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Effects of Temperature on Intraspecific Competition in Ectotherms

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abstract: Understanding how temperature influences population regulation through its effects on intraspecific competition is an important question for which there is currently little theory or data. Here we develop a theoretical framework for elucidating temperature effects on competition that integrates mechanistic descriptions of life-history trait responses to temperature with population models that realistically capture the variable developmental delays that characterize ectotherm life cycles. This framework yields testable comparative predictions about how intraspecific competition affects reproduction, development, and mortality under alternative hypotheses about the temperature dependence of competition. The key finding is that ectotherm population regulation in seasonal environments depends crucially on the mechanisms by which temperature affects competition. When competition is strongest at temperatures optimal for reproduction, effects of temperature and competition act antagonistically, leading to more complex dynamics than when competition is temperature independent. When the strength of competition increases with temperature past the optimal temperature for reproduction, effects of temperature and competition act synergistically, leading to dynamics qualitatively similar to those when competition is temperature independent. Paradoxically, antagonistic effects yield a higher population floor despite greater fluctuations. These findings have important implications for predicting effects of climate warming on population regulation. Synergistic effects of temperature and competition can predispose populations to stochastic extinction by lowering minimum population sizes, while antagonistic effects can increase the potential for population outbreaks through greater fluctuations in abundance.

Keywords: ectotherm, intraspecific competition, population dynamics, seasonality, temperature, temperature variation.

Introduction

It is well known that differential responses to temperature variation (e.g., through differences in emergence times or

activity patterns) allow species to coexist by concentrating intraspecific competition relative to interspecific competition (temporal niches; Chesson 2000). However, very little is known about the mechanisms by which temperature effects on life-history traits (reproduction, development, survivorship) that operate at the level of individuals translate into species-specific responses at the level of populations. A trait-based understanding of temperature effects is important because it allows us to identify the types of life-history strategies that facilitate or constrain species coexistence in thermally variable environments, information that is crucial in predicting how perturbations such as climate warming influence biodiversity.

A trait-based framework for elucidating temperature effects on species interactions necessarily begins with intraspecific competition. This is because intraspecific competition is the major mechanism of negative density-dependent feedback underlying population regulation, a critical prerequisite for species coexistence. Empirical studies show that the effects of intraspecific competition on life-history traits is strongly temperature dependent (Ritchie 1996; Reigada and Godoy 2006; Laws and Belovsky 2010). However, theoretical work on temperature effects on species interactions has considered intraspecific competition to be temperature independent. For instance, Vasseur and McCann (2006) developed a bioenergetic consumer-resource model without age or stage structure, in which intraspecific competition in the resource species, the source of negative feedback that stabilizes the interaction, is temperature independent. Van de Wolfshaar et al. (2008) and Ohlberger et al. (2011) developed size-structured models that more realistically capture ectotherm life cycles, but they also assumed intraspecific competition in the resource species to be temperature independent. All of these previous studies considered constant thermal environments in which there is no diurnal or seasonal temperature variation. Despite the fact that ectotherms play key roles as resources, predators, parasites, and mutualists

in virtually all communities, there is currently no theory that investigates how temperature effects on intraspecific competition influence ectotherm population dynamics in thermally variable environments.

Here we develop a trait-based mathematical framework for investigating this question. We start with a mechanistic description of temperature responses of life-history traits derived from temperature effects on the underlying biochemical processes (e.g., reaction kinetics, enzyme inactivation). We incorporate these responses into population models, described by delay differential equations, that can realistically capture the temperature-induced developmental delays characteristic of ectotherm life cycles. We investigate how the joint effects of temperature and competition on life-history traits translate into population dynamics under different types of seasonal temperature regimes. We derive comparative predictions that can be tested with experimental or time-series data.

Conceptual Framework

Elucidating the mechanisms by which temperature affects intraspecific competition requires three types of information. First, we have to understand how temperature affects life-history traits in the absence of competition. This is important because temperature responses of life-history traits determine the physiological optima for reproduction and the lower and upper thermal limits to viability (Adolph and Porter 1993; van der Have and de Jong 1996; van der Have 2002; Buckley 2008; Kingsolver 2009; Kingsolver et al. 2011; Kearney 2013). Second, we have to understand how temperature affects intraspecific competition, specifically, how it influences the relationship between vital rates (birth, maturation, and mortality) and density. Third, we need to know the characteristics of the seasonal temperature regime experienced by the species in question. Of particular importance are the mean habitat temperature, in relation to the physiological temperature optima, and the amplitude of seasonal fluctuations, in relation to the lower and upper thermal limits to viability. For instance, tropical ectotherms tend to experience mean habitat temperatures close to their physiological optima and seasonal fluctuations of relatively small amplitude; Mediterranean and temperate species experience mean habitat temperatures well below their physiological optima and seasonal fluctuations of large amplitude (Deutsch et al. 2008; Amarasekare and Savage 2012). The extent to which this difference influences temperature effects on competition is an important question.

Effects of Temperature on Life-History Traits

Temperature responses of life-history traits in the absence of competition have been well studied for a large number of ectotherm species (Angilletta 2009; Kingsolver 2009; Kingsolver et al. 2011), and their mechanistic basis is well understood. Briefly, 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 and enzyme inactivation) give rise to temperature responses at the organismal level that are monotonic or left-skewed. 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).

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):

$$d_X(T) = d_{X_{T_R}} e^{A_{d_X}[(1/T_R)-(1/T)]}, \qquad (1)$$

where $d_X(T)$ is the mortality rate of stage X (e.g., juvenile, adult) at temperature T (in kelvins), $d_{X_{T_R}}$ is the mortality rate at a reference temperature (typically between 20° and 30°C, the commonest being 24°–25°C; Sharpe and DeMichele 1977; Schoolfield et al. 1981), and A_{d_X} is the Arrhenius constant, which quantifies the temperature sensitivity of mortality, that is, how fast it increases with increasing temperature.

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):

$$m(T) = \frac{(m_{T_R} T/T_R) e^{A_{m_I}[(1/T_R)-(1/T)]}}{1 + e^{A_L[(1/T_{L/2})-(1/T)]} + e^{A_H[(1/T_{H/2})-(1/T)]}}, \qquad (2)$$

where $m(T)$ is the maturation rate at temperature T (in kelvins), m_{T_R} is the maturation rate at the reference tem-

perature T_R at which the enzyme is 100% active, A_{m_J} (enthalpy of activation divided by the universal gas constant R) quantifies temperature sensitivity, $T_{L/2}$ and $T_{H/2}$ are, respectively, the low and high temperatures at which the enzyme is 50% active, and A_L and A_H are 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).

The per capita birth rate of most ectotherms exhibits a symmetric, unimodal temperature response (e.g., Dreyer and Baumgartner 1996; Carrière and Boivin 1997; Morgan et al. 2001; Parajulee 2006; Zamani et al. 2006; Dannon et al. 2010; Hou and Weng 2010; Jandricic et al. 2010; Dell et al. 2011; Amarasekare and Savage 2012) that is well described by a Gaussian function:

$$b(T) = b_{T_{opt}}e^{-(T-T_{opt_b})^2/2s_b^2}, \tag{3}$$

where T_{opt_b} is the temperature (in kelvins) at which the birth rate is maximized ($b_{T_{opt}}$), and s_b depicts the variability in the temperature response, that is, the temperature range over which the birth rate deviates from the optimum.

Effects of Intraspecific Competition on Life-History Traits

It is well established that intraspecific competition for resources (e.g., food, nutrients, space) causes per capita birth rates to decrease and per capita mortality rates to increase with increasing conspecific density (Begon et al. 2005). These density-dependent relationships can be linear or nonlinear (table 1), with nonlinear responses leading to overcompensation or undercompensation in the feedback of density on the per capita growth rate (Kot 2001; Gurney and Nisbet 1998).

Effects of Temperature on Intraspecific Competition

Elucidating the effects of temperature on intraspecific competition requires that we understand how temperature modifies life-history traits' responses to density. Density dependence in life-history traits can arise from intraspecific competition for abiotic or biotic resources. We consider the situation where the resource supply does not change with temperature on the timescales relevant to the consumer's population dynamics. This applies to abiotic resources (e.g., space, nutrients), whose supply does not directly depend on the environmental temperature, or biotic resources such as perennial plants, whose biomass change in response to temperature is slow relative to the life span of insect herbivores that feed on them. For instance, Ritchie (1996) and Laws and Belovsky (2010) investigated the effects of temperature and density on the fecundity and survivorship of grasshoppers and found that grass biomass and chemical solubility (an index of plant quality) did not vary significantly with temperature within and between years.

We construct two hypotheses for how temperature affects intraspecific competition in ectotherms. The first, based on metabolic-scaling theory (Savage al. 2004), is that the strength of competition increases monotonically with increasing temperature. This is because higher activity levels at higher temperatures increase the per-individual resource acquisition, which reduces the carrying capacity when resources are limiting. In this case, the temperature response of competition should be monotonic:

$$q(T) = q_{T_R}e^{A_q[(1/T_R)-(1/T)]}, \tag{4}$$

where q_{T_R} is the per capita competitive effect at a reference temperature T_R (in kelvins) and A_q is the Arrhenius constant that quantifies the temperature sensitivity of competition, that is, how fast the competition coefficient increases with increasing temperature.

The second hypothesis, based on ecological theory

Table 1: Functions used to depict density dependence in life-history traits

Trait	Density response	Parameters	Sources
Fecundity	$B(A) = be^{-q_bA}$, $B(A) = b/(1 + q_bA)$	b: density-independent per capita birth rate; q_b: per capita competitive effect; A: adult abundance	Gurney et al. 1983; Nisbet and Gurney 1983; Murdoch et al. 2003
Development[a]	$M(X) = m_Xe^{q_{m_X}X}$, $M(X) = m_X/(1 + q_{m_X}X)$	m_X: density-independent per capita maturation rate; q_{m_X}: per capita competitive effect; X: abundance of development stage X (egg, juvenile)	Gurney et al. 1983
Mortality	$D(Y) = d_Y + q_{d_Y}Y$, $D(Y) = d_y/(1 - q_{d_Y}Y)$	d_Y: density-independent per capita mortality rate; q_{d_Y}: per capita competitive effect, Y: abundance of stage Y (juvenile, adult)	Nisbet 1997; Murdoch et al. 2003

[a] Competition is likely to slow development by impeding both growth and differentiation (van der Have and de Jong 1996; van der Have 2002). The functional forms given are the most plausible, in the absence of any studies that have quantified the density response of the maturation rate.

(Begon et al. 2005), is that competition is strongest at temperatures that are optimal for reproduction. This is because of the greater demand for resources during periods of high reproductive activity. In this case, the temperature response of competition should be unimodal:

$$q(T) = q_{T_{\mathrm{opt}}} e^{-(T - T_{\mathrm{opt_q}})^2 / 2 s_q^2}, \qquad (5)$$

where $T_{\mathrm{opt_q}}$ is the temperature (in kelvins) at which competition is strongest ($q_{T_{\mathrm{opt}}}$) and s_q depicts the variability in $q(T)$ about the optimum. Note that a Gaussian function is being used for purposes of illustration. Once empirical data become available, any other form of unimodal relationship (e.g., left- or right-skewed) can be used to depict the temperature response.

Joint Effects of Temperature and Competition on Life-History Traits

Building on the above information, we can depict temperature effects on density responses of life-history traits through the function $k(T, X)$ where k is the trait value, T is temperature, and X is the density of the life-history stage affected by competition ($X = J, A$). The function $k(T, X)$ can take different forms, that is, $k(T)e^{-q(T)X}$, $k(T)/(1 \pm q(T)X)$, or $k(T) + q(T)X$, where $k(T)$ is the temperature response of trait k in the absence of competition (eqq. [1]–[3]) and $q(T)$ depicts temperature effects on the strength of intraspecific competition (eqq. [4], [5]).

