the fitness of an individual with phenotype x ($W(x,J,A)$), which is given by its per capita growth rate. In stage-structured models, the per capita growth rate is calculated as the dominant eigenvalue of the system of equations (eq. [12] in our case; see app. A for details; apps. A–G are available online):

$$\begin{aligned}W(x,J,A) = -\frac{1}{2}e^{-B}(-[&e^{2B}(C + D)^2\\ &- 4e^B(b(T,x)E\\ &+ C(De^B)) + e^B(CD)]^{1/2}),\end{aligned} \tag{13}$$

where $B = Aq_b(T)$, $C = d_{\mathrm{J}}(T) + 2Jq_{d_{\mathrm{J}}}(T) + m_{\mathrm{J}}(T)$, $D = d_{\mathrm{A}}(T) + 2Aq_{d_{\mathrm{A}}}(T)$, and $E = m_{\mathrm{J}}(T)(B - 1)$. When density dependence operates on only one or two traits, equation (13) simplifies accordingly.

We obtain the mean fitness of the population by integrating the fitnesses of all individuals over all values of the phenotype x:

$$\begin{aligned}\bar{W}(\bar{x},J,A) &= \int_{-\infty}^{\infty} W(x,J,A)p(x,\bar{x})\mathrm{d}x\\ &= -\frac{1}{2}e^{-B}(-[e^{2B}(C + D)^2 - 4e^B(\bar{b}(T,\bar{x})E\\ &\qquad + C(De^B)) + e^B(CD)]^{1/2}).\end{aligned} \tag{14}$$

The eco-evolutionary dynamics are given by

$$\begin{aligned}\frac{dJ}{dt} &= \bar{b}(T,\bar{x})Ae^{-q_b(T)A} - m_{\mathrm{J}}(T)J - J(d_{\mathrm{J}}(T) + q_{d_{\mathrm{J}}}(T)J),\\ \frac{dA}{dt} &= m_{\mathrm{J}}(T)J - A(d_{\mathrm{A}}(T) + q_{d_{\mathrm{A}}}(T)A),\\ \frac{d\bar{x}}{dt} &= h^2\sigma^2\frac{\partial \bar{W}}{\partial \bar{x}},\end{aligned} \tag{15}$$

where h^2 is the narrow-sense heritability (Falconer and McKay 1996) and $\partial\bar{W}/\partial\bar{x}$ is the selection gradient (the rate at which mean fitness changes with the mean trait value).

An eco-evolutionary model in which reaction norms of all life-history traits simultaneously evolve would be immensely complicated and analytically intractable within the quantitative genetics framework. We therefore focus on the evolution of the thermal reaction norm for fecundity and consider the empirically observed reaction norms of development and mortality in the organism's typical thermal environment to constitute evolved adaptations to that environment. Investigations of how thermal reaction norms of different life-history traits coevolve is an important future direction (see "Discussion").

Theory predicts—and data confirm—that different life-history traits exhibit qualitatively different types of nonlinear responses to temperature (e.g., exponential, Gaussian, left-skewed; Sharpe and DeMichele 1977; Schoolfield et al. 1981; Van der Have and de Jong 1996; Gillooly et al. 2001, 2002; Van der Have 2002; Savage et al. 2004; Ratkowsky et al. 2005; Kingsolver 2009; Kingsolver et al. 2011; Amarasekare and Savage 2012). We therefore need to consider how these different response types influence eco-evolutionary dynamics. We start by providing mechanistic descriptions of these temperature responses.

Temperature Responses of Life-History Traits

Temperature responses of reproduction, development, and mortality are determined by 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). For instance, temperature effects on biochemical rate processes (e.g., reaction kinetics, enzyme inactivation) give rise to temperature responses at the organismal level that are monotonic or left-skewed. Mortality and maturation rates tend to exhibit this type of response. In contrast, 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: rate processes on the left- and right-hand sides push the system toward an intermediate optimum. These effects result in temperature responses that are unimodal and symmetric (e.g., Gaussian). Reproductive traits tend to exhibit this type of response.

The per capita mortality rate of all ectotherms exhibits a monotonic temperature response that is well described by the Boltzmann-Arrhenius function for reaction kinetics (Van der Have and de Jong 1996; Gillooly et al. 2001, 2002; Savage et al. 2004):

$$d_L(T) = d_{L_{\mathrm{TR}}} e^{A_{d_L}\left(\frac{1}{\mathrm{TR}}-\frac{1}{T}\right)}, \tag{16}$$

where $d_L(T)$ is the mortality rate of stage L (e.g., juvenile, adult) at temperature T (K), $d_{L_{\mathrm{TR}}}$ is the mortality rate at a reference temperature (TR), and A_{d_L} is the Arrhenius constant, which quantifies the temperature sensitivity of mortality, that is, how fast it increases with increasing temperature (app. A).

As described in the "Mathematical Framework" section, data show that the temperature response of per capita fecundity is symmetric unimodal and well described by a Gaussian function (eq. [1]; fig. 1).

The maturation rate of ectotherms exhibits a left-skewed temperature response (Sharpe and DeMichele 1977; Schoolfield et al. 1981; Van der Have and de Jong 1996; Van der Have 2002; Kingsolver 2009; Kingsolver et al. 2011) that results from the reduction in reaction rates at low and high temperature extremes due to enzyme inactivation. This response is well described by a thermodynamic rate process model (Sharpe and DeMichele 1977; Schoolfield et al. 1981; Ratkowsky et al. 2005); (app. A):

$$m(T) = \frac{\frac{m_{\mathrm{TR}}T}{\mathrm{TR}} e^{A_{m_{\mathrm{J}}}\left(\frac{1}{\mathrm{TR}}-\frac{1}{T}\right)}}{1 + e^{A_{\mathrm{L}}\left(\frac{1}{T_{\mathrm{L}/2}}-\frac{1}{T}\right)} + e^{A_{\mathrm{H}}\left(\frac{1}{T_{\mathrm{H}/2}}-\frac{1}{T}\right)}}, \tag{17}$$

where $m(T)$ is the maturation rate at temperature T (K); m_{TR} is the maturation rate at the reference temperature TR at which the enzyme is 100% active; $A_{m_{\mathrm{J}}}$ (enthalpy of activation divided by the universal gas constant R) quantifies temperature sensitivity; $T_{\mathrm{L}/2}$ and $T_{\mathrm{H}/2}$ are, respectively, the low and high temperatures at which the enzyme is 50% active; and A_{L} and A_{H} are, respectively, the enthalpy changes associated with low and high temperature enzyme inactivation divided by R (Johnson and Lewin 1946; Sharpe and DeMichele 1977; Schoolfield et al. 1981; Van der Have and de Jong 1996; Van der Have 2002; Ratkowsky et al. 2005).

