Functional Ecology
British Ecological Society

Functional Ecology 2015 doi: 10.1111/1365-2435.12583

Effects of temperature and resource variation on insect population dynamics: the bordered plant bug as a case study

Christopher A. Johnson*,[1,2], Renato M. Coutinho[3], Erin Berlin[1], Kimberly E. Dolphin[1], Johanna Heyer[1], Britney Kim[1], Alice Leung[1], Jamie Lou Sabellon[1] and Priyanga Amarasekare[1]

[1]Department of Ecology and Evolutionary Biology, University of California Los Angeles, Los Angeles, CA 90095, USA; [2]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA; and [3]Instituto de Física Teórica, Universidade Estadual Paulista, Rua Quirino de Andrade, 215, São Paulo, 01049-010, Brazil

Summary

1. In species with complex life cycles, population dynamics result from a combination of intrinsic cycles arising from delays in the operation of negative density-dependent processes (e.g. intraspecific competition) and extrinsic fluctuations arising from seasonal variation in the abiotic environment. Abiotic variation can affect species directly through their life-history traits and indirectly by modulating the species' interactions with resources or natural enemies.

2. We investigate how the interplay between density-dependent dynamics and abiotic variability affects population dynamics of the bordered plant bug (*Largus californicus*), a Hemipteran herbivore inhabiting the California coastal sage scrub community. Field data show a striking pattern in abundance: adults are extremely abundant or nearly absent during certain periods of the year, leading us to predict that seasonal forcing plays a role in driving observed dynamics.

3. We develop a stage-structured population model with variable developmental delays, in which fecundity is affected by both intraspecific competition and temporal variation in resource availability and all life-history traits (reproduction, development, mortality) are temperature-dependent. We parameterize the model with experimental data on temperature responses of life-history and competitive traits and validate the model with independent field census data.

4. We find that intraspecific competition is strongest at temperatures optimal for reproduction, which theory predicts leads to more complex population dynamics. Our model predicts that while temperature or resource variability interacts with development-induced delays in self-limitation to generate population fluctuations, it is the interplay between all three factors that drive the observed dynamics. Considering how multiple abiotic factors interact with density-dependent processes is important both for understanding how species persist in variable environments and predicting species' responses to perturbations in their typical environment.

Key-words: competition, ectotherms, environmental variability, life-history traits, mathematical modelling, population dynamics, resource variability, temperature variation

Introduction

Elucidating the mechanisms that drive species' population dynamics is a central challenge in ecology. In organisms with complex life cycles, time delays due to juvenile development lead to delays in the operation of negative feedback processes (e.g. intraspecific competition), which can generate population cycles (Gurney, Nisbet & Lawton 1983; Nisbet & Gurney 1983; Murdoch *et al.* 1987; Murdoch & Walde 1989; Nisbet 1997; Gurney & Nisbet 1998; Murdoch, Briggs & Nisbet 2003).

It is well known that species' responses to abiotic environmental variation can interact with density-dependent feedback processes to drive population dynamics

---

*Correspondence author: E-mail: johnsonc@email.arizona.edu

(Kingsolver 1989; Urbaneja *et al.* 1999; Huey & Berrigan 2001; Crozier 2004; Savage *et al.* 2004; Frazier, Huey & Berrigan 2006; Zamani *et al.* 2006a; Amarasekare & Sifuentes 2012). Abiotic variation can have both direct and indirect effects on population dynamics. Direct effects arise from the abiotic factor's impact on species' life-history traits, such as reproduction, development and mortality (Dreyer & Baumgartner 1996; Liu & Tsai 2000; Morgan, Walters & Aegerter 2001; Urbaneja *et al.* 2001; Medeiros *et al.* 2003; Bommiredyy, Parajulee & Porter 2004; Matadha, Hamilton & Lashomb 2004; Castillo *et al.* 2006; Parajulee 2006; Ulmer *et al.* 2006; Huang, Ren & Musa 2008; Ragland & Kingsolver 2008; De Conti *et al.* 2010; Hou & Weng 2010; Jandricic *et al.* 2010; Nishikawa *et al.* 2010), and interaction traits, such as competition coefficients and attack rates (Zamani *et al.* 2006b; Dannon *et al.* 2010; Englund *et al.* 2011; Lang *et al.* 2011; Amarasekare & Coutinho 2014). Temperature is perhaps the most important abiotic factor that exerts such direct effects. Indirect effects arise from the impacts of an abiotic factor on other species (resources, natural enemies, competitors, mutualists) with which a focal species interacts. For example, rainfall and/or temperature may drive the phenology of a plant species on which an herbivore feeds, and temporal variation in resource availability arising from the plant's phenological response can, in turn, affect the herbivore's population dynamics. Understanding how direct and indirect effects of abiotic variation influence density-dependent population dynamics is crucial in predicting how species may respond to atypical environmental variability such as climate change (Bale *et al.* 2002; Walther *et al.* 2002; Root *et al.* 2003; Parmesan 2006; Deutsch *et al.* 2008; Tewksbury, Huey & Deutsch 2008; Kingsolver 2009; Kingsolver *et al.* 2011; McMahon *et al.* 2011; Sheldon, Yang & Tewksbury 2013).