Empirical Evidence on the Effects of Temperature and Competition on Life-History Traits

Ritchie (1996) and Laws and Belovsky (2010) used field-enclosure experiments to investigate the effects of temperature and density on grasshopper life-history traits. Laws and Belovsky (2010) found that temperature had a strong effect on density-dependent mortality but little or no effect on density-dependent fecundity. Both studies showed that the strength of density-dependent mortality increased with increasing temperatures. Because these experiments were conducted on a relatively narrow temperature range (20°–26°C in Laws and Belovsky 2010 and 33°–36°C in Ritchie 1996), the data are insufficient to elucidate the nature of the temperature-response function for density-dependent mortality. However, the fact that the strength of competition increased with increasing temperature over both temperature ranges studied suggests that the temperature response of competition may be monotonic in this grasshopper species (*Melanoplus sanguinipes*). This is further supported by the fact that neither the biomass nor the quality of the plant species on which the grasshoppers fed changed with temperature (Ritchie 1996; Laws and Belovsky 2010). This suggests that grass-

hoppers' resource supply remained constant over the temperature range studied. This should cause the strength of competition to increase with increasing temperature, because increased activity levels at higher temperatures should increase the greater per-individual resource requirement.

Reigada and Godoy (2006) studied the effects of density on the fecundity and survivorship of the blowfly (*Chrysomya megacephala*) at two temperatures (20° and 30°C). They found that temperature had no effect on density-dependent mortality but that the density-dependent decline in fecundity was stronger at 20°C than at 30°C. The fact that only two temperatures were studied makes it difficult to draw any conclusions about the nature of the temperature-response function for density-dependent fecundity. However, on the basis of this study's findings it is unlikely that the strength of competition increases monotonically with temperature, because in that case we would expect to see a greater decline in fecundity with density at higher, rather than lower, temperatures.

Gao et al. (2013), who investigated the effects of temperature and density on the fecundity of the cotton aphid (*Aphis gossypii*), found that the strength of competition declined monotonically with increasing temperature over the range 32°–40°C. This finding argues against a monotonically increasing temperature response because such a response would mean that competition would be strongest at the coldest temperatures. The fact that the species is able to reproduce within the temperature range 10°–35°C suggests that the temperature response of competition may well be unimodal, with competition strength increasing with temperature to the maximum observed at 32°C. Other authors (C. Johnson, R. Coutinho, E. Berlin, K. Dolphin, J. Heyer, B. Kim, A. Leung, J. Sabellon, and P. Amarasekare, unpublished manuscript) investigated the effects of temperature and density on the bordered plant bug (*Largus californicus*). They observed density-dependent effects on per capita fecundity but not on juvenile and adult mortality. Importantly, density-dependent fecundity exhibited a unimodal temperature response, with the greatest decline in fecundity occurring at the optimal temperature for plant bug reproduction.

Taken together, these studies suggest that temperature affects density-dependent fecundity or mortality but not both. There is some indication that the temperature response of density-dependent mortality is monotonic and increasing while the temperature response of density-dependent fecundity is unimodal, but more data are necessary before any general conclusions can be made about the joint effects of temperature and competition on life-history traits (see "Discussion").

Effects of Temperature and Competition
on Population Dynamics

The next step is to determine how the joint effects of temperature and competition on life-history traits translate into population dynamics. We start with a simple model of the ectotherm life cycle, with juvenile and adult stages. Temperature affects all vital rates (birth, maturation, mortality), while intraspecific competition can affect one or more of these traits. At present, very little is known about how the interplay between temperature and competition shapes trait responses. Here we investigate how vital rates that are affected only by temperature interact with vital rates that are affected by both temperature and competition to influence population dynamics.

Most ectotherms, invertebrates in particular, exhibit life cycles involving distinct developmental stages (e.g., eggs, larvae/nymphs). Such stage structure leads to developmental delays that are directly affected by temperature. Delay differential equations with time-dependent parameters (Nisbet and Gurney 1983; Nisbet 1997) provide a natural mathematical context for analyzing stage-structured population dynamics. They have their origins in the continuous age-/size-structured models of Gurney et al. (1983) and de Roos et al. (2008) and hence can be extended to represent ectotherms with continuous growth (e.g., fish, lizards). We build on the seminal early work of Gurney et al. (1983) and Nisbet and Gurney (1983) to develop models in which the time dependence arises from trait responses to temperature. Our new contribution is to develop a framework that integrates mechanistic descriptions of trait-level responses to temperature with variable-delay models of population dynamics.

The dynamics of a two-stage delay model with birth, death, and development are given by

$$\frac{dJ(t)}{dt} = B\big(T(t), A(t)\big)A(t) - M_J(t) - D_J\big(T(t), J(t)\big)J(t),$$

$$\frac{dA(t)}{dt} = M_J(t) - D_A\big(T(t), A(t)\big)A(t),$$

$$M_J(t) = B\big(T(t - \tau(t)), A(t - \tau(t))\big)A(t - \tau(t))$$

$$\times \ \frac{m_J(T(t))}{m_J(T(t - \tau(t)))} S_J(t), \tag{6}$$

$$\frac{dS_J(t)}{dt} = S_J(t)\Bigg[\frac{m_J(T(t))D_J(T(t - \tau(t)), J(t - \tau(t)))}{m_J(T(t - \tau(t)))}$$

$$- D_J(T(t), J(t))\Bigg],$$

$$\frac{d\tau(t)}{dt} = 1 - \frac{m_J(T(t))}{m_J(T(t - \tau(t)))},$$

where J and A depict juvenile and adult densities, respectively, and the functions $B(T(t), A(t))$, and $D_X(T(t), X(t))$, where $(X = J, A)$, describe the joint effects of temperature and density on per capita birth and mortality rates, respectively (see app. A for details; apps. A–C are available online). We use an exponential function to depict density-dependent birth rate and a linear function to depict the density-dependent mortality rate (see table 1) because data show these to be the most commonly observed density responses (Murdoch et al. 2003). The function $M_J(t)$ is the temperature-dependent recruitment rate, which is the product of the recruitment rate into the juvenile stage $\tau(t)$ time units ago and the fraction of juveniles that survive to adulthood ($S_J(t)$). The latter can be density dependent if intraspecific competition affects juvenile mortality. The function $m_J(T(t))$ depicts variation in the per-individual maturation rate with time due to the temperature dependence of juvenile developmental delay (τ). Note that vital rates are both temperature dependent and time dependent to accommodate trait responses to variable temperature regimes (e.g., seasonal; see below). Because the model incorporates variable developmental delays, it can depict the life histories of organisms that reproduce continuously (e.g., tropical ectotherms) or seasonally (e.g., Mediterranean and temperate ectotherms).

Model Analysis

We investigate the long-term outcomes (equilibria) of equation (6) under a constant thermal environment (i.e., the organism in question experiences the same temperature, on average, with few or no fluctuations around the mean). We also conduct numerical analyses of equation (6) to understand how population dynamics are affected by seasonal temperature variation.

We incorporate seasonal temperature variation into the population model as $T = s(t)$, where T is the temperature in kelvins, t is time in days, and $s(t)$ depicts seasonal temperature variation. Then,

$$s(t) = M_T - A_T \cos\left(\frac{2\pi t}{\text{year}}\right), \tag{7}$$

where M_T is the mean annual temperature, A_T is the amplitude of seasonal temperature fluctuations within the year, and year = 365 days. We run the model for a period of 100 years and calculate long-term abundances, population variability (coefficient of variation in abundance), and minimum population size over the last 5 years.

We analyze four cases along two axes of biological rel-

evance. The first axis is the stability of equilibria in the absence of temperature variation, which depends on the life-history attributes of the species. Species with low lifetime fecundity and short developmental delays relative to adult longevity attain a stable equilibrium in the absence of temperature variation. Species with high lifetime fecundity and long developmental delays relative to adult longevity exhibit delayed feedback cycles when intraspecific competition affects fecundity and single-generation cycles when competition affects juvenile mortality (see Murdoch et al. 2003 for a detailed description of cyclic behavior in delay models). When intraspecific competition affects adult mortality, the equilibrium is stable, regardless of life-history characteristics, unless fecundity exhibits overcompensating density dependence (Nisbet 1997).

The second axis comprises the characteristics of the seasonal temperature regime. We consider two types of seasonal temperature regime. The first is representative of a tropical habitat, with a mean habitat temperature close to the optimal temperature for reproduction and seasonal temperature fluctuations of low amplitude (1°C–3°C). The second is representative of a Mediterranean/temperate habitat, with a mean habitat temperature well below the optimal temperature for reproduction and seasonal temperature fluctuations of high amplitude (9°C–12°C). These values reflect the seasonal temperature regimes experienced by insect species at different latitudes. For instance, the tropical pod-sucking bug *Clavigralla shadabi*, from Benin (Dreyer and Baumgartner 1996), experiences a mean annual temperature of 27.2°C (SE = 0.09°C) and an amplitude of seasonal fluctuations (difference between maximum and minimum monthly temperature) of 3.3°C. The Mediterranean pod-sucking bug *Murgantia histrionica*, in coastal southern California, experiences a mean annual temperature of 17.2°C (SE = 0.28°C) and seasonal fluctuations of 9.5°C. The pea aphid *Acyrthosiphon pisum*, in eastern England, experiences a mean habitat temperature of 9.75°C (SE = 0.41°C) and seasonal fluctuations of 12°C.

In analyzing the model, we used parameter values that are representative of insect species (Sharpe and DeMichele 1977; Schoolfield et al. 1981; Kooijman 1993; van der Have and de Jong 1996; Amarasekare and Savage 2012). In accordance with empirical findings (Gao et al. 2013; C. Johnson, R. Coutinho, E. Berlin, K. Dolphin, J. Heyer, B. Kim, A. Leung, J. Sabellon, and P. Amarasekare, unpublished manuscript), we considered the unimodal temperature response of competition to have the same parameter values as the temperature response of reproduction, that is, that competition is strongest at the temperature optimal for reproduction ($T_{\mathrm{opt_q}} = T_{\mathrm{opt_b}}$) and operates on the same temperature range within which the species can reproduce ($s_q = s_b$). To ensure that the rate at which competition strength increases with temperature does not exceed that

of the maturation rate when the temperature response of competition is monotonic, we considered the Arrhenius constant for the temperature response of competition (A_q) to be the same as that for the maturation rate (A_m). This is a reasonable approximation because thermodynamical constraints dictate that the Arrhenius constants, both within and between species, fall within a narrow range for all ectotherms (Gillooly et al. 2001, 2002; Savage et al. 2004). To facilitate comparisons between monotonic and unimodal temperature responses of competition, $q_{T_{\mathrm{opt}}}$ was scaled such that $q_{T_{\mathrm{opt}}} = q_{T_{\mathrm{R}}} e^{A_q[(1/T_R)-(1/T_{\max})]}$, where $T_{\max}$ is the maximum temperature experienced by the species, calculated as $T_{\max} = M_{\mathrm{T}} + A_{\mathrm{T}}$.

Results

Effects of Temperature and Competition on Life-History Traits

Temperature has both direct and indirect effects on life-history traits. Direct effects arise from temperature effects on the biochemical processes underlying life-history traits (e.g., reaction kinetics, enzyme inactivation), which cause birth and maturation rates to decline at both low and high temperatures (and to cease altogether as temperatures reach extreme levels) and the mortality rate to increase with increasing temperature (once temperatures exceed the lower limit for viability; fig. 1).

Temperature also affects life-history traits indirectly through its effects on intraspecific competition: the decline in birth and maturation rates and the increase in the mortality rate with increasing density are now dependent on the environmental temperature. Importantly, the direct and indirect effects of temperature can operate at the same time or at different times, depending on the mechanism by which temperature affects competition.

When the strength of intraspecific competition increases monotonically with temperature, competition is strongest at temperatures that exceed the optimum for reproduction, at which the per capita birth rate is already declining because of the direct effects of temperature on fecundity. Hence, the effects of temperature and competition act synergistically, causing a decrease in the upper temperature limit at which reproduction ceases and an overall reduction in the birth rate without altering the unimodal nature of the temperature response of reproduction (fig. 1*a*). A similar outcome is observed in the case of development (fig. 1*c*). In the case of the mortality rate, which increases monotonically with increasing temperature in the absence of competition, temperature effects on competition merely amplify this effect (fig. 1*e*). The key point is that when the strength of competition increases with increasing temperature, effects of temperature and competition act syn-

ergistically to reinforce the decline in birth and maturation rates and the increase in the mortality rate that occur at high temperatures in the absence of competition.