Effects of Temperature on Intraspecific Competition

To investigate temperature effects on population dynamics, we need to know how temperature affects population regulation. Following previous theoretical studies (Savage et al. 2004; Amarasekare and Coutinho 2014) we consider two hypotheses for the temperature response of competition. First, if higher activity levels at higher temperatures increase the per-individual resource acquisition, reducing the carrying capacity when resources are limiting, we expect the strength of competition to increase monotonically with temperature. This relationship can be described using the Boltzmann-Arrhenius function:

$$q(T) = q_{\mathrm{TR}} e^{A_q\left(\frac{1}{\mathrm{TR}}-\frac{1}{T}\right)}, \tag{18}$$

where q_{TR} is the per capita competitive effect at a reference temperature TR and A_q is the Arrhenius constant, which quantifies how fast competition strength increases with temperature.

The second hypothesis is that competition is strongest at temperatures that are physiologically optimal for reproduction (Begon et al. 2005). This is because of the increased energetic requirements during periods of peak reproductive activity, which increase the per-individual requirement for food and other limiting factors. In this case, the temperature response of competition should be unimodal:

$$q(T) = q_{T_{\max}} e^{-\frac{(T-T_{\max_q})^2}{2s_q{}^2}}, \tag{19}$$

where $T_{\max_q}$ is the temperature at which competition is strongest ($q_{T_{\max}}$) and s_q depicts the response width. There is empirical support for both hypotheses (Ritchie 1996; Reigada and Godoy 2006; Laws and Belovsky 2010; Gao et al. 2013; Johnson et al. 2015).

Now we have all the elements necessary to fully specify our eco-evolutionary model. The next step is to analyze the model, which proceeds in two steps: model parameterization using empirical data for ectotherm species and analysis of eco-evolutionary dynamics under different regimes of seasonal temperature variation.

Model Parameterization

We parameterize the eco-evolutionary dynamics model with data for three Hemipteran insect species from tropical, Mediterranean, and temperate latitudes. We use these particular species because they have the most complete data on the temperature responses of fecundity, maturation, and mortality rates, thus enabling us to accurately estimate the reaction norm parameters.

The tropical species is a pod-sucking bug (*Clavigralla shadabi*; Hemiptera: Coreidae) from Benin (8°20′N; Dreyer and Baumgartner 1996), the Mediterranean species is the harlequin bug (*Murgantia histrionica*; Hemiptera: Pentatomidae) from coastal southern California (33°37′8″N; Amarasekare 2000), and the temperate species is the pea aphid (*Acyrthosiphon pisum*; Hemiptera: Aphididae) from York, England (53°57′30″N; Morgan et al. 2001). The tropical species, which experiences a mean annual temperature of 27.2°C ($\mathrm{SE} = 0.09$) and amplitude of seasonal fluctuations (difference between maximum and minimum monthly temperature) of 3.5°, achieves its maximum birth rate at 27.4°C. The Mediterranean species, which experiences a mean annual temperature of 17.2°C ($\mathrm{SE} = 0.28$) and seasonal fluctuations of 10.5°, achieves its maximum birth rate at 25.3°C. The temperate species, which experiences a mean habitat temperature of 9.5°C ($\mathrm{SE} = 0.41$) and seasonal fluctuations of 13°, achieves its maximum birth rate at 18.5°C. All three species have multiple generations per year.

If the species are adapted to their current thermal environments—a reasonable assumption, since they are either native to their respective habitats or have been established in these habitats for more than a century—one would expect the observed temperature optimum for fecundity to be close to the optimum it is expected to achieve under stabilizing selection. We therefore consider the observed maximum fecundities and the temperature optima as approximations of β and T_{opt_β} and the observed response width as an approximation of $s_{\max}$.

Since the heritability of phenotypic traits tends to be low (Falconer and McKay 1996), we used a value of $h^2 = 0.1$ throughout. Higher heritabilities lead to faster evolutionary dynamics but do not have a qualitative effect on the long-term evolutionary outcome (Schreiber et al. 2011; Vasseur et al. 2011). Initial values of the quantitative trait x were set to values ($0.01-0.05$) well below that ($\mu = 1$) at which maximum fecundity (β) is achieved, after verifying that initial conditions did not affect the long-term ecological or evolutionary outcomes.

Model Analysis

To analyze the model, we need to specify the seasonal temperature regime under which reaction norm evolution occurs and the timescales over which we analyze eco-evolutionary dynamics. We describe these steps next.

Seasonal Temperature Variation. We use a sinusoidal function to incorporate seasonal temperature variation into the model. Specifically,

$$T(t) = M_T - A_T \cos\left(\frac{2\pi t}{t_m}\right),$$

where M_T and A_T depict, respectively, the mean annual temperature (K) and the amplitude of seasonal fluctuations, t is the time in days, and $t_m = 365$. The sinusoidal function ensures that the daily temperature fluctuates around the mean annual temperature with an amplitude given by A_T and a period of 365 days. The dependence of temperature on time ensures that the eco-evolutionary model captures the changes in activity levels and the resulting phenological patterns exhibited by each species in its typical thermal environment (fig. B1, app. B; figs. B1, C1, D1–D3, E1, F1, G1–G3 are available online). For example, let $k(T)$ be the temperature response function of the trait k (e.g., birth, maturation, or mortality rate). Since temperature is a function of time, the trait value also changes over time, taking high values when the temperature is favorable and low values when the temperature is unfavorable (fig. B1).

Eco-Evolutionary Dynamics. To investigate eco-evolutionary dynamics, we numerically integrated equation (15) under the seasonal regime experienced by each species. Because mean fitness is quantified as the dominant eigenvalue of the system of equations depicting ecological dynamics (eq. [12]), it is important to determine whether the population can attain a stable stage distribution (i.e., a constant juvenile-to-adult ratio) and, if so, how quickly. It has been shown previously that a population experiencing seasonal temperature variation can attain a stable age/stage distribution provided the nature of seasonal variation (e.g., mean temperature and amplitude of seasonal fluctuations) remains approximately constant across years (Amarasekare and Coutinho 2013). Simulations of the ecological model (eq. [12]), parameterized with data for the three species, show that a stable stage distribution is achieved within 1 year (fig. C1, app. C). To ensure that reaction norm evolution occurred in a population that had attained a stable stage distribution, we allowed stage-structured population dynamics to proceed for 50 years before initiating eco-evolutionary dynamics. We calculated the optimal temperature ($T_{\mathrm{opt}_b}(\bar{b}_{T_{\mathrm{opt}}}(\bar{x}))$) after 250 years of eco-evolutionary dynamics (750–1,000 generations, depending on the species). This time frame allowed sufficient time for eco-evolutionary dynamics to reach their long-term outcomes.