Here, we use the bordered plant bug (*Largus californicus*; Fig. 1), a Hemipteran herbivore inhabiting the California coastal sage scrub, as a model system to investigate this issue. Motivated by a distinctive pattern observed in the bug's population dynamics, we develop a mathematical model to generate predictions for two hypotheses about the underlying mechanisms. While the model is motivated by the biology of the bordered plant bug, the theory is more general and can be applied to any ectotherm whose dynamics are influenced by direct and indirect abiotic effects.

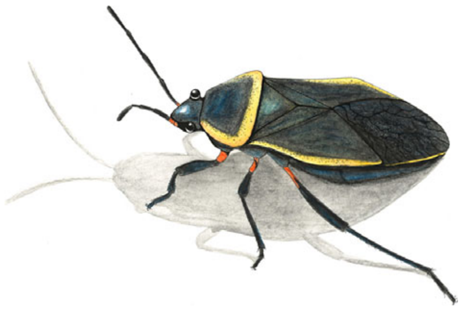

Fig. 1. Illustration of an adult bordered plant bug (*Largus californicus*).

Materials and methods

STUDY SYSTEM

We studied the bordered plant bug at the Main Campus Reserve of the University of California, Santa Barbara. This is essentially a closed population as the reserve is a small (150 m by 250 m) region of coastal bluffs bounded by the Pacific Ocean and a lagoon. The population was studied in 1986 by Booth (1990) and 25 years later by us (see Appendix S1 in Supporting Information).

The bordered plant bug is a generalist herbivore (Booth 1990) whose main food source at this site is bush lupine (*Lupinus arboreus*). Abundance patterns in the field exhibit a distinctive pattern that cannot be explained by density-dependent dynamics alone: adults are extremely abundant in summer and fall, but are almost completely absent in late spring and late summer (Fig. 2). This suggests that bug dynamics may be subject to seasonal environmental forcing.

Bordered plant bugs are attacked by three parasitoid species: an egg parasitoid (*Gryon largi*) and a tachinid fly (*Trichopoda pennipes*) (Booth 1990) as well as an unidentified parasitoid wasp. Here, we do not include the effects of natural enemies on plant bug dynamics. We discuss how incorporating parasitoids in this framework offers promising future directions in the Discussion.

CONCEPTUAL FRAMEWORK

Based on the population dynamics observed in the field, we can make two hypotheses about the mechanisms underlying the observed abundance patterns. First, if abundance patterns result from developmental time lags that cause delays in the operation of negative feedback, one would expect to see population cycles if adult longevity is short relative to the juvenile developmental period (Murdoch, Briggs & Nisbet 2003). Otherwise, one would expect stable (non-oscillatory) dynamics. Secondly, if abundance patterns result from the interplay between developmental delay-driven cycles and direct and/or indirect effects of abiotic variation, we expect more complex dynamics due to the effects of seasonal forcing on density-dependent population dynamics.

To test which hypothesis better explains the observed census data, we develop a mathematical framework that can accommodate both time delays in the operation of density dependence and seasonal forcing of key parameters. To do this, we first quantify the temperature responses of life-history and competitive traits via laboratory experiments (see Appendix S2). We then incorporate these responses within a variable delay model. Finally, we explain how seasonal variation in temperature and resource availability is quantified in the field and incorporated within the model.