When the strength of competition varies unimodally with temperature, competition is strongest at intermediate temperatures that are optimal for reproduction, at which birth and maturation rates are high and the mortality rate is low. Hence, the effects of temperature and competition act antagonistically, with direct effects of temperature causing birth and maturation rates to decline and mortality rates to increase during periods of low and high temperature extremes and indirect effects of temperature (mediated via competition) causing birth and maturation rates to decline and mortality rates to increase at temperatures that are favorable to reproduction and development (fig. 1). The key consequence of the antagonistic effects of temperature and competition is an increase in the nonlinearity of temperature responses of life-history traits. For instance, there is a qualitative change in the temperature response from unimodal to bimodal in the case of birth and maturation rates and a change from monotonic to unimodal in the case of the mortality rate (fig. 1). These qualitative outcomes are unaltered when the unimodal temperature response is depicted by a modified Gaussian function that allows for a minimum level of competition at temperatures near the lower and upper limits below and above which reproduction ceases (i.e., $q(T) = q_{\min} + q_{T_{opt}} e^{-(T - T_{opt_q})^2/(2s_q^2)}$).

### Effects of Temperature and Competition on Population Dynamics

Constant Thermal Environment. When environmental temperatures are constant, the stage-structured model (eq. [6]) yields analytical results on long-term (equilibrium) abundances (see app. A for details). There are two key results. First, regardless of whether intraspecific competition affects fecundity, juvenile mortality, or adult mortality, variation in equilibrium abundance with temperature is greater when competition is strongest at temperatures optimal for reproduction than when the strength of competition increases monotonically with increasing temperature (fig. 2). For instance, when competition affects fecundity and its temperature response is unimodal, equilibrium abundance shows a bimodal pattern, with a large peak at low temperatures and a much smaller peak at high temperatures (fig. 2a, 2d). This is because while competition is relaxed at higher temperatures, fecundity is lower and mortality is higher (recall that fecundity exhibits a unimodal temperature response while mortality exhibits a monotonic temperature response; fig. 1), thus making for a smaller increase in abundance once temperatures exceed the optimal range for reproduction. The bimodality in abundances resulting from a unimodal

temperature response of competition is much stronger when competition affects juvenile mortality (fig. 2b, 2e). This is because density dependence in juvenile mortality affects both survivorship and development; that is, it reduces the number of juveniles maturing into adults and slows down the maturation rate. Hence, adult abundance is lowest at intermediate temperatures at which competition is strongest.

Second, the mechanism by which temperature affects competition determines the temperature at which equilibrium abundance reaches a maximum. When competition is strongest at the optimal temperature for reproduction, abundance is highest at temperatures below this optimum, regardless of whether it is fecundity or mortality that is affected by competition. This is because mortality is low at temperatures below the optimum for reproduction, at which competition is also weak. When the strength of competition increases with temperature, abundance peaks at temperatures below the optimum for reproduction when competition affects fecundity or juvenile mortality and at temperatures near this optimum when competition affects adult mortality (fig. 2c, 2f). The former outcome ensues because when the strength of competition increases with temperature, the upper temperature limit at which reproduction ceases is lowered, with a corresponding decrease in the temperature at which the birth rate is highest (fig. 1a). The latter outcome ensues because when competition affects adult mortality, reproduction is unconstrained, which leads to higher abundances at temperatures optimal for reproduction. These results underscore the nonintuitive outcomes arising from the interplay between direct and indirect effects of temperature on life-history traits.

Seasonally Varying Thermal Environment. Numerical analysis of the stage-structured model (eq. [6]) under seasonal temperature variation leads to three key insights. First, seasonal variation leads to qualitatively different long-term abundance patterns, depending on the mechanism by which temperature affects competition: a unimodal temperature response of competition leads to more complex dynamics (a greater increase in the frequency and amplitude of population fluctuations) than a monotonic temperature response of competition, the nature of which depends on the life-history trait affected by competition and the type of seasonal regime experienced by the species (tropical vs. Mediterranean/temperate; fig. 3). Second, intra-annual fluctuations are qualitatively similar to those observed under temperature-independent competition when the temperature response of competition is monotonic but not when it is unimodal. Third, despite greater complexity of population dynamics, a unimodal temperature response of competition leads to a higher population

Monotonic temperature response of competition
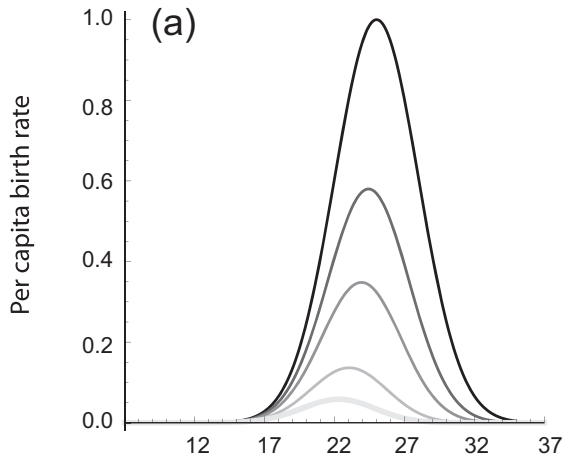
Unimodal temperature response of competition
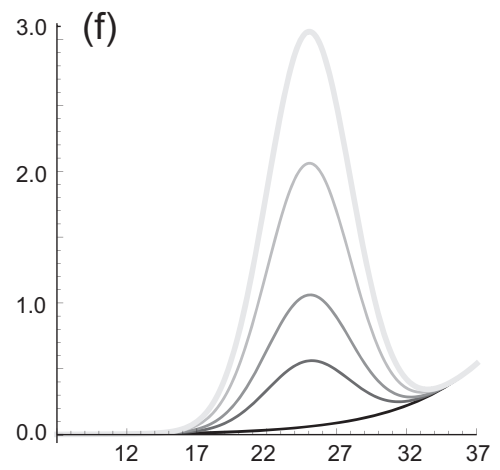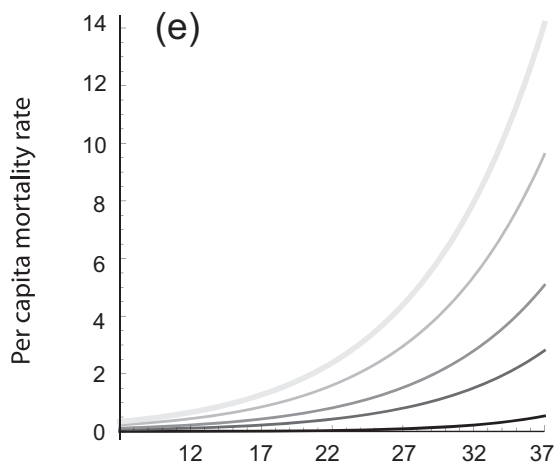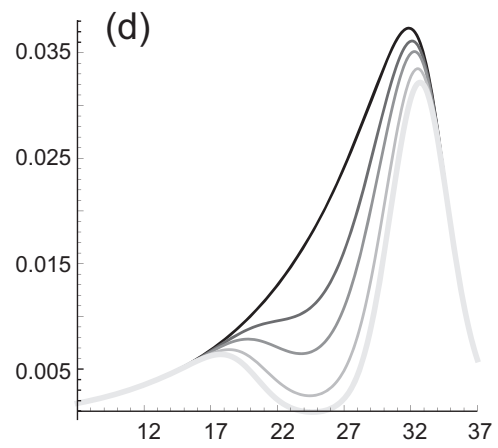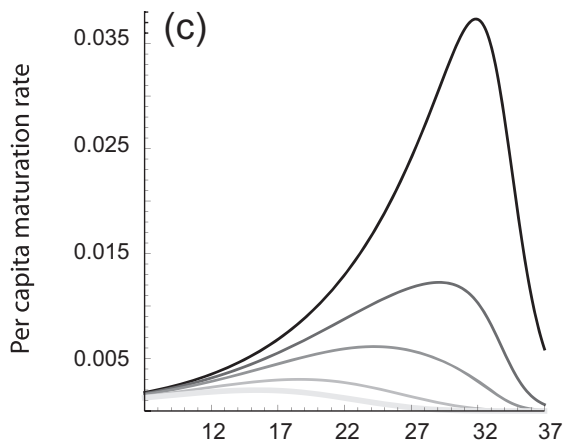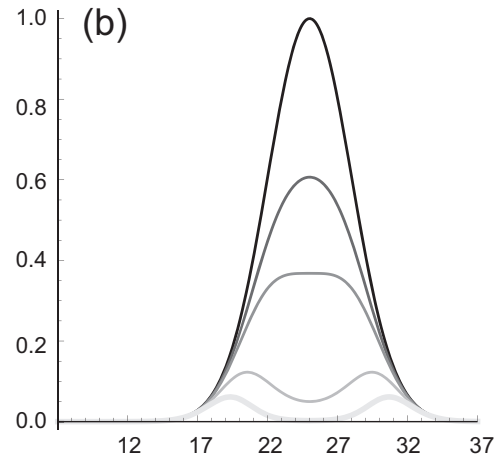
floor (i.e., minimum population size) than a monotonic temperature response (fig. 4). Below, we explain how these results come about.

When temperature affects life-history traits but not competition, abundances decline at low and high temperatures because mortality exceeds reproduction and development. They also decline following periods of favorable temperatures for reproduction and development because an excess of births and recruitment over deaths increases intraspecific competition. When temperature affects both life-history traits and competition, the mechanism by which temperature affects competition determines how this basic pattern is altered.

When competition is strongest at intermediate temperatures that are optimal for reproduction, intra-annual fluctuations are out of phase with those observed when competition is temperature independent, and they exhibit an increase in both the amplitude and the frequency of fluctuations (fig. 3). This is because extreme temperatures and strong competition reduce fecundity, development, and survivorship at different times, leading to additional nonlinearities in life-history traits' response to temperature and density (fig. 1). When the strength of competition increases monotonically with temperature, intra-annual fluctuations in abundance are in phase with those observed when competition is temperature independent, and they exhibit a small increase in the amplitude of fluctuations but no change in the frequency (fig. 3). This is because extreme temperatures and strong competition reduce fecundity, development, and survivorship at the same time, thus only enhancing the existing nonlinearities in life-history traits' response to temperature and density. The only exception occurs when competition affects juvenile mortality in species that experience a Mediterranean or temperate temperature regime (mean habitat temperature below the optimum for reproduction, seasonal fluctuations of large amplitude). In this case, a monotonic temperature response of competition leads to fluctuations that are more out of phase than those when competition is temperature independent but less so than those when the temperature response of competition is unimodal. (The degree to which fluctuations are out of phase can be quantified as the correlation between time series; fig. 4). This difference arises because while intraspecific competition affecting fecundity or adult mortality generates negative density dependence in that trait only, competition affecting juvenile mortality generates negative density dependence in both maturation and mortality rates. The resulting increase in nonlinearity, combined with strong seasonal fluctuations, causes intra-annual fluctuations to deviate from those under temperature-independent competition even when the temperature response of competition is monotonic. These qualitative outcomes are unaltered when the unimodal temperature response of competition is depicted by a modified Gaussian function that allows for a minimum level of competition at temperatures near the lower and upper limits for reproduction.

Somewhat paradoxically, antagonistic effects of temperature and competition lead to more complex dynamics but a higher minimum population size. This is because competition is relaxed at temperatures above the optimum for reproduction. The resulting increase in abundance buffers the subsequent decline in abundance as temperatures decline to winter levels. The strength of this buffering is determined by how strongly the direct effects of temperature (a decrease in the birth rate and an increase in the mortality rate at temperatures above the optimum) oppose the indirect effects (weaker competition at higher temperatures due to a unimodal temperature response of competition). Species in which the increase in the mortality rate at high temperatures is lower than the decrease in birth rate and whose upper temperature limit for viability is high relative to the temperature optimum for reproduction (i.e., those with greater tolerance of high temperatures) are likely to exhibit a stronger buffering effect and hence a higher minimum population size.