Stochastic Extinction. The interaction between the nonlinear temperature response functions of life-history traits and seasonal temperature variation can lead to complex dynamics characterized by large fluctuations in abundance. This predisposes species to extinction via demographic stochasticity during periods of low abundances. To investigate the effects of stochastic extinction on reaction norm evolution,

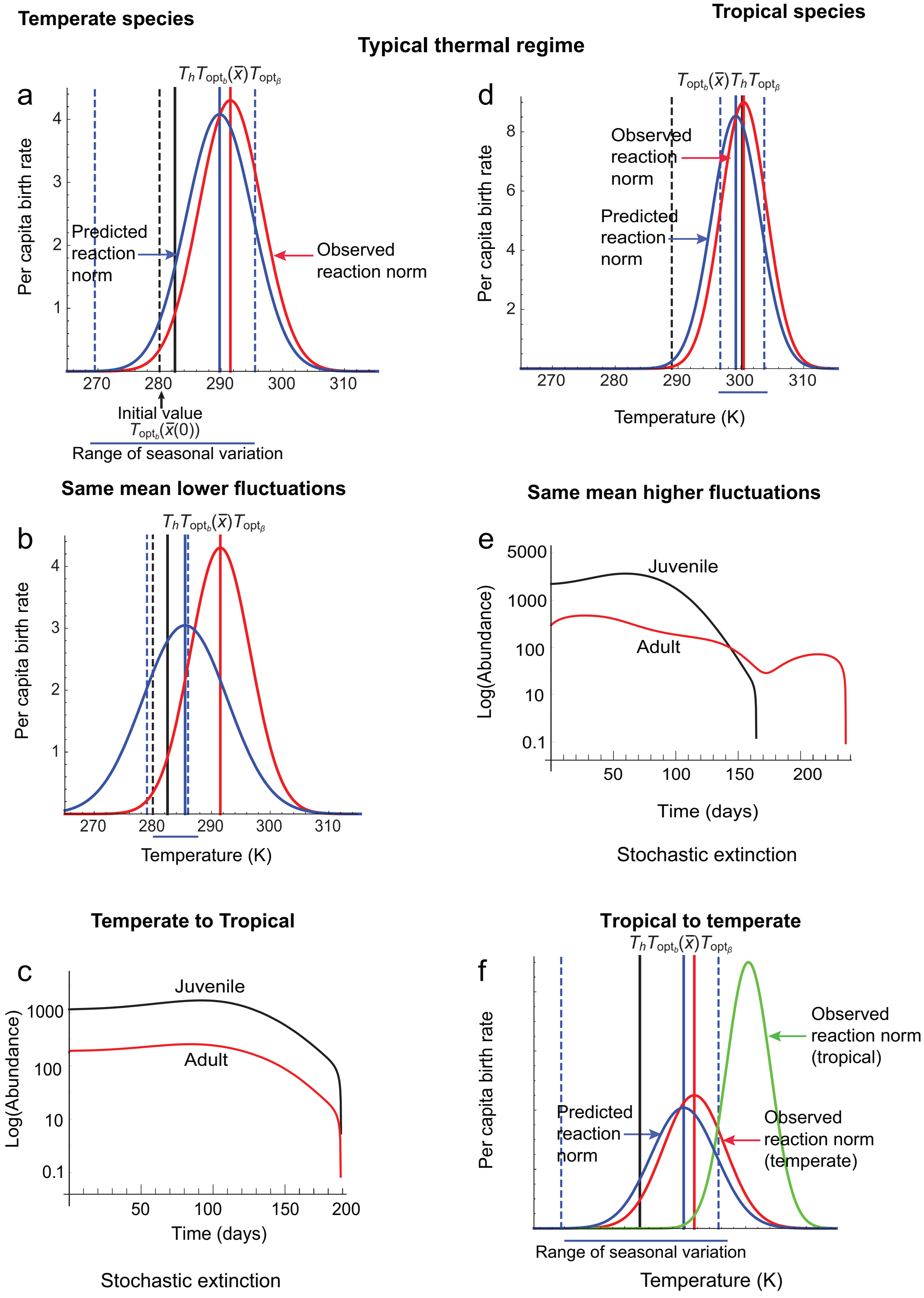

Figure 2: Thermal reaction norms for the temperate (*left*) and tropical (*right*) species when the temperature response of competition is unimodal and a trade-off exists between maximum fecundity and response breadth. Panels *a* and *d* depict the case when each species (tropical or temperate) is subject to its typical thermal regime. Panels *b* and *e* depict the case when each species experiences the same habitat mean but lower (temperate species) or higher (tropical species) fluctuations. Panels *c* and *f* depict the case when a temperate species is subject to a

we introduced an extinction threshold such that if the population size at any time fell below one individual, it was considered to have become extinct.

Testing Predictions. We conduct three types of analyses. In the first analysis, we investigate reaction norm evolution when each species is subject to its typical thermal environment. In the second analysis, we increase or decrease the magnitude of seasonal fluctuations while holding the mean temperature at the value typically experienced by the species. For example, we subject the temperate species, which typically experiences large seasonal fluctuations, to lower fluctuations characteristic of a tropical climate (3.5°C) while keeping the mean habitat temperature it experiences in a temperate climate (9.5°C). This allows us to determine the effect that seasonal fluctuations themselves have on reaction norm evolution. In the third analysis, we change both the mean and the amplitude of seasonal fluctuations, that is, we subject each species to a thermal regime different from the one it typically experiences. This allows us to investigate how the thermal reaction norm for fecundity evolves when a tropical ectotherm invades a temperate habitat and vice versa.

Since each species is native or naturalized to the habitat it resides in, it is reasonable to expect that natural selection has shaped the reaction norm for fecundity so as to maximize fitness in the organism's current thermal environment. These empirically observed reaction norms provide a basis for comparison with the reaction norms that evolve in our model.

Results

We begin with the temperate species, looking first at how the reaction norm evolves in the species' typical thermal environment. When the temperate species experiences the low habitat mean and high amplitude seasonal fluctuations characteristic of its typical thermal environment, maximum fecundity evolves at a temperature that is well above the mean habitat temperature and close to the empirically observed temperature optimum (fig. 2*a*). When it experiences the same habitat mean but weaker seasonal fluctuations, maximum fecundity evolves at a temperature that is only slightly above the habitat mean and well below the empirically observed temperature optimum (fig. 2*b*). When the temperate species is subject to a tropical thermal regime, exposure to high tropical temperatures cause abundances to fall so low that stochastic extinction occurs before the species can adapt to the new thermal environment (fig. 2*c*).