EFFECTS OF TEMPERATURE ON LIFE-HISTORY TRAITS

The per capita birth rate of most ectotherms exhibits a symmetric and unimodal response to temperature that is well-described by a Gaussian function:

$$b(T) = b_{T_{\text{opt}}} e^{-\frac{(T-T_{\text{opt}})^2}{2\sigma_b^2}} \qquad \text{eqn 1}$$

where $b(T)$ is the per capita birth rate at temperature T (in degrees Kelvin), $b_{T_{\text{opt}}}$ is the maximum birth rate, attained at an optimal temperature T_{opt}, and σ_b is the variability about the optimum. Plant bug reproduction exhibits a unimodal temperature response

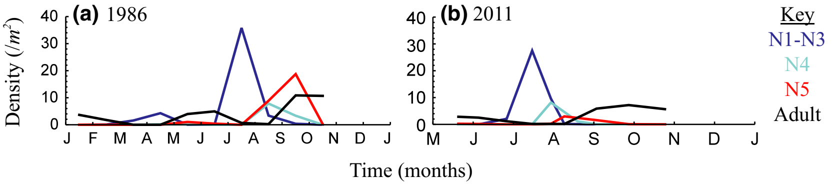

Fig. 2. Time-series plots show the density of bordered plant bug life stages at the Main Campus Reserve at the University of California, Santa Barbara. Panel (a) is census data collected in 1986 by Booth (1990), and panel (b) is data that we collected in 2011. There are no census data of egg density in the field. As it is impossible to distinguish between pre-reproductive and reproductive adults in the field, the two life stages are combined into a single adult class.

with data providing a significant fit to eqn 1 (Table S1). Reproduction is therefore greatest at intermediate temperatures and declines at higher and lower temperatures (Fig. 3a). The optimum temperature for reproduction is 23·9 ± 0·3 °C, which is near the maximum temperature in the field (1986: 24·5 °C, 2011: 25·7 °C).

In ectotherms, development and mortality exhibit monotonic temperature responses (Gillooly *et al.* 2001; Brown *et al.* 2004; Savage *et al.* 2004) given by the Boltzmann–Arrhenius function:

$$k_i(T) = k_{i,T} e^{A_{i,k}\left(\frac{1}{T_{i,k}}-\frac{1}{T}\right)} \qquad \text{eqn 2}$$

where $k_i(T)$ is the trait value (i.e. $k = m$ for maturation rate and $k = d$ for mortality) for stage i at temperature T, $k_{i,T}$ is the trait value k at a reference temperature $T_{i,k}$ for stage i, and $A_{i,k}$ is the Arrhenius constant of trait k for stage i, measuring its temperature sensitivity (how fast it changes with varying temperature). We find that development rate and mortality increase monotonically with temperature in a manner described by the Boltzmann–Arrhenius function (eqn 2; Table S1).

EFFECTS OF TEMPERATURE ON COMPETITIVE TRAITS

To our knowledge, there are no empirical data on the temperature response of competitive traits; however, theory offers two hypotheses for how temperature affects the strength of competition. First, metabolic scaling theory predicts that the strength of competition increases monotonically with temperature within biologically realistic temperature ranges (Savage *et al.* 2004). Secondly, ecological theory predicts that competitive traits exhibit a unimodal response to temperature such that competition is strongest near the optimal temperature for reproduction (Begon, Harper & Townsend 2005).

We find that the strength of competition is a unimodal function of temperature with data providing a significant fit to the following Gaussian function (Table S1):

$$\alpha(T) = \alpha_{T_{\max}} e^{-\frac{(T-T_\alpha)^2}{2\sigma_\alpha^2}} \qquad \text{eqn 3}$$

where $\alpha(T)$ is the competitive effect at temperature T, $\alpha_{T_{\max}}$ is the maximum competitive effect, occurring at temperature T_{max}, and σ_α is the variability about the maximum. This suggests that in plant bugs, competition is strongest at intermediate temperatures (23·1 ± 0·3 °C) near the optimum for reproduction (23·9 ± 0·3 °C) and declines at both higher and lower temperatures (Fig. 4). This is an important finding because theory predicts that when competition is strongest near the optimal temperature for reproduction, the effects of temperature and competition interact antagonistically, driving more complex dynamics (Amarasekare & Coutinho 2014).