Competition Affects Multiple Life-History Traits. When intraspecific competition affects fecundity and adult mortality, the outcomes for population dynamics are similar to those observed when competition affects only adult mortality (figs. B1, B2; figs. A1–A3, B1, B2, and C1–C3 are available online). This is because fecundity affects the juvenile stage directly and the adult stage only indirectly, while mortality affects the adult stage directly and hence has a more direct effect on population dynamics. When competition affects juvenile mortality and fecundity or juvenile mortality and adult mortality, joint effects of temperature and competition on juvenile mortality dominate those on fecundity and adult mortality (figs. B1, B2). This

Figure 1: Effects of temperature and competition on life-history traits when competition increases with temperature (*a*, *c*, *e*) and when competition is strongest at temperatures optimal for reproduction (*b*, *d*, *f*). The dark solid line depicts the temperature response in the absence of competition, and the gray lines depict the temperature responses in the presence of competition (lighter lines reflect increasing density—i.e., 2, 3, 4, and 5 individuals/cm²—and hence a stronger competitive response). Parameter values are as follows: $b_{T_{opt}} = 1.0$, $T_{opt_b} = T_{opt_q} = 298$ K, $s_b = s_q = 3.0$, $T_R = 297$ K, $m_{J_{T_R}} = 0.0167(T_{J_{T_R}} = 60)$, $q_{T_R} = 0.2$, $A_m = A_q = 10{,}500$, $T_{L/2} = 287$ K, $A_L = -50{,}000$, $T_{H/2} = 307$ K, $A_H = 75{,}000$, $d_{T_R} = 0.02$, $A_d = 15{,}000$.
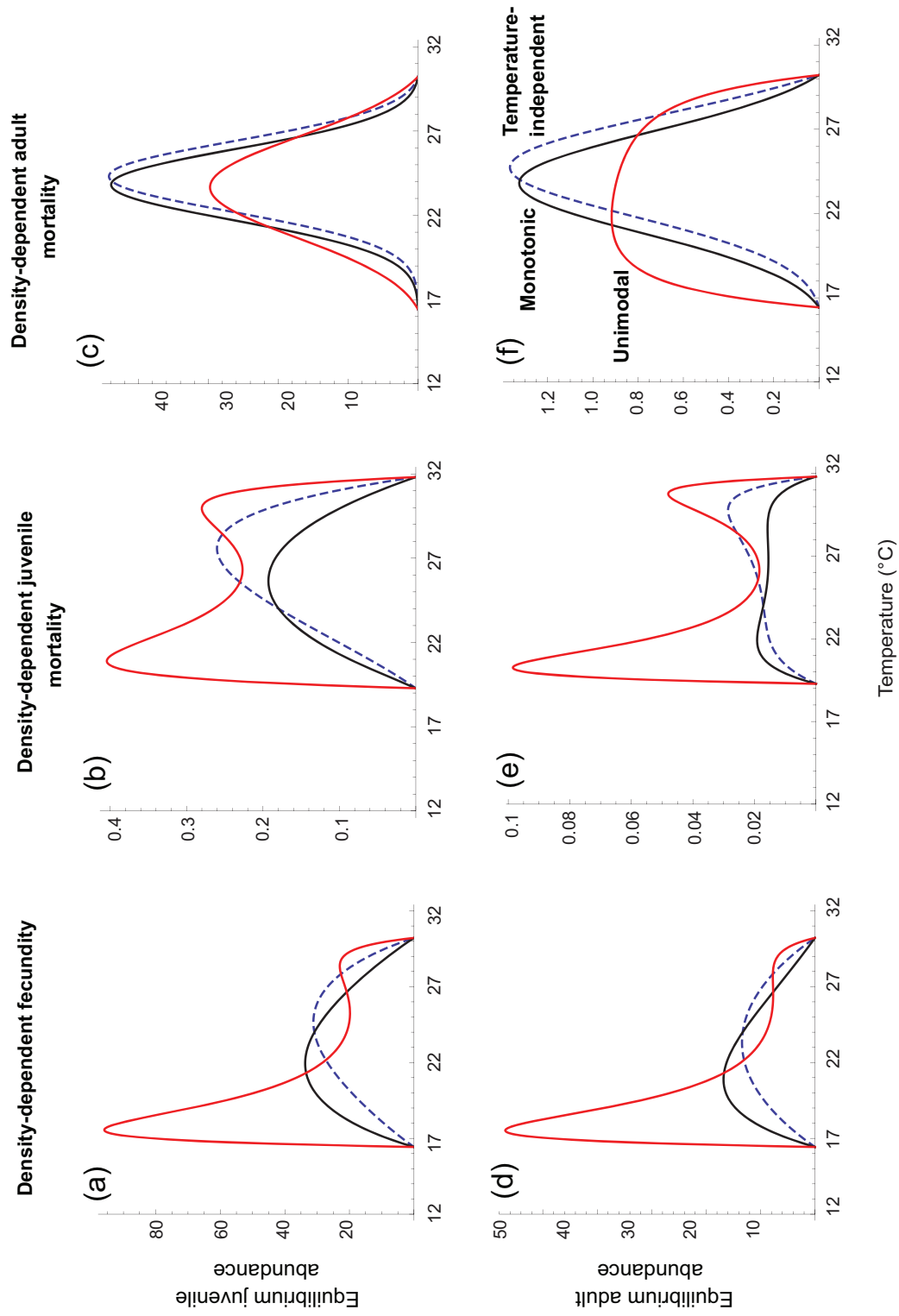
Figure 2: Equilibrium abundances of juveniles (*a–c*) and adults (*d–f*) in a constant thermal environment (eq. [6]; see app. A for analytical details). In all panels, the dashed line shows the outcomes when competition is temperature independent, the black line the outcomes when competition strength increases with temperature, and the red line the outcomes when competition is strongest at temperatures optimal for reproduction. Panels *a* and *d* depict equilibrium abundances as a function of temperature when intraspecific competition affects fecundity, *b* and *e* the abundances when competition affects juvenile mortality, and *c* and *f* the abundances when competition affects adult mortality. Parameter values are as follows: $d_{J_{T_R}} = d_{A_{T_R}} = 0.02$, $A_{d_J} = 12{,}000$, $A_{d_A} = 15{,}000$; other values are as in figure 1.
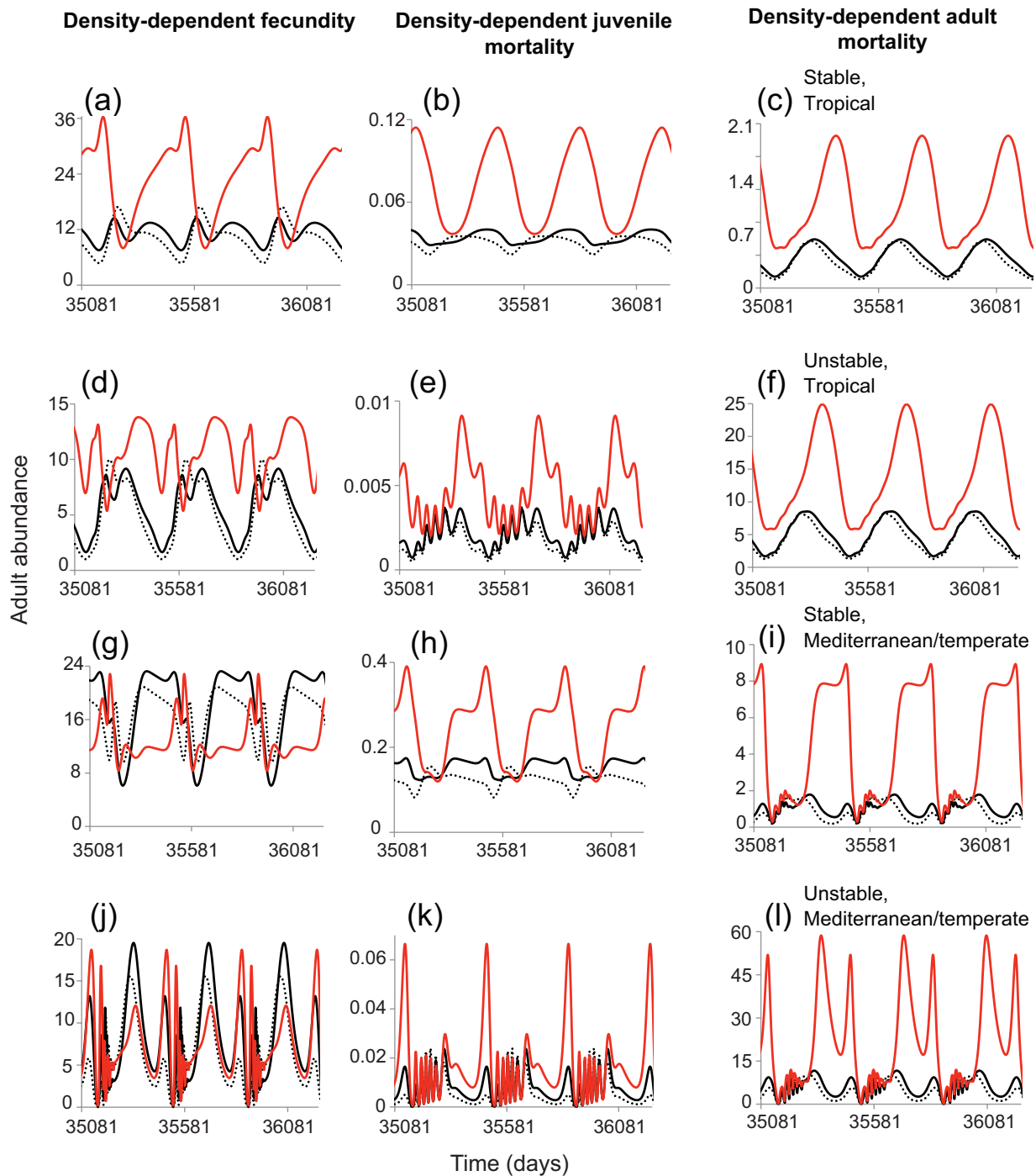
E59

Figure 3: Long-term adult abundances for species that attain a stable point equilibrium or stable limit cycles in the absence of seasonal temperature variation and experience a tropical or Mediterranean/temperate temperature regime (see text for descriptions of the types of long-term outcomes and temperature regimes). In each panel, the dotted line depicts abundances when intraspecific competition is independent of temperature, the black solid line abundances when the temperature response of competition is monotonic, and the red line abundances when the temperature response of competition is unimodal. Abundances shown are for the last 3–4 years of a 100-year time series. For species experiencing a stable point equilibrium in the absence of temperature variation (a–c, g–i), $b_{T_{opt}} = 1.0$ and $d_{A_{T_R}} = 0.05$; for species experiencing limit cycles (d–f, j–l), $b_{T_{opt}} = 5.0$, $m_{J_{T_R}} = 0.0167$, $d_{J_{T_R}} = 0.005$, and $d_{A_{T_R}} = 0.5$. Parameters for the tropical temperature regime are $M_T = 27°C$ and $A_T = 3.0°C$, and those for the Mediterranean/temperate regime are $M_T = 17°C$ and $A_T = 9.0°C$. Other parameters, which are common to all panels, are as in figures 1 and 2.