When the tropical species experiences the high habitat mean and low-amplitude fluctuations characteristic of its typical thermal environment, maximum fecundity evolves at a temperature that is close to the mean habitat temperature and the empirically observed temperature optimum (fig. 2*d*). When it experiences stronger seasonal fluctuations at the same high habitat mean, abundances fall so low that stochastic extinction occurs before the species can adapt to the new thermal regime (fig. 2*e*). However, when the tropical species is exposed to a temperate thermal regime with a low habitat mean and high-amplitude fluctuations, it evolves a reaction norm characteristic of a temperate species with a lower maximum fecundity and a wider response breadth (fig. 2*f*).

The Mediterranean species exhibits an intermediate situation. When subject to its typical environment, maximum fecundity evolves at a temperature that is well above the mean habitat temperature and close to the empirically observed optimum (fig. 3*a*). When it experiences the same habitat mean but weaker seasonal fluctuations, the Mediterranean species exhibits an evolutionary response similar to that of the temperate species, with maximum fecundity evolving at a temperature that is well below the empirically observed maximum (fig. 3*b*). When subject to a tropical thermal regime, the Mediterranean species evolves a reaction norm characteristic of a tropical species with higher maximum fecundity and lower response breadth; when subject to a temperate thermal regime, it evolves a reaction norm characteristic of a temperate species with lower maximum fecundity and higher response breadth (fig. 3*c*). This flexibility arises because the Mediterranean species' thermal reaction norm exhibits attributes of both tropical and temperate species. For example, it has a narrow response breadth, which allows it to withstand the higher mean temperatures and lower seasonal fluctuations of a tropical climate, and a thermal optimum that exceeds the mean habitat

tropical thermal regime and vice versa. Panels *c* and *e* depict the temporal dynamics in cases when stochastic extinction occurs. In *a*, *b*, and *d*, the red curve depicts the empirically observed reaction norm for a given thermal regime, and the blue curve depicts the reaction norm that evolves in our model under that thermal regime. In *f*, the green curve is the empirically observed reaction norm under a tropical thermal regime, and the red curve is the empirically observed reaction norm under a temperate thermal regime. In each panel, the vertical red and blue lines depict the observed and predicted temperature optima, the dashed blue lines depict the range of seasonal temperature variation, and the solid black line depicts the mean habitat temperature; the dashed black line represents the temperature corresponding to the value of maximum fecundity that provides the initial condition for eco-evolutionary dynamics. In *c* and *e*, the black and red curves depict, respectively, juvenile and adult abundances. The detailed eco-evolutionary dynamics underlying these reaction norms are depicted in figures D1 and D3 (app. D). Parameter values are as follows: $q_{\mathrm{TR}} = q_{\mathrm{opt}} = 1/5$, $A_q = 10{,}000$, $T_{\mathrm{opt}_q} = T_{\mathrm{opt}_\beta}$, and $s_q = s_{b_{\max}}$. Other parameter values are as in table B1, appendix B.

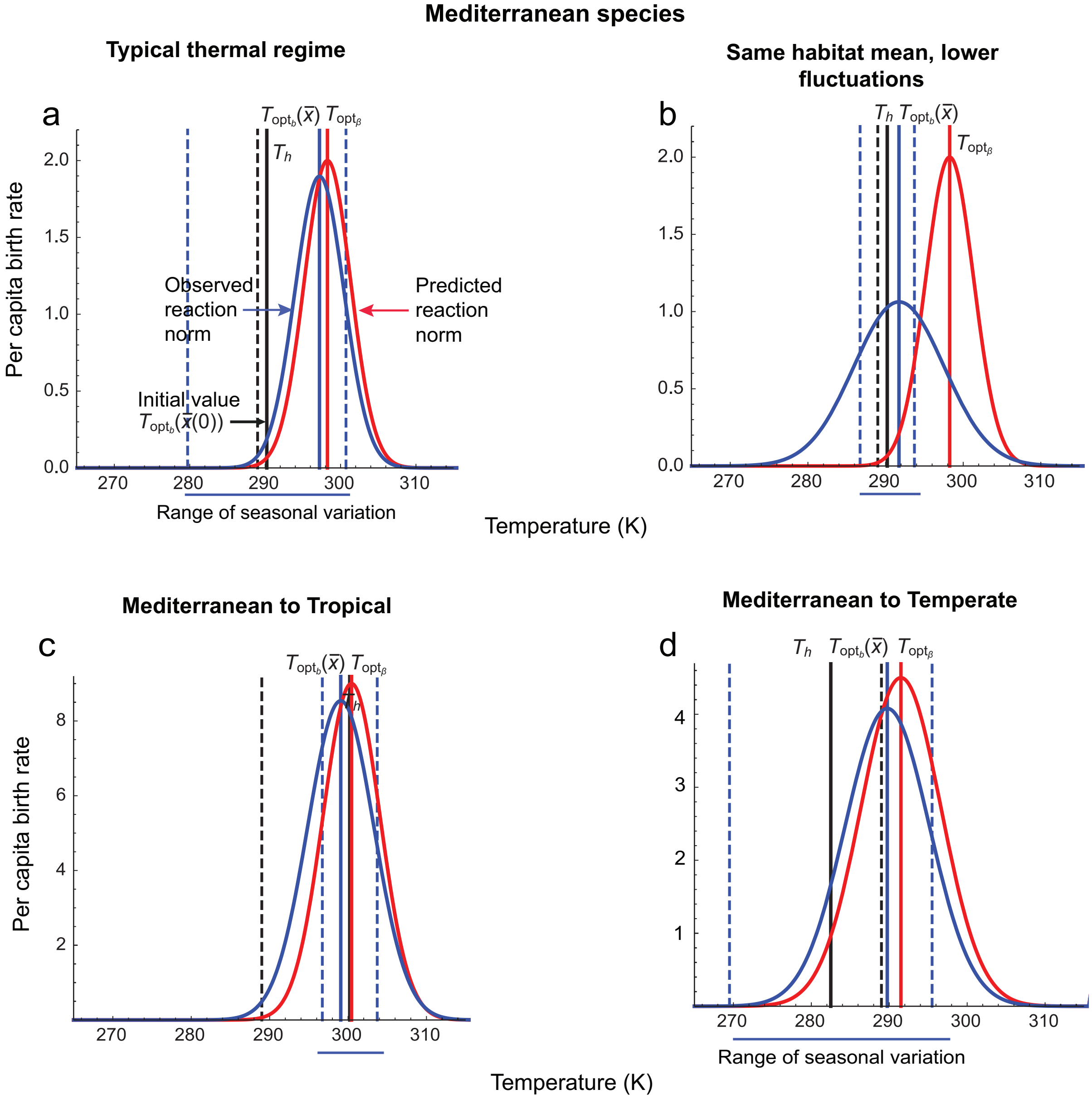

Figure 3: Thermal reaction norms for the Mediterranean species when the temperature response of competition is unimodal and a trade-off exists between maximum fecundity and response breadth. Panel *a* depicts the case when the species is subject to its typical thermal regime, *b* depicts the case when the species experiences the same habitat mean but lower fluctuations, and *c* and *d* depict, respectively, the cases when the Mediterranean species is subject to a tropical and temperate thermal regime. In each panel, the red curve depicts the empirically observed reaction norm for a given thermal regime, and the blue curve depicts the reaction norm that evolves in our model under that thermal regime. The detailed eco-evolutionary dynamics underlying these reaction norms are depicted in figure D2 (app. D). Parameter values are as in figure 2.

temperature, which allows it to withstand the lower mean temperatures and higher seasonal fluctuations of a temperate climate.