Now that the temperature responses of life-history and competitive traits have been quantified, the next step is to incorporate these responses into a mathematical framework to generate predictions about population-level outcomes.

MATHEMATICAL FRAMEWORK

We develop a stage-structured delay-differential equation (DDE) model to investigate bordered plant bug population dynamics.

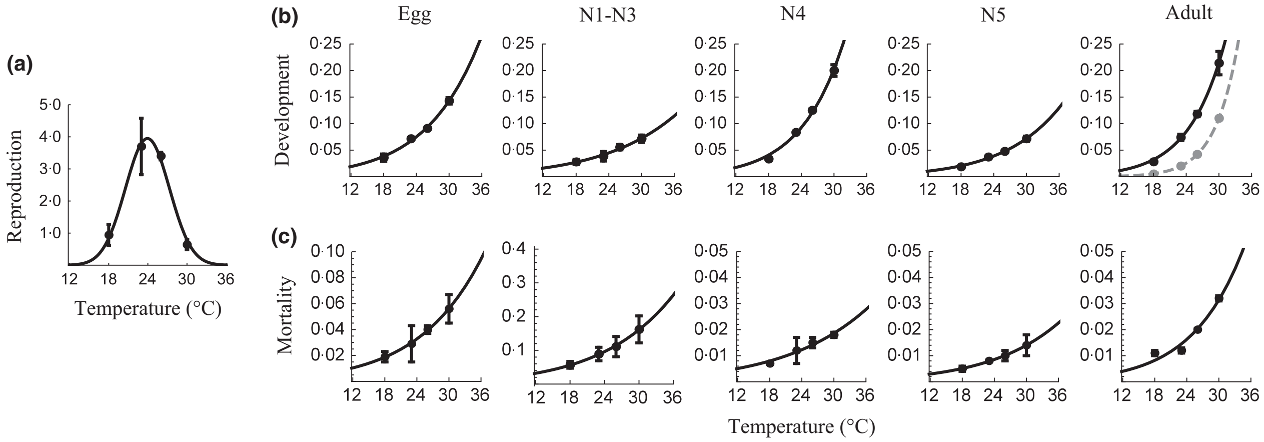

Fig. 3. Temperature responses of life-history traits. Reproduction (panel a) is described by a Gaussian function (eqn 1), while development rate (panels b) and mortality (panels c) are described by the Boltzmann–Arrhenius function (eqn 2). See Tables S1 for parameter estimates.

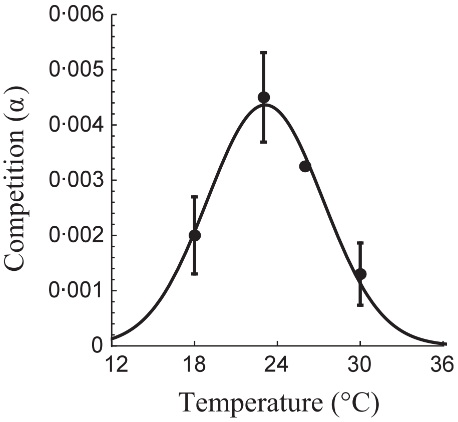

Fig. 4. Temperature response of competitive traits. Intraspecific competition (quantified by the decline in fecundity with adult density; see Fig. S1) exhibits a unimodal response to temperature, which is well-described by a Gaussian function (eqn 3). See Table S1 for parameter estimates.

DDE models provide a natural way to describe the dynamics of species with stage-structured life cycles (Gurney, Nisbet & Lawton 1983; Nisbet & Gurney 1983; Murdoch *et al.* 1987; Murdoch & Walde 1989; Nisbet 1997; Gurney & Nisbet 1998; Murdoch, Briggs & Nisbet 2003). The model is mechanistic because all parameters are explicitly temperature-dependent and temperature-driven variability in developmental delays is explicitly modelled. Although motivated by the biology of the bordered plant bug, the model can be easily modified to investigate the dynamics of other ectotherms that inhabit variable environments.