E60
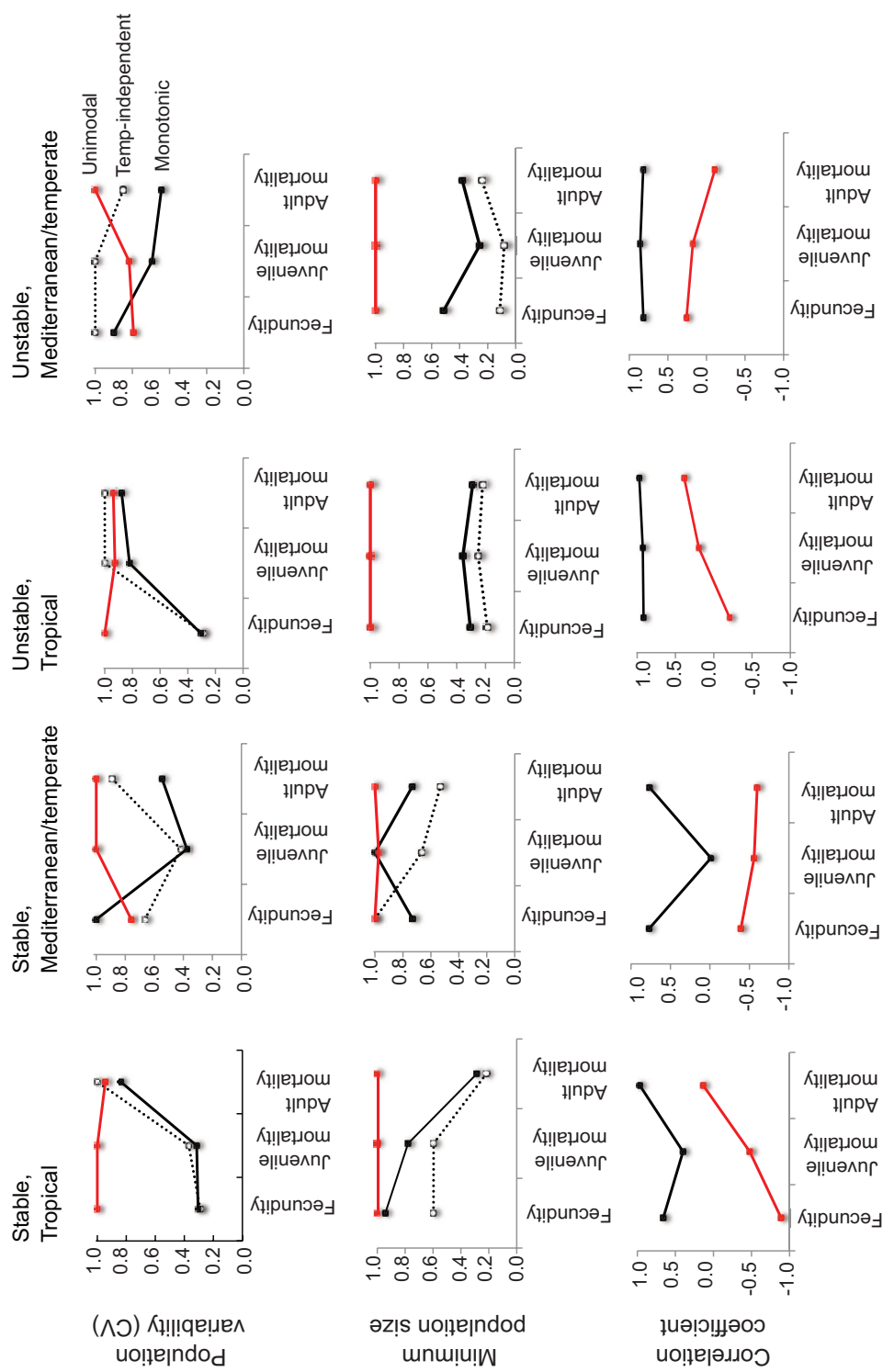
Figure 4: Metrics of population characteristics when temperature affects competition. The first two columns depict a population that attains a stable equilibrium in the absence of temperature variation, and the last two columns a population that exhibits cycles. Plots in the third row depict the correlation coefficient between time series of abundances (for the last 5 years of a 100-year run) when competition is temperature independent versus that when the temperature response is monotonic or unimodal. Lines are drawn for ease of visual comparison. When the temperature response is monotonic, population dynamics are in phase with those observed under temperature-independent competition (statistically significant positive correlation; $n = 1,825$, $P < .005$), but when the temperature response is unimodal, dynamics are out of phase (a smaller positive or negative correlation; $n = 1,825$, $P < .005$). CV = coefficient of variation. Parameter values are as in figures 2 and 3.

is because temperature and competition acting on fecundity or adult mortality affect that trait only, while temperature and competition acting on juvenile mortality affect both that trait and development. Thus, the temperature and density responses of juvenile mortality drive the patterns of population dynamics, even when all three traits are simultaneously affected by competition. These results emerge regardless of whether the species exhibits a stable point equilibrium or limit cycles (e.g., generation cycles or delayed feedback cycles) in the absence of temperature variation.

Importantly, competition affecting more than one life-history trait does not have any qualitative effects on the population dynamical outcomes under the two mechanisms by which temperature affects competition. Antagonistic effects of temperature and competition lead to more complex dynamics and a higher population floor regardless of (1) whether the species exhibits a stable point equilibrium or a limit cycle in the absence of temperature variation, (2) which combination of life-history traits is affected by density, and (3) the type of seasonal temperature regime (tropical vs. Mediterranean/temperate) experienced by the species. This finding suggests that the emergent antagonistic versus synergistic effects are fundamental properties of the temperature dependence of population regulation that are robust to the nature of the long-term steady state in the absence of temperature variation (i.e., point equilibrium vs. limit cycle), the nature of negative feedback (i.e., one or more vital rates are functions of density), and the pattern of abiotic (temperature) variation (i.e., small temperature fluctuations with the mean habitat temperature close to the physiological optimum vs. large fluctuations with a mean below the optimum).

Applicability of Model to High-Latitude Species. We have analyzed the model using temperature regimes that are characteristic of tropical, Mediterranean, and temperate latitudes. Ectotherms inhabiting continental climates at higher latitudes can experience seasonal fluctuations stronger than those we have analyzed. Such species can also exhibit seasonal diapause. The question therefore arises as to how well the stage-structured delay model applies to high-latitude ectotherms. In appendix C, we show that neither seasonal diapause nor high-amplitude seasonal temperature fluctuations alter the qualitative results we have obtained on temperature effects on competition. Specifically, the dynamics are more complex and minimum population sizes are higher when the temperature response of competition is unimodal than when it is monotonic. This finding is encouraging because it suggests that the stage-structured delay model is applicable to ectotherms occupying a wide range of latitudes.

Discussion

We have presented a trait-based mathematical framework for elucidating the mechanisms by which temperature affects intraspecific competition. This framework yields testable comparative predictions about how intraspecific competition affects reproduction, development, and mortality under alternative hypotheses about the temperature dependence of competition. It identifies the conditions under which temperature-dependent competition leads to population dynamics that are qualitatively different from those observed when competition is temperature independent. To our knowledge, this is the first attempt at developing a theoretical framework that integrates mechanistic descriptions of trait responses to temperature with population models that realistically capture the developmental delays characteristic of ectotherm life cycles.

The novelty of our approach is its strong mechanistic basis, which leads to insights that could not otherwise have been obtained. For instance, we find that the interplay between direct and indirect effects of temperature on life-history traits can have qualitatively different effects on population dynamics, depending on the mechanism by which temperature affects competition. Direct effects arise from temperature effects on biochemical processes (e.g., reaction kinetics, enzyme inactivation) that underlie the temperature responses of fecundity, development, and mortality, which can be derived from first principles with thermodynamic rate process models (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). Indirect effects arise from temperature effects on life-history traits' response to density, which can be quantified with competition experiments conducted at different temperatures. When the strength of competition increases monotonically with temperature, direct and indirect effects of temperature act synergistically; when competition is strongest at temperatures optimal for reproduction, direct and indirect effects act antagonistically. Antagonistic effects increase the nonlinearity in the trait responses to temperature and density, leading to an increase in the frequency and/or amplitude of intra-annual population fluctuations. In contrast, synergistic effects enhance existing nonlinearities in trait responses, leading to a small increase in the amplitude of fluctuations without altering the frequency. Counter to intuition, antagonistic effects of temperature and competition lead to a higher minimum population size than do synergistic effects, despite the greater tendency for population fluctuations.

These results have important implications for understanding how temperature variation influences population persistence. If the strength of competition increases monotonically within the biologically relevant temperature

range, we expect populations to become more susceptible to stochastic extinction during periods of low abundances, because the synergistic effects of temperature and competition could lead to a population floor lower than would otherwise be the case. In contrast, if competition is strongest at temperatures optimal for reproduction, we expect populations to be more prone to population outbreaks, because the antagonistic effects of temperature and competition could result in large fluctuations in abundance. The former situation could be detrimental to biodiversity if native species exhibit a monotonic temperature response of competition, while the latter could be detrimental if invasive pests and pathogens exhibit a unimodal temperature response of competition. These differences in the way joint effects of temperature and competition influence population regulation underscore the importance of incorporating intraspecific competition into studies that investigate effects of climate warming on population viability and biodiversity.

An important question is the extent to which these theoretical predictions are borne out by empirical data. There are no more than a few studies that we have been able to find, all of which focus on insects (Orthoptera, Hemiptera, and Diptera). They find that temperature affects the density-dependent decline in fecundity or in survivorship but not in both. None of these studies spanned a sufficiently wide temperature range to characterize the nature of the temperature response of competition, but there is a suggestion that the temperature response of density-dependent mortality is monotonic and increasing while that of density-dependent fecundity is unimodal. There are no empirical studies we are aware of that have investigated the population-level consequences of temperature effects on intraspecific competition. This is at least in part due to lack of predictive theory on the subject, a gap that our framework takes a first step toward filling.

Theoretical studies of temperature effects on population dynamics and species interactions have assumed that intraspecific competition is temperature independent (e.g., Savage et al. 2004; Vasseur and McCann 2006; van de Wolfshaar et al. 2008; Ohlberger et al. 2011). An important contribution of our work is in identifying the conditions under which the temperature dependence of competition should be incorporated into studies of temperature effects on species interactions. We find that intra-annual fluctuations in abundance are qualitatively similar to, and in phase with, those observed under temperature-independent competition when the temperature response of competition is monotonic but not when it is unimodal. Even when the temperature response of competition is monotonic, the degree to which intra-annual fluctuations deviate from those under temperature-independent competition depends on the life-history trait affected by competition and the characteristics of the temperature regime experienced by the

species. These results suggest that while the assumption of temperature-independent self-limitation may be reasonable for species in which competition affects fecundity and/or adult mortality and increases in strength with increasing temperature, it may not be reasonable (1) when competition affects juvenile mortality in species that experience a Mediterranean or temperate temperature regime or (2) when the temperature response of competition is unimodal, regardless of the life history affected by competition or the seasonal temperature regime experienced by the species. This finding is particularly important for theoretical investigations of climate-warming effects on consumer-resource interactions. Whether warming increases the amplitude of consumer-resource fluctuations that predispose species to stochastic extinction during periods of low abundances will depend crucially on whether self-limitation in resource species, typically the source of negative density dependence that allows stable consumer-resource coexistence (i.e., at a point attractor; Gurney and Nisbet 1998; Murdoch et al. 2003), increases with increasing temperature or peaks at intermediate temperatures.

A second important contribution of our work is in providing testable comparative predictions about the joint effects of temperature and competition on life-history traits, which can be tested via controlled experiments. For instance, temperature effects on the strength of intraspecific competition (the parameter q) can be measured by conducting competition experiments at a series of temperatures and using linear or nonlinear regression to estimate q as the slope of the relationship between per capita birth/maturation/mortality rate and density. Values of q thus estimated at a series of temperatures constitute the temperature response of competition for a given life-history trait. Once these data are at hand, one can use nonlinear regression to determine the relationship between temperature and q. If temperature effects on competition affect life-history traits in the way predicted by theory, experimentally quantified temperature responses should provide a significant fit to the predicted temperature responses under monotonic (eq. [4]) or unimodal (eq. [5]) temperature responses of competition (fig. 1). Because the theory makes comparative predictions under alternative hypotheses, experiments not only can quantify the joint effects of temperature and competition but also can identify the mechanisms by which temperature affects competition. Although there are a few empirical studies that have investigated the joint effects on temperature and density, none has spanned a sufficiently wide temperature range to characterize the temperature response of competition. Such studies are urgently needed if we are to understand and predict the effects of perturbations such as climate warming on population viability and species diversity.

Our findings also provide guidelines for investigating

temperature effects on population dynamics using time-series data. Depending on the mechanism by which temperature affects competition, long-term abundances exhibit distinctive signatures determined by the life-history trait affected by competition and the type of seasonal temperature regime experienced by the species. These can be detected by parameterizing the model we have developed (or appropriate modifications thereof) and comparing its output with independent time-series data from experiments or field observations. Even if data are unavailable to parameterize a model, statistical analyses could be used to detect signatures in time-series data that are consistent with particular combinations of temperature responses and seasonal temperature regimes.

A particular advantage of the predictions emerging from our framework is their utility for comparative studies of temperature effects on different species within the same community or the same species in different habitats. Such studies are potentially important in assessing which combinations of life-history traits and density responses make species more or less vulnerable to perturbations such as climate warming.

Our framework considers competition for resources whose supply does not depend on the environmental temperature (e.g., abiotic resources such as space, light, and nutrients) or does not change with temperature on timescales relevant to consumer-resource dynamics (e.g., biotic resources with slow turnover, such as perennial plants). It does so because it provides a tractable starting point for developing biologically realistic models to investigate temperature effects on population regulation. Elucidating temperature effects on intraspecific competition for resources whose supply does change with temperature requires extending the theory to consumer-resource interactions, in which temperature effects on the resource species' population dynamics determine the strength of the consumers' competition for the resource. Developing mechanistic models of consumer-resource interactions that investigate this feedback is an important future direction, as are investigations of the joint effects of temperature and competition on body size. Our framework also focuses on ectotherm population dynamics, which constitute a good starting point because ectotherm body temperatures vary with the environmental temperature. However, endotherms are also affected by temperature variation through their interactions with resources, natural enemies, and mutualists that are ectothermic. Exploring the effects of temperature and competition on ectotherm-endotherm interactions is another important research priority.