The key result to emerge from this analysis is that the evolutionary response to a change in the thermal environment depends on the species' latitudinal origin and its susceptibility to stochastic extinction. We see that when the tropical species is subject to a temperate thermal regime its reaction norm evolves to resemble that of a temperate species. However, when the temperate species is subject to a tropical thermal regime, stochastic extinction prevents any opportunity of reaction norm evolution. This is counterintuitive at first glance since the temperate species is a thermal generalist and the tropical species is a thermal specialist. The explanation lies in the different ways in which temperature affects the population dynamics of tropical and temperate species. When the temperate species is subject to a tropical thermal regime, it experiences temperatures that are above its physiological optimum for most of the year. Birth and maturation rates are the lowest and mortality rate is the highest during the long periods of warmer temperatures (fig. 4*a*–4*c*). As a result, abundances drop to low levels that cause stochastic extinction before the species has had time to adapt to the tropical climate (fig. 4*d*; fig. D3, app. D). In contrast, when a tropical species is subject to a temperate thermal regime, its high physiological optimum allows it to capitalize on the times of the year when temperatures exceed the habitat mean. Birth and maturation rates are highest during the warmest periods of the year, and while the mortality rate is also high during this time, it is much lower than that which the species experiences during the warmest days in the tropical habitat (fig. 4*e*–4*g*). As a result, abundances do not reach the low levels at which stochastic extinction occurs, and the species can persist long enough to adapt to a temperate climate regime (fig. 4*h*; fig. D1, app. D).

Importantly, it is the temperature effects on ectotherm development that drives the differential susceptibility of tropical and temperate species to stochastic extinction. When we omit the juvenile stage and focus only on adult population dynamics, the temperate species can just as well invade tropical habitats as does tropical species temperate habitats (fig. E1, app. E). When we consider the entire life cycle, the multiplicative effects of the temperature responses of juvenile development, juvenile mortality, and adult mortality (and any density-dependent effects thereof) come into play in determining the species' per capita growth rate when rare. It is this interaction that causes species' abundances to fall to the low levels at which extinction occurs due to demographic stochasticity. Since such interactive effects are absent when only the adult stage is considered, stochastic extinction is prevented and temperate species can increase when rare in a tropical habitat and adapt to that environment (fig. E1, app. E).

In our eco-evolutionary model, energetic constraints impose a trade-off between maximum fecundity and response breadth such that response breadth evolves as a correlated trait. Analysis of the model without this trade-off (i.e., maximum fecundity evolves while response breadth remains unchanged) yields the same outcome, that is, maximum fecundity evolves at a temperature well above the mean habitat temperature in Mediterranean and temperate species and to coincide with the mean habitat temperature in the tropical species (fig. F1, app. F). However, since the response breadth does not evolve, each species, when subject to a thermal environment different from the one it is adapted to, evolves a reaction norm that is mismatched with the new thermal environment. For instance, when the tropical species is subject to a temperate climate, maximum fecundity evolves at a temperature that is closer to the mean habitat temperature but the response breadth remains narrow, making the species unable to take advantage of time periods when seasonal fluctuations cause temperatures to exceed the habitat mean. Similarly, maximum fecundities of Mediterranean and temperate species evolve at temperatures that exceed the habitat mean, but the response breadth remains wider than the range of seasonal fluctuations experienced in a tropical climate. If plasticity incurs a cost, which one expects would be the case (DeWitt et al. 1998; Relyea 1998), this would be maladaptive. These results highlight the important role that selection and constraints jointly play in thermal adaptation.

The temperature response of intraspecific competition (monotonic vs. unimodal) affects reaction norm evolution through its effect on stochastic extinction (figs. G1, G2, app. G). Minimum population sizes (the lowest abundance observed in the time series) of all species are lower when the temperature response of competition is monotonic (fig. G3, app. G), thus increasing the risk of stochastic extinction.

Discussion

We investigate the mechanisms underlying the latitudinal variation in the relationship between thermal optima and the mean habitat temperature. We focus on the evolution of the thermal reaction norm for fecundity, as it is a major component of fitness. We hypothesize, on the basis of Jensen's inequality, that thermal optima should evolve to temperatures above the habitat mean when seasonal fluctuations are strong and to coincide with the habitat mean when seasonal fluctuations are weak. We test this hypothesis by developing an eco-evolutionary model that integrates quantitative genetics of reaction norm evolution with stage-structured population dynamics. The novelty of our framework is the mechanistic descriptions, derived from first principles of thermodynamics, of life-history trait responses to temperature, inclusion of the stage structure that characterizes the complex life cycles of multicellular ectotherms, and consideration of stochastic extinction at low abundances as a constraint on reaction norm evolution.

We find that, when exposed to the typical thermal regimes characterized by large seasonal fluctuations, thermal optima of Mediterranean and temperate species do evolve to exceed the mean habitat temperature. When exposed to the typical thermal regime characterized by weak seasonal fluctuations, the tropical species' thermal optimum evolves to coincide with the mean habitat temperature.

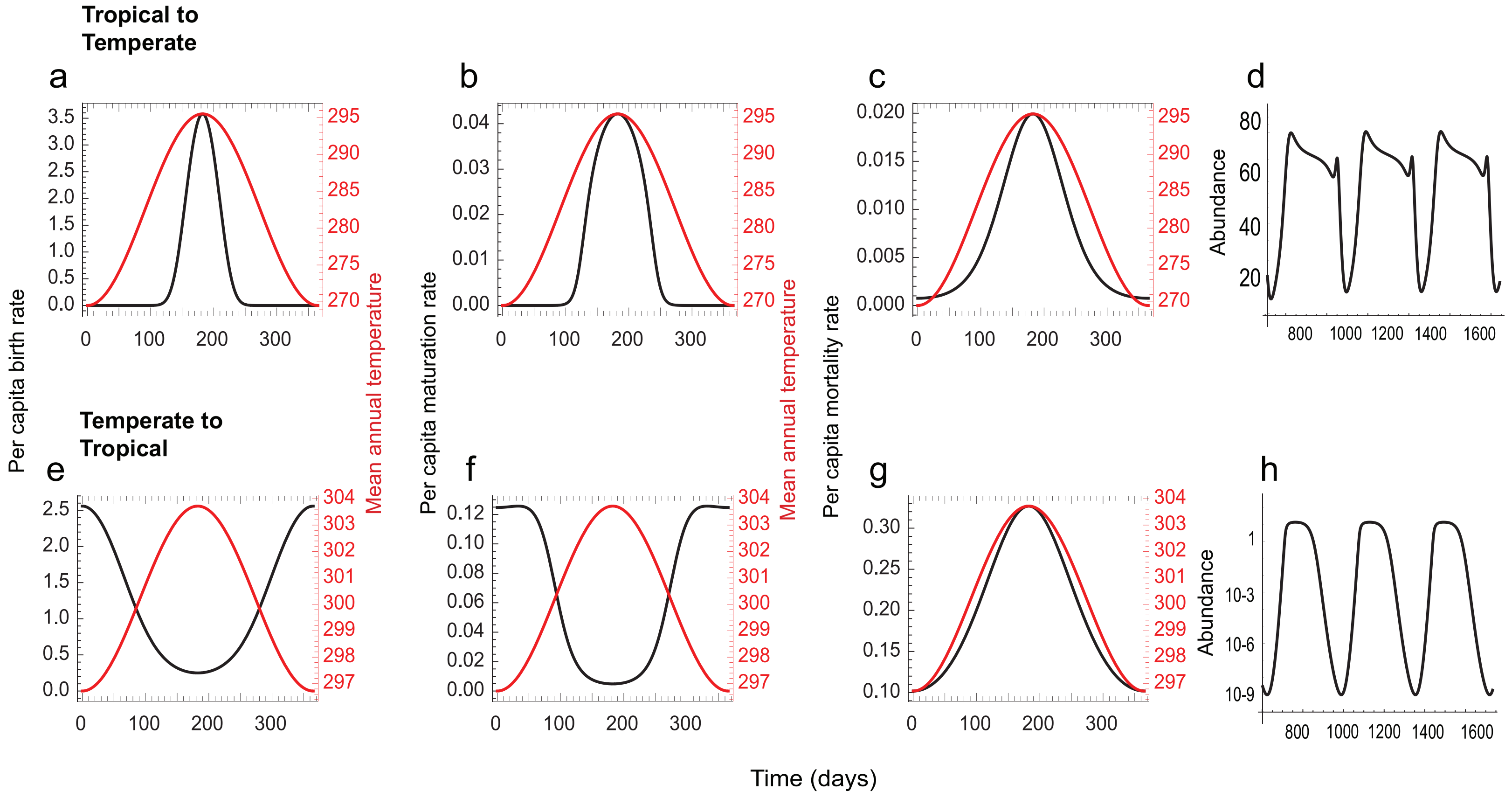

Figure 4: Temperature responses of life-history traits and population dynamics for the tropical species when subject to a temperate climate regime (*a*–*d*) and for the temperate species when subject to a tropical climate regime (*e*–*f*). In all panels, the red curves depict the seasonal temperature variation over a year. The black curves depict the per capita birth rate in *a* and *e*, the per capita maturation rate in *b* and *f*, and the per capita mortality rate in *c* and *g*. Panels *d* and *h* depict abundances over the year for each case. Parameter values are as in figure 2.

Two key insights emerge from our analysis. The first is the role of ecological dynamics as a constraint on reaction norm evolution. We see that the tropical species cannot tolerate an increase in seasonal fluctuations at the high mean habitat temperature it currently experiences, while the temperate species cannot tolerate a decrease in fluctuations if the mean habitat temperature is higher that what it typically experiences. In both cases, a change in the thermal regime causes abundances to fall to levels that predispose the species to stochastic extinction, thus precluding the opportunity to adapt to a novel thermal environment. Stochastic extinction risk is greater when the strength of intraspecific competition increases monotonically with increasing temperature. This is because both temperature and competition act synergistically to reduce abundances at high temperatures, leading to a lower minimum population size as temperatures approach winter levels. Minimum population size is higher when the temperature response of competition is unimodal because the negative effects of competition and temperature are felt at different times, that is, competition is strongest at the physiologically optimal temperature for reproduction while negative effects of temperature are strongest during temperature extremes above the physiological optimum.

Importantly, it is the multiplicative effects of temperature responses of juvenile development and mortality (and any density-dependent effects thereof) that drive the differential susceptibility of tropical and temperate species to stochastic extinction. This is evidenced by the absence of such differential effects when stage structure is eliminated from the model (app. E). This finding illustrates the crucial importance of incorporating the complex life cycles of multicellular ectotherms into investigations of thermal reaction norm evolution.

The second key result is a potential directionality in colonization success. Tropical ectotherms, because of their high thermal optima, can persist in sufficiently high abundances to avoid stochastic extinction during the initial invasion phase. This gives them the opportunity to adapt to the new thermal regime and successfully establish in temperate habitats. Temperate ectotherms, because of their lower thermal optima, are more likely to succumb to stochastic extinction during the initial invasion phase. They are therefore less likely to establish in tropical habitats. Interestingly, the Mediterranean species, which resembles a tropical ectotherm in having a relatively narrow temperature response of reproduction and a temperate ectotherm in exhibiting a temperature optimum well above the mean habitat temperature, can invade and establish in both tropical and temperate habitats. This result, combined with the finding that tropical ectotherms can successfully colonize temperate habitats despite having a narrow response breadth, suggests that ectotherm species' ability to adapt to novel thermal environments may hinge on having a high thermal optimum rather than a wide response breadth.

Although we have not attempted a comprehensive analysis, our review of the invasion literature suggests that the predicted directionality in colonization success may well exist. For example, some of the most successful invasive species are ectotherms of tropical origin that have successfully colonized temperate habitats (e.g., the cane toad [McCann et al. 2014], the Asian tiger mosquito [Juliano and Lounibos 2005], the fire ant [Morrison et al. 2004], scale insects [Miller et al. 2005], and marine invertebrates [Jablonski et al. 2006, 2013; Freestone et al. 2013]). While there are instances of temperate ectotherms successfully colonizing subtropical habitats, such as Hawaii (Meyer and Cowie 2010), the most successful temperate invaders of tropical habitats are endotherms (e.g., birds and rodents [Wiens and Graham 2005]). Of note, our findings serve to explain the differential success of tropical and temperate species in colonizing novel thermal environments. Whether this directionality in colonization success translates into superior competitive ability during the establishment phase is an intriguing question that we hope to address in future work.