In conclusion, our study constitutes a first step in investigating the effects of temperature variation on intraspecific competition in ectotherms. It is intended to provide a predictive framework for future empirical studies on the temperature effects on competition and a mechanistic basis for future theoretical studies on temperature effects on population dynamics and species interactions.

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Appendix A from P. Amarasekare and R. M. Coutinho, "Effects of Temperature on Intraspecific Competition in Ectotherms"

(Am. Nat., vol. 184, no. 3, p. E50)

Long-Term Outcomes of the Stage-Structured Variable Delay Model in a Constant Thermal Environment

Intraspecific Competition Affects Fecundity

When intraspecific competition affects fecundity, the per capita birth rate is a decreasing function of density. In a constant thermal environment (i.e., the species experiences the same temperature, on average, over the year), this gives us the following version of equation (6):

$$\frac{dJ(t)}{dt} = b(T)A(t)e^{-q(T)A(t)} - M_J(T) - d_J(T)J(t),$$

$$\frac{dA(t)}{dt} = M_J(T) - d_A(T)A(t), \tag{A1}$$

$$M_J(t) = b(T)A(t - \tau(T))e^{-q(T)A(t-\tau(T))}e^{-d_J(T)\tau(T)},$$

where the functions $b(T)$, $d_X(T)$ ($X = J, A$) and $M_J(t)$ depict the density-independent per capita birth, maturation, and mortality rates at temperature T. Since maturation and mortality rates are no longer time dependent, development delay (τ) and juvenile survivorship (S) do not vary over time and are equal to, respectively, $e^{-d_J(T)\tau(T)}$ and $1/m_J(T)$.

At equilibrium, $dJ(t)/dt = 0$, $dA(t)/dt = 0$, $J(t) = J(t - \tau(T)) = J^*$, and $A(t) = A(t - \tau(T)) = A^*$. The nontrivial equilibrium is given by

$$J^* = \frac{d_A(T)[\exp(d_J(T)/m_J(T)) - 1][\ln(b(T)/d_A(T)) - d_J(T)/m_J(T)]}{d_J(T)q(T)},$$

$$A^* = \frac{\ln(b(T)/d_A(T)) - d_J(T)/m_J(T)}{q(T)}. \tag{A2}$$

Note that the developmental delay is expressed in terms of the maturation rate; that is, $\tau(T) = 1/m_J(T)$. Figures 2*a* and 2*d* depict the effects of temperature on equilibrium abundance.

In a constant thermal environment, the equilibrium is a function of the strength of competition ($q(T)$) but the stability of the equilibrium is not (Nisbet and Gurney 1983; Nisbet 1997; Murdoch et al. 2003). The local stability criterion for a fixed delay model with density-dependent fecundity is given in Gurney et al. (1980) and Nisbet (1997).

Intraspecific Competition Affects Juvenile Mortality

When intraspecific competition affects juvenile mortality in a constant thermal environment we have the following version of equation (6):

$$\frac{dJ(t)}{dt} = b(T)A(t) - M_J(t) - (d_J(T) + q(T)J(t))J(t),$$

$$\frac{dA(t)}{dt} = M_J(t) - d_A(T)A(t), \tag{A3}$$

$$M_J(T) = b(T)A(t - \tau(T))e^{-\int_{t-\tau(T)}^{t}(d_J(T)+q(T)J(x))dx},$$

$$\frac{dS_J(t)}{dt} = S_J(t)(q(T)J(t - \tau) - q(T)J(t)).$$

The nontrivial equilibrium is

$$J^* = \frac{m_{\mathrm{J}}(T)\ln\left(b(T)/d_{\mathrm{A}}(T)\right) - d_{\mathrm{J}}(T)}{q(T)},$$

$$A^* = \frac{(d_{\mathrm{J}}(T) + q(T)J^*)J^*}{b(T) - d_{\mathrm{A}}(T)}. \tag{A4}$$

Figures 2*b* and 2*e* depict the effects of temperature on equilibrium abundance. The stability analysis of this model cannot be conducted analytically. Nisbet (1997) provides a numerical analysis of the stability boundary.

Intraspecific Competition Affects Adult Mortality

When intraspecific competition affects adult mortality in a constant thermal environment, we have the following version of equation (6):

$$\frac{dJ(t)}{dt} = b(T)A(t) - M_{\mathrm{J}}(t) - d_{\mathrm{J}}(T)J(t),$$

$$\frac{dA(t)}{dt} = M_{\mathrm{J}}(t) - (d_{\mathrm{A}}(T) + q(T)A(t))A(t), \tag{A5}$$

$$M_{\mathrm{J}}(T) = b(T)A(t - \tau(T))e^{-d_{\mathrm{J}}(T)\tau(T)},$$

with the nontrivial equilibrium

$$J^* = \frac{b(T)A^*(1 - e^{-d_{\mathrm{J}}(T)\tau(T)})}{d_{\mathrm{J}}(T)},$$

$$A^* = \frac{b(T)e^{d_{\mathrm{J}}(T)\tau(T)} - d_{\mathrm{A}}(T)}{q(T)}. \tag{A6}$$

Figures 2*c* and 2*f* depict the effects of temperature on equilibrium abundance.

Murdoch et al. (2003) provide a detailed, and accessible, derivation of the fixed delay models, and Nisbet and Gurney (1983) and Nisbet (1997) provide the formalism for delay models with variable instar duration driven by resource competition.

Long-Term Outcomes of the Stage-Structured Variable Delay Model in a Seasonally Variable Thermal Environment

An important question when investigating density-dependent population dynamics under seasonally fluctuating temperatures is whether the resulting periodic solution is stable to perturbations of the species abundance. We investigated this issue by analyzing the basin of attraction of the periodic solutions; that is, given different initial conditions, does the population converge to the same periodic attractor in the long term? This constitutes a rigorous perturbation analysis of the periodic attractor because, by setting the initial values to both small and large numbers of adults, we are investigating the stability of the periodic solution to both small and large perturbations of the state variables. We varied the initial population of adults from 0.01 up to 40 under the three regimes of density dependence for the cases when the tropical and Mediterranean/temperate species exhibit a stable point equilibrium in the absence of season variation (in which case a periodic solution is driven only by seasonal temperature variation) and when the two types of species exhibit delayed feedback cycles (in which case the periodic solution that arises because of developmental delays is modified by seasonal temperature variation). We found that the long-term periodic solution is robust to changes in the initial conditions in all cases, confirming that there are no alternative states. Thus, our analyses shows that the periodic solutions obtained in a seasonally varying thermal environment are indeed stable to perturbations of the state variables.
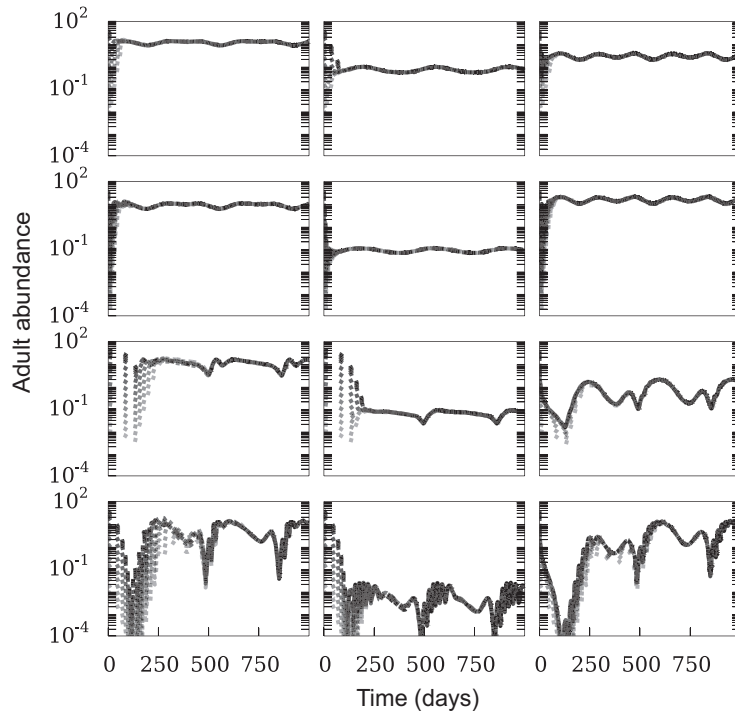
Figure A1: Analysis of the basin of attraction of the periodic solutions for abundances by varying initial abundances for the four cases presented in figure 3 when competition is temperature independent. As can be seen, all initial conditions converge to the same periodic attractor, suggesting that the periodic solutions obtained under seasonal temperature variation are stable to perturbations. The time to convergence varies from 1 month to 2 years, depending on the type of density dependence and the seasonal temperature regime. Convergence takes longer in Mediterranean/temperate species. All parameter values are as in figure 3, and the 12 panels correspond to those in figure 3.
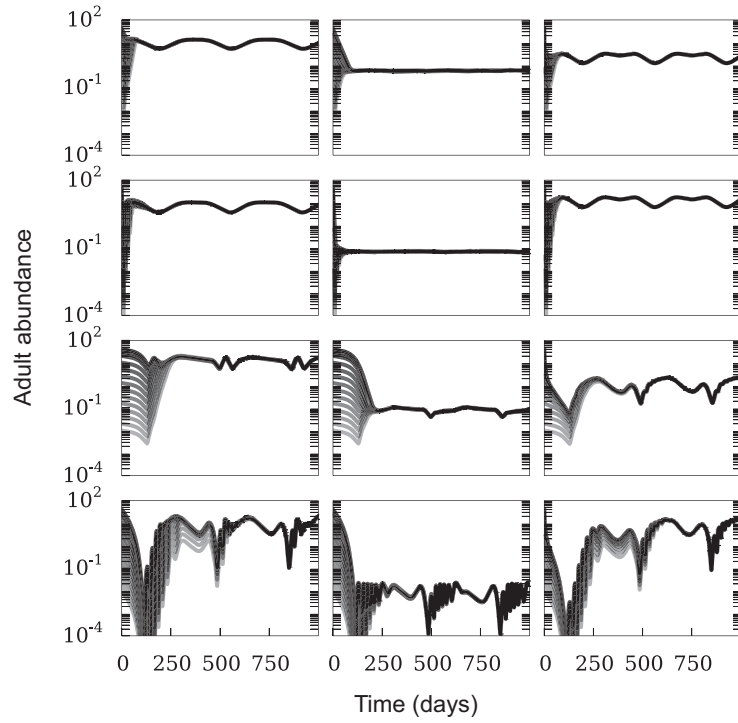
Figure A2: Analysis of the basin of attraction of the periodic solutions for abundances by varying initial abundances for the four cases presented in figure 3 when the strength of competition increases monotonically with temperature. All parameter values are as in figure 3, and the 12 panels correspond to those in figure 3.
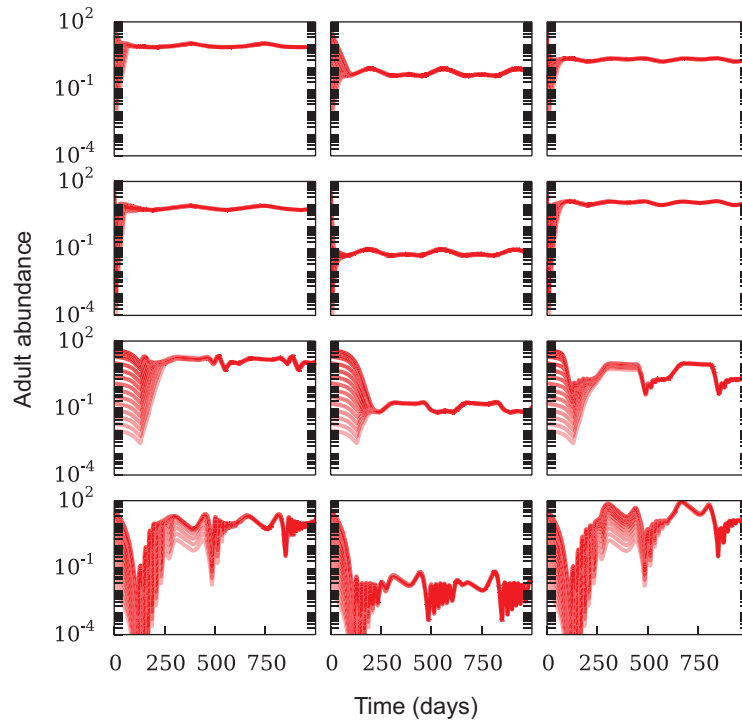
Figure A3: Analysis of the basin of attraction of the periodic solutions for abundances by varying initial abundances for the four cases presented in figure 3 when competition is strongest at temperatures optimal for reproduction. All parameter values are as in figure 3, and the 12 panels correspond to those in figure 3.