Here we have developed an eco-evolutionary framework that combines the quantitative genetics of reaction norm evolution with stage-structured population dynamics. In doing so, we have used ordinary differential equations to depict stage-structured population dynamics. A realistic depiction of temperature effects on ectotherm development requires the use of delay differential equations (Gurney et al. 1983; Nisbet 1997; Murdoch et al. 2003), but we currently do not have the techniques to combine these equations with models of trait evolution. Developing the mathematical and computational techniques necessary to do so is an important future direction. While our model focuses on seasonal temperature variation, most ectotherm species also experience diurnal temperature fluctuations. Our focus on seasonal temperature variation alone is, in part, in the interest of parsimony: as our results show, seasonal variation alone is sufficient to explain the latitudinal variation in the relationship between thermal optima and the mean habitat temperature. It is also in part due to the lack of detailed information on patterns of diurnal temperature variation on the same species for which data on thermal reaction norms are available. In the absence of such data, it is difficult to make an informed inference about the role of diurnal temperature variation in driving latitudinal patterns. Preliminary analyses we have conducted, assuming a sinusoidal pattern of diurnal variation, show that such variation does not qualitatively alter our main finding that thermal optima of species experiencing high amplitude seasonal variation evolve to exceed the mean habitat temperature.

In the interests of tractability, we have investigated the evolution of the reaction norm for fecundity while considering reaction norms of other life-history traits to reflect adaptations to the organism's typical thermal environment.

In reality, reaction norms of different life-history traits are likely to coevolve. Investigating the coevolutionary dynamics of reaction norm evolution is an important future direction. Our formulation also considers ecological and evolutionary dynamics to operate on comparable timescales. While the increasingly strong evidence for rapid evolution, especially in response to changes in the thermal environment (e.g., Rodriguez-Trelles and Rodriguez 1998; Maron et al. 2004; Wiens and Graham 2005; Franks et al. 2007), validates this approach, it is important to test how robust our results are when evolutionary dynamics operate on a slower timescale than ecological dynamics. We are currently developing adaptive dynamics models to investigate the issue of timescales in reaction norm evolution.

Acknowledgments

This research was supported by a Complex Systems Scholar grant from the James S. McDonnell Foundation and National Science Foundation grant DEB-1457815 to P.A. We thank three anonymous referees whose constructive comments greatly improved the manuscript.

Literature Cited

Amarasekare, P. 2000. Coexistence of competing parasitoids on a patchily distributed host: local vs. spatial mechanisms. Ecology 81:1286–1296.

Amarasekare, P., and R. Coutinho. 2013. The intrinsic growth rate as a predictor of population viability under climate warming. Journal of Animal Ecology 82:1240–1253.

———. 2014. Effects of temperature on intra-specific competition in ectotherms. American Naturalist 184:E50–E65.

Amarasekare, P., and V. Savage. 2012. A mechanistic framework for elucidating the temperature dependence of fitness. American Naturalist 179:178–191.

Begon, M., J. Harper, and C. Townsend. 2005. Individuals, populations and communities. Blackwell Science, Oxford.

Carriere, Y., and G. Boivin. 1997. Evolution of thermal sensitivity of parasitization capacity in egg parasitoids. Evolution 51:2028–2032.

Dannon, E. A., M. Tamo, A. van Huis, and M. Dicke. 2010. Functional response and life history parameters of *Apanteles taragamae*, a larval parasitoid of *Maruca vitrata*. BioControl 55:363–378.

Dell, A., S. Pawar, and S. M. Savage. 2011. Systematic variation in the temperature dependence of physiological and ecological traits. Proceedings of the National Academy of Sciences of the USA 108:10591–10596.

Deutsch, C. J., J. Tewksbury, R. B. Huey, K. Sheldon, C. Ghalambor, D. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proceedings of the National Academy of Sciences of the USA 105:6668–6672.

DeWitt, T., A. Sih, and D. Wilson. 1998. Costs and limits of phenotypic plasticity. Trends in Ecology and Evolution 13:77–81.

Dreyer, H., and J. Baumgartner. 1996. Temperature influence on cohort parameters and demographic characteristics of the two cowpea coreids *Clavigralla tomentosicollis* and *C. shadabi*. Entomologia Experimentalis et Applicata 78:201–213.

Falconer, D. S., and T. McKay. 1996. Introduction to quantitative genetics. Benjamin Cummings, New York.

Franks, S., S. Sim, and A. Weis. 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. Proceedings of the National Academy of Sciences of the USA 104:1278–1282.

Frazier, M., R. Huey, and D. Berrigan. 2006. Thermodynamic constraints on the evolution of insect growth rates: "warmer is better." American Naturalist 168:512–520.

Freestone, A., G. Ruiz, and M. Torchin. 2013. Stronger biotic resistance in tropics relative to temperate zone: effects of predation on marine invasion dynamics. Ecology 94:1370–1377.

Gao, G., Z. Lu, D. Xia, P. Sun, J. Ma, and Y. Xu. 2013. Effects of temperature and density on the mortality and reproduction of cotton aphid *Aphis gossypii*. Chinese Journal of Applied Ecology 24:1300–1304.

Gilchrist, G. 1995. Specialists and generalists in changing environments. I. Fitness landscapes of thermal sensitivity. American Naturalist 146:252–270.

Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. Science 293:2248–2251.

Gillooly, J. F., E. L. Charnov, G. B. West, V. M. Savage, and J. H. Brown. 2002. Effects of size and temperature on developmental time. Nature 417:70–73.

Gurney, W., R. Nisbet, and J. Lawton. 1983. The systematic formulation of tractable single-species population models incorporating age structure. Journal of Animal Ecology 52:479–495.

Hochachka, P., and G. Somero. 2002. Biochemical adaptation. Oxford University Press, New York.

Hou, Y., and Z. Weng. 2010. Temperature-dependent development and life table parameters of *Octodonta nipae* (coleoptera: Chrysomelidae). Environmental Entomology 39:1676–1684.

Huey, R., and D. Berrigan. 2001. Temperature, demography, and ectotherm fitness. American Naturalist 158:204–210.

Jablonski, D., C. Belanger, S. Berke, S. Huang, A. Krug, K. Roy, A. Tomasovych, and J. Valentine. 2013. Out of the tropics, but how? fossils, bridge species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient. Proceedings of the National Academy of Sciences of the USA 110:10487–10494.

Jablonski, D., K. Roy, and J. Valentine. 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. Science 314:101–106.