Literature Cited Only in Appendix A

Gurney, W., S. Blythe, and R. Nisbet. 1980. Nicholson's blowflies revisited. Nature 287:17–21.

Appendix B from P. Amarasekare and R. M. Coutinho, "Effects of Temperature on Intraspecific Competition in Ectotherms"

(Am. Nat., vol. 184, no. 3, p. E50)

Population Dynamics When Intraspecific Competition Affects More than One Life-History Trait

Figures B1 and B2 depict the joint effects of temperature and competition on population dynamics when competition affects more than one life-history trait. See "Competition Affects Multiple Life-History Traits" in the main text for details.
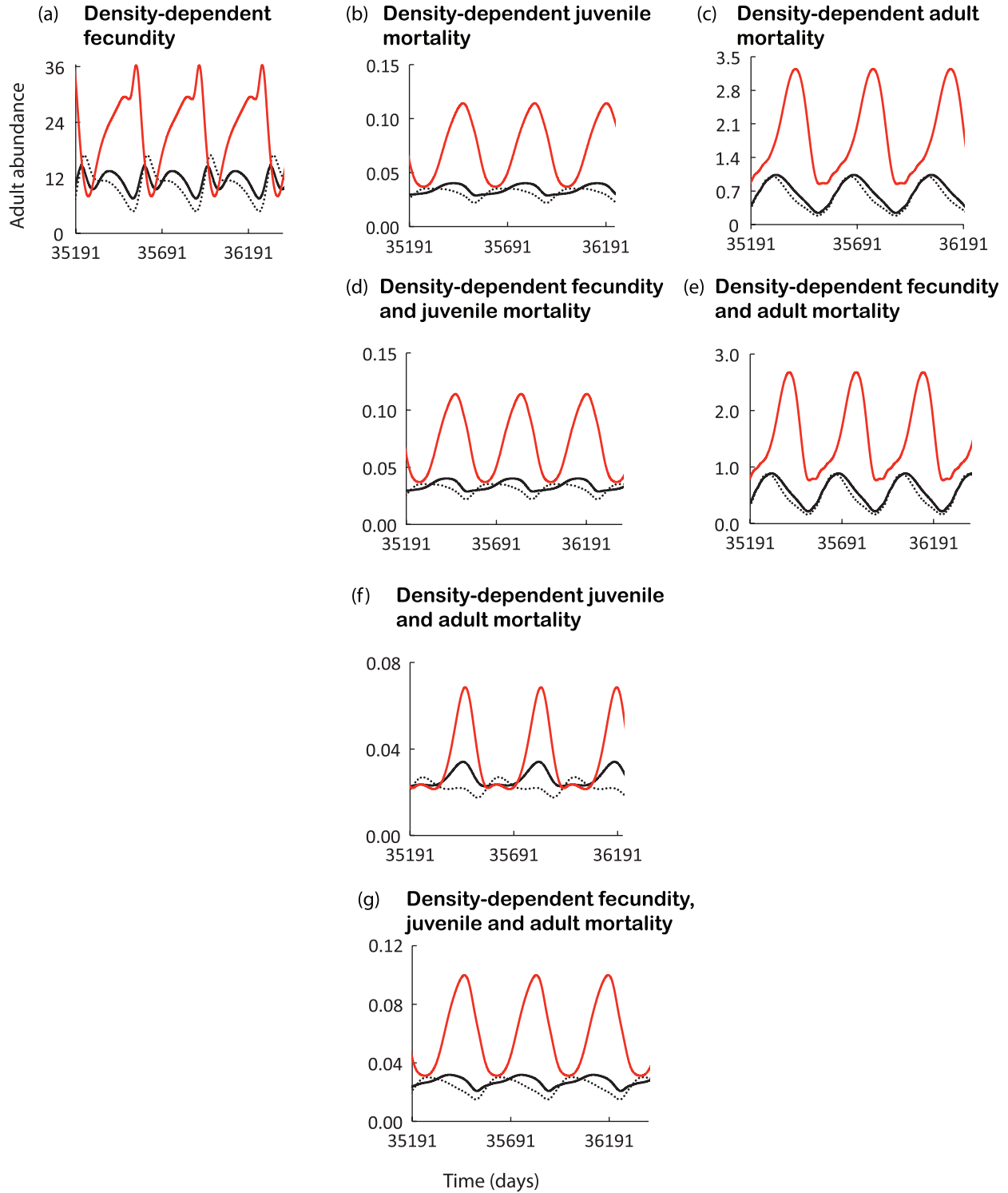
Figure B1: Long-term adult abundances in a tropical seasonal environment for a species that attains a stable equilibrium in the absence of temperature variation and experiences density dependence in more than one life-history trait. In each panel, the dotted line depicts abundances when intraspecific competition is independent of temperature, the black solid line abundances when the temperature response of competition is monotonic, and the red line abundances when the temperature response of competition is unimodal. Parameter values are as in figures 2 and 3.
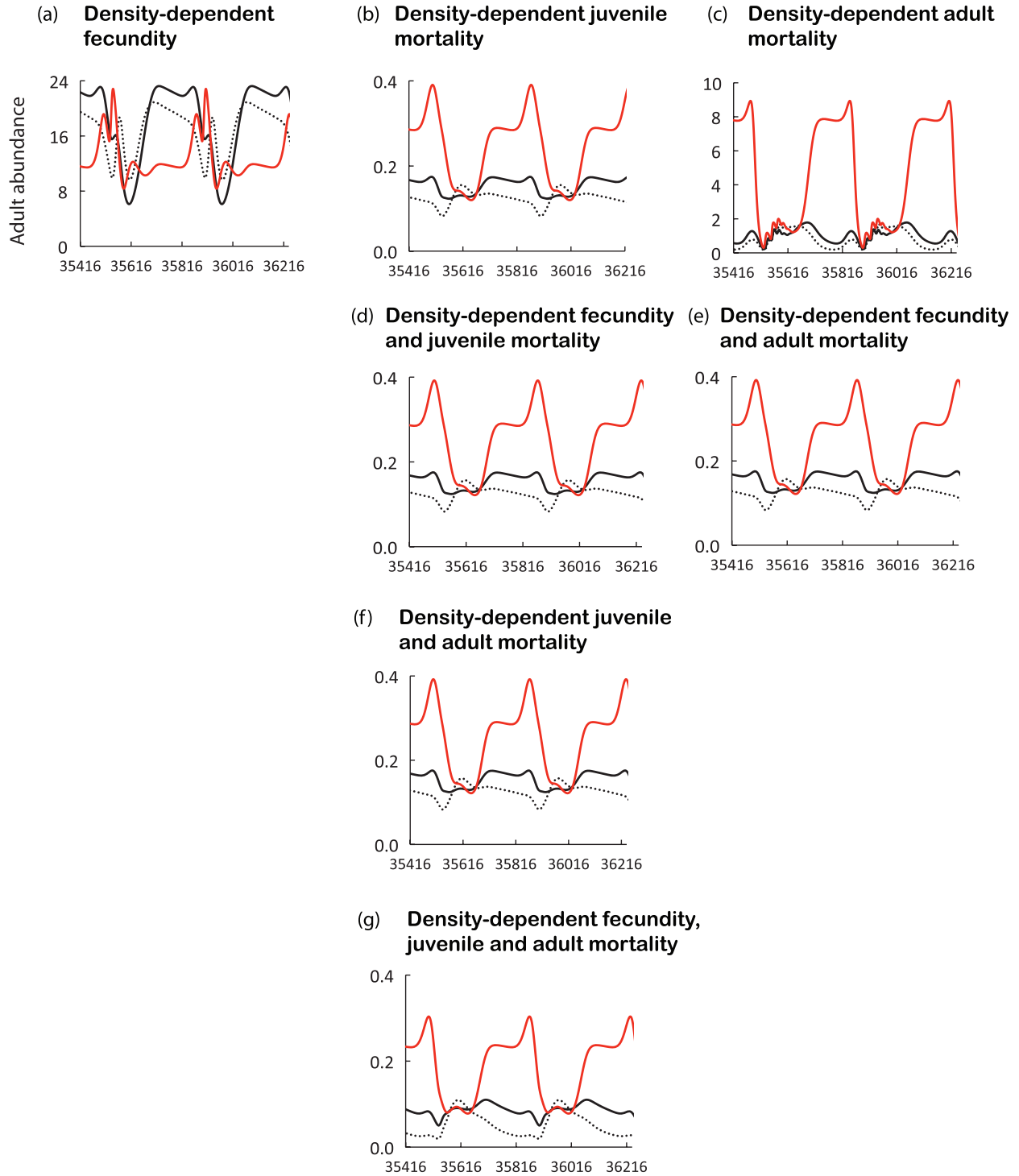
(a) **Density-dependent fecundity**

(b) **Density-dependent juvenile mortality**

(c) **Density-dependent adult mortality**

(d) **Density-dependent fecundity and juvenile mortality**

(e) **Density-dependent fecundity and adult mortality**

(f) **Density-dependent juvenile and adult mortality**

(g) **Density-dependent fecundity, juvenile and adult mortality**

Figure B2: Long-term adult abundances in a Mediterranean/temperate environment for a species that attains a stable equilibrium in the absence of temperature variation and experiences density dependence in more than one life-history trait. In each panel, the dotted line depicts abundances when intraspecific competition is independent of temperature, the black solid line abundances when the temperature response of competition is monotonic, and the red solid line abundances when the temperature response of competition is unimodal. Parameter values are as in figures 2 and 3.

Appendix C from P. Amarasekare and R. M. Coutinho, "Effects of Temperature on Intraspecific Competition in Ectotherms"

(Am. Nat., vol. 184, no. 3, p. E50)

Application of the Delay Differential Equation Model to High-Latitude Species Experiencing Large Temperature Fluctuations and to Seasonal Diapause

Effects of High-Amplitude Seasonal Temperature Fluctuations

How well the stage-structured delay model (eq. [6]) applies to temperate species experiencing high-amplitude seasonal fluctuations is an important issue. We have conducted numerical simulations of the model with data for an insect species (the pea aphid *Acyrthosiphon pisum*) that is found in both maritime temperate and continental temperate climates (Morgan et al. 2001). These simulations show (figs. C1, C2) that an increase in seasonal fluctuations does not lead to a qualitative change in the model's predictions. Specifically, the dynamics are more complex and minimum population sizes are higher when the temperature response of competition is unimodal than when it is monotonic. This result underscores the important point that seasonal fluctuations in themselves cannot alter the qualitative effect of intraspecific competition on population dynamics because seasonal temperature variation is an abiotic factor that is outside the biotic feedback loop that characterizes density-dependent population regulation. What seasonal fluctuations can do is increase the amplitude of population fluctuations without altering the frequency (figs. C1, C2).

Effects of Seasonal Diapause

We have also investigated how well the stage-structured delay model applies to species that experience seasonal diapause. We incorporated diapause into the model by causing all but the diapausing stage to die at low temperatures. As can be seen (fig. C3), the existence of a diapausing stage does not alter any of the qualitative outcomes of the model. This is because at temperatures low enough to cause diapause, there is no reproduction or development and no competition. Hence, the fact that the life history of an ectotherm contains a diapausing stage per se does not alter our findings on temperature effects on competition, either at the level of life-history traits or at the level of population dynamics. This, in turn, means that using stage-specific developmental thresholds as we do in the model is sufficient to capture the lack of reproductive activity and the consequent lack of increase in population size to levels at which competition starts to operate.