Jandricic, S. E., S. P. Wraight, K. C. Bennett, and J. P. Sanderson. 2010. Developmental times and life table statistics of *Aulacorthum solani* (hemiptera: Aphididae) at six constant temperatures, with recommendations on the application of temperature-dependent development models. Environmental Entomology 39:1631–1642.

Jensen, J. L. 1906. Sur les fonctions convexes et les inégalités entre les valeurs moyennes. Acta Mathematica 30:175–193.

Johnson, C., R. Coutinho, E. Berlin, K. Dolphin, J. Heyer, B. Kim, A. Leung, J. Sabellon, and P. Amarasekare. 2015. Effects of temperature and resource variation on insect population dynamics: the bordered plant bug (*Largus californicus*) as a case study. Functional Ecology 30:1122–1131.

Johnson, F., and I. Lewin. 1946. The growth rate of *E. coli* in relation to temperature, quinine and coenzyme. Journal of Cellular and Comparative Physiology 28:47–75.

Juliano, S., and L. Lounibos. 2005. Ecology of invasive mosquitoes: effects on resident species and on human health. Ecology Letters 8:558–574.

Kingsolver, J. 2009. The well-temperatured biologist. American Naturalist 174:755–768.

Kingsolver, J., A. Woods, L. B. Buckley, L. Potter, H. MacLean, and J. Higgins. 2011. Complex life cycles and the responses of insects to climate change. Integrative and Comparative Biology 51:719–732.

Laws, A., and G. Belovsky. 2010. How will species respond to climate change? examining the effects of temperature and population density on an herbivorous insect. Environmental Entomology 39:312–319.

Long, M., and M. Fee. 2008. Using temperature to analyse temporal dynamics in the songbird motor pathway. Nature 456:189–194.

Lynch, M., and B. Walsh. 1998. Genetics and analysis of quantitative traits. Sinauer, Sunderland, MA.

Maron, J., M. Vila, R. Bommarco, S. Elmendorf, and P. Beardsley. 2004. Rapid evolution of an invasive plant. Ecological Monographs 74:261–280.

Martin, T., and R. Huey. 2008. Why "suboptimal" is optimal: Jensen's inequality and ectotherm thermal preferences. American Naturalist 171:E102–E118.

McCann, S., M. Greenlees, D. Newell, and R. Shine. 2014. Rapid acclimation to cold allows the cane toad to invade montane areas within its Australian range. Functional Ecology 28:1166–1174.

Meyer, W., and R. Cowie. 2010. Invasive temperate species are a threat to tropical island biodiversity. Biotropica 42:732–738.

Miller, D., G. Miller, G. S. Hodges, and J. Davidson. 2005. Introduced scale insects (Hemiptera: Coccoidea) of the United States and their impact on agriculture. Proceedings of the Entomological Society of Washington 107:123–158.

Morgan, D., K. F. A. Walters, and J. N. Aegerter. 2001. Effect of temperature and cultivar on the pea aphid, *Acyrthosiphon pisum* (Hemiptera: Aphididae) life history. Bulletin of Entomological Research 91:47–52.

Morrison, L., S. Porter, E. Daniels, and M. Korzukhin. 2004. Potential global range expansion of the invasive fire ant, *Solenopsis invicta*. Biological Invasions 6:183–191.

Murdoch, W., C. J. Briggs, and R. Nisbet. 2003. Consumer resource dynamics. Princeton University Press, Princeton, NJ.

Nijhout, H. 1994. Insect hormones. Princeton University Press, Princeton, NJ.

Nisbet, R. 1997. Delay-differential equations for structured populations. Pages 89–116 *in* S. Tuljapurkar and H. Caswell, eds. Structured-population models in marine, terrestrial, and freshwater systems. Chapman & Hall, New York.

Parajulee, M. 2006. Influence of constant temperatures on life history parameters of the cotton aphid, *Aphis gossypii*, infesting cotton. Environmental Entomology 36:666–672.

Ratkowsky, D., J. Olley, and T. Ross. 2005. Unifying temperature effects on the growth rate of bacteria and the stability of globular proteins. Journal of Theoretical Biology 233:351–362.

Reigada, C., and W. Godoy. 2006. Larval density, temperature and biological aspects of *Chrysomya megacephala* (Diptera: Calliphoridae). Arquivo Brasileiro de Medicina Veterinária e Zootecnia 58:562–566.

Relyea, R. 1998. Costs of phenotypic plasticity. American Naturalist 159:272–282.

Ritchie, M. E. 1996. Interaction of temperature and resources in population dynamics: a test of theory. Pages 79–89 *in* R. Floyd, A. Sheppard, and P. De Barro, eds. Frontiers of population ecology. CSIRO, Melbourne.

Rodriguez-Trelles, F., and M. Rodriguez. 1998. Rapid micro-evolution and loss of chromosomal diversity in *Drosophila* in response to climate warming. Evolutionary Ecology 12:829–838.

Ruel, J., and M. Ayers. 1997. Jensen's inequality predicts effects of environmental variation. Trends in Ecology and Evolution 14:361–366.

Savage, V. M., J. F. Gillooly, J. H. Brown, G. B. West, and E. L. Charnov. 2004. Effects of body size and temperature on population growth. American Naturalist 163:429–441.

Schoolfield, R., J. Sharpe, and C. Magnuson. 1981. Non-linear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. Journal of Theoretical Biology 88:719–731.

Schreiber, S., R. Bürger, and D. Bolnick. 2011. The community effects of phenotypic and genetic variation within a predator population. Ecology 92:1582–1593.

Sharpe, P., and D. DeMichele. 1977. Reaction kinetics of poikilotherm development. Journal of Theoretical Biology 64:649–670.

Tewksbury, J. J., R. B. Huey, and C. Deutsch. 2008. Climate warming puts the heat on tropical ectotherms. Science 320:1296–1297.

Van der Have, T. M. 2002. A proximate model for thermal tolerance in ectotherms. Oikos 98:141–155.

Van der Have, T. M., and G. de Jong. 1996. Adult size in ectotherms: temperature effects on growth and differentiation. Journal of Theoretical Biology 183:329–340.

Vasseur, D. A., P. Amarasekare, V. H. W. Rudolf, and J. M. Levine. 2011. Eco-evolutionary dynamics of coexistence via neighbor dependent selection. American Naturalist 178:E96–E109.

Wiens, J., and C. Graham. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review of Ecology, Evolution, and Systematics 36:519–539.

Zamani, A., A. Talebi, Y. Fathipour, and V. Baniameri. 2006. Effect of temperature on biology and population growth parameters of *Aphis gossypii* glover (Hom., Aphididae) on greenhouse cucumber. Journal of Applied Entomology 130:453–460.

Associate Editor: Charles J. Goodnight
Editor: Alice A. Winn