 Taken together, these additional analyses illustrate the broad applicability of the stage-structured delay model to ectotherms inhabiting different latitudes.
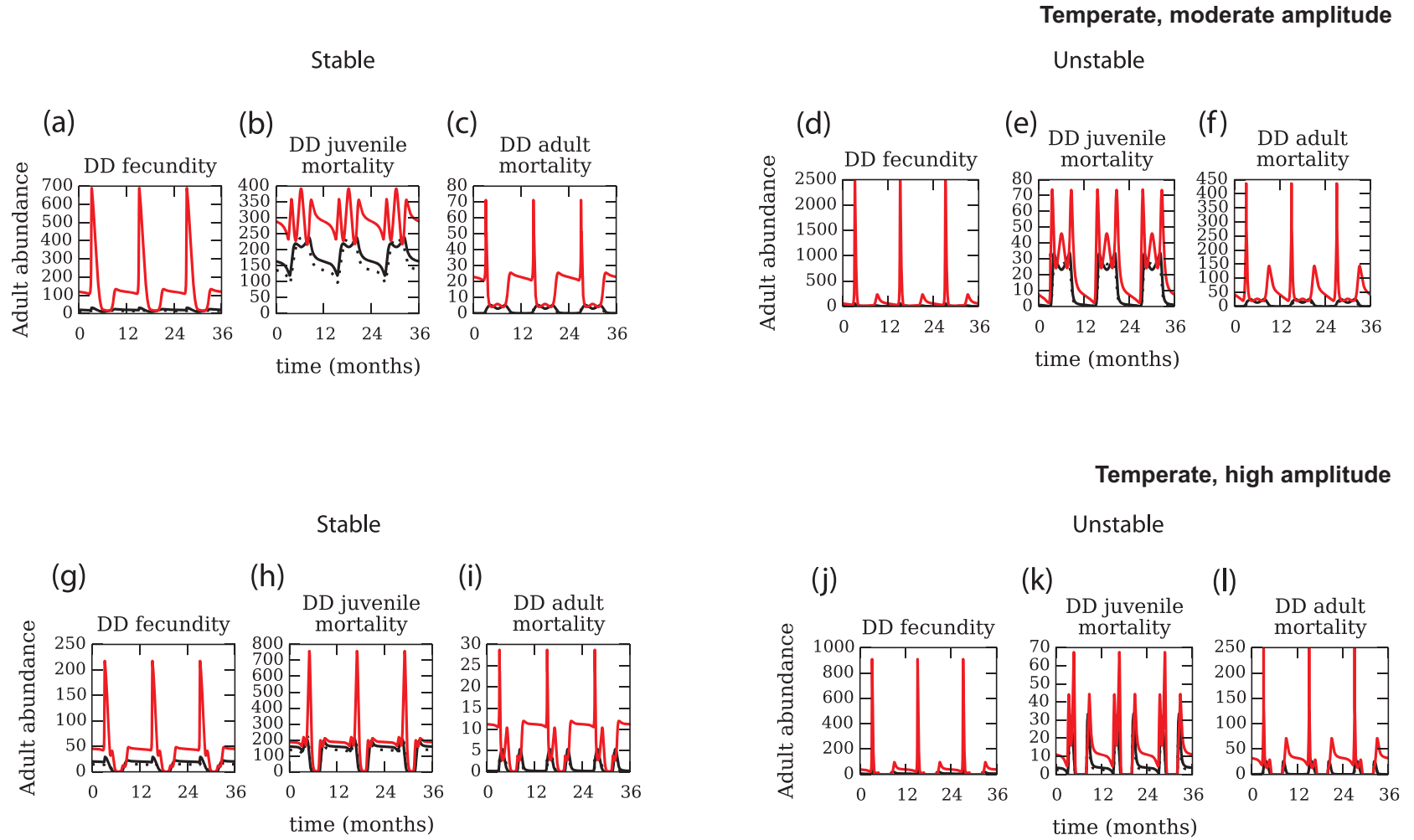
Figure C1: Long-term adult abundances for species that attain a stable point equilibrium or a stable limit cycle in the absence of seasonal temperature variation and experience a temperate climate with moderate (12.5°C) versus large (20°C) seasonal fluctuations. The dotted line depicts abundances when competition is temperature independent, and the black and red solid lines depict, respectively, abundances under monotonic and unimodal temperature responses of competition. For species experiencing a stable equilibrium in the absence of temperature variation (a–c, g–i), $b_{T_{opt}} = 1.0$, $d_{J_{T_R}} = 0.02$, and $d_{A_{T_R}} = 0.05$; for species experiencing limit cycles (d–f, j–l), $b_{T_{opt}} = 5.0$, $d_{J_{T_R}} = 0.005$, and $d_{A_{T_R}} = 0.5$. Other parameter values are as follows: $T_{opt_b} = T_{opt_q} = 291.5$ K, $s_b = s_q = 5.12$, $T_R = 292.6$ K, $m_{J_{T_R}} = 0.1$ ($\tau_{J_{T_R}} = 10$), $q_{T_R} = 0.2$, $A_m = A_q = 5,108$, $T_{L/2} = 285$ K, $A_L = -50,000$, $T_{H/2} = 300$ K, $A_H = 75,000$, $A_{d_J} = 14,518$, and $A_{d_A} = 15,004$. Mean temperature is 282.5 K for all cases. DD = density-dependent.
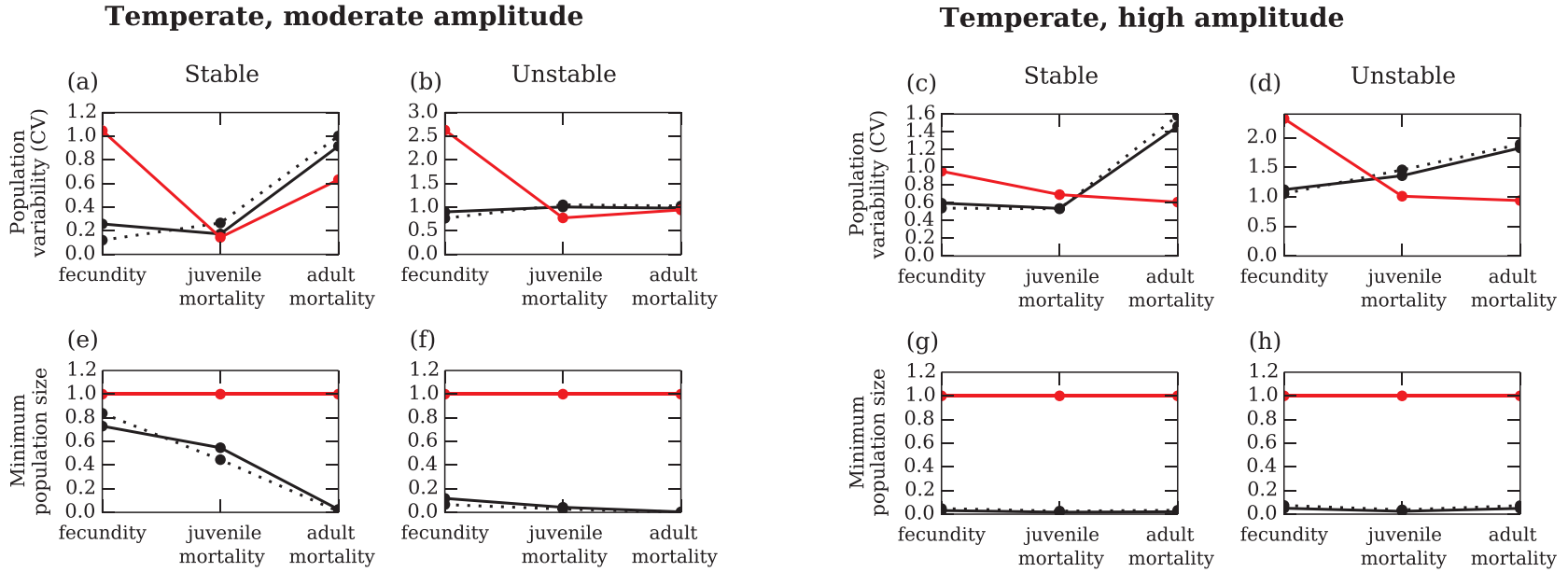
Figure C2: Population variability (*a*–*d*) and minimum population sizes (*e*–*h*) for species that attain a stable point equilibrium or stable limit cycles in the absence of seasonal temperature variation and experience a temperate climate with moderate (12.5°C) or high (20°C) seasonal fluctuations. Parameter values are as in figure C1. CV = coefficient of variation.
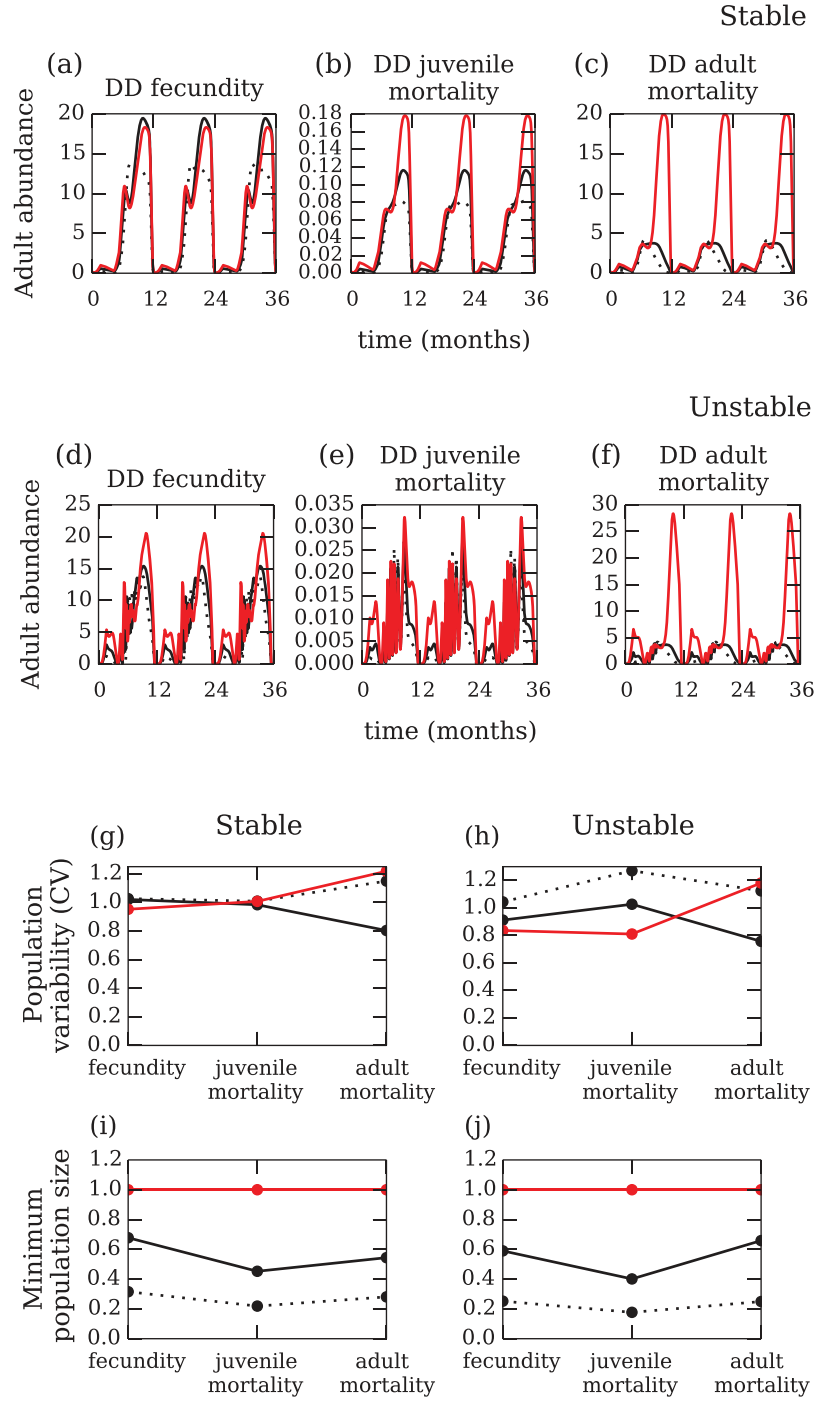
Figure C3: Effects of seasonal diapause on long-term adult abundances (*a–f*), population variability (*g, h*), and minimum population sizes (*i, j*). We incorporated diapause into the model by introducing a second juvenile stage and imposing extreme mortality at low temperatures on adult and nondiapausing juvenile stages. Because the total developmental delay is kept constant (the duration of the diapausing stage is a fraction of the original juvenile stage duration), this model is completely equivalent to the original model. Extreme winter mortality was imposed by setting the mortality rate (d_X, where $X = J, A$) to be $d_X(1 + e^{-5(T - 282)})$, which results in a steep decline in juvenile and adult abundances as temperatures reach winter levels. Parameter values are as in the Mediterranean/temperate case (figs. 1, 3). DD = density-dependent; CV = coefficient of variation.