POPULATION DYNAMICS

The bug's life cycle consists of six life stages: eggs (E), early nymphal instars ($N_1 - N_3$; denoted N_E in the model), 4th and 5th nymphal instars (N_4 and N_5), pre-reproductive adults (P) and reproductive adults (R). Population dynamics are given by the following system of DDEs:

$$\frac{\mathrm{d}E(t)}{\mathrm{d}t} = b\big(T(t)\big)Q(t)R(t)e^{-\alpha(T(t))R(t)} - g_E(t) - \mathrm{d}_E\big(T(t)\big)E(t) \qquad \text{eqn 4}$$

$$\frac{\mathrm{d}N_E(t)}{\mathrm{d}t} = g_E(t) - g_{N_E}(t) - \mathrm{d}_{N_E}\big(T(t)\big)N_E(t)$$

$$\frac{\mathrm{d}N_4(t)}{\mathrm{d}t} = g_{N_E}(t) - g_{N_4}(t) - d_{N_4}\big(T(t)\big)N_4(t)$$

$$\frac{\mathrm{d}N_5(t)}{\mathrm{d}t} = g_{N_4}(t) - g_{N_5}(t) - \mathrm{d}_{N_5}\big(T(t)\big)N_5(t)$$

$$\frac{\mathrm{d}P(t)}{\mathrm{d}t} = g_{N_5}(t) - g_P(t) - \mathrm{d}_P\big(T(t)\big)P(t)$$

$$\frac{\mathrm{d}R(t)}{\mathrm{d}t} = g_P(t) - g_R(t) - d_R\big(T(t)\big)R(t)$$

where $b(T(t))$ is the temperature response of the birth rate and $Q(t)$ depicts the time-varying effect of resource variability on the birth rate (i.e. $Q(t) = 1$ if resource availability remains constant over time, and $Q(t) \neq 1$ if resource availability varies seasonally). The function $\alpha(T(t))$ is the temperature response of intraspecific competition; $g_i(t)$ depicts maturation through-stage i (g_R describes adult senescence); and $d_i(T(t))$ depicts the temperature response of mortality of stage i.

There are three key points to note about this model. First, resource variability ($Q(t)$) affects reproduction rather than development or mortality because laboratory experiments show that reproduction is the only trait exhibiting density dependence (Fig. S1; Table S2). Because it is difficult to experimentally quantify how resource variability affects reproduction, we assume that laboratory estimates of reproduction reflect the maximum values possible.

The second point we want to emphasize concerns development ($g_i(t)$). Because development is temperature-dependent, stage duration is not constant, and thus, developmental delays vary over time. We use the following maturation functions based on previous theory on dynamically varying time delays (Gurney, Nisbet & Lawton 1983; Nisbet & Gurney 1983):

$$g_E(t) = b\big(T(t')\big)Q(t')R(t')e^{-\alpha T(t')R(t')}\frac{m_E\big(T(t)\big)}{m_E\big(T(t')\big)}s_E(t) \qquad \text{eqn 5}$$

$$g_i(t) = g_i\big(t - \tau_i(t)\big)\frac{m_i\big(T(t)\big)}{m_i\Big(T\big(t - \tau_i(t)\big)\Big)}s_i(t)$$

where

$$t' = t - \tau_E(t) \qquad \text{eqn 6}$$

$$\frac{\mathrm{d}s_i(t)}{\mathrm{d}t} = s_i(t)\left(\frac{m_i\big(T(t)\big)}{m_i\Big(T\big(t - \tau_i(t)\big)\Big)}\mathrm{d}_i\Big(T\big(t - \tau_i(t)\big)\Big) - d_i(T(t))\right)$$

$$\frac{\mathrm{d}\tau_i(t)}{\mathrm{d}t} = 1 - \frac{m_i\big(T(t)\big)}{m_i\Big(T\big(t - \tau_i(t)\big)\Big)}$$

Note that t' denotes the time at which eggs hatching at time t were laid (where τ_E is the time delay involved in egg development), $s_i(t)$ describes through-stage survivorship of stage i, and $\tau_i(t)$ is the developmental time delay of stage i. Maturation of eggs to 1st nymphal instars ($g_E(t)$) is a function of the rate at which eggs were laid a time $\tau_E(t)$ ago and survivorship through the egg stage ($s_E(t)$). Similarly, maturation of successive stages ($g_i(t)$) is functions of the rate at which individuals mature from the previous life stage and through-stage survivorship. The ratio $m_i(T(t))/m_i(T(t - \tau_i(t)))$ determines how temperature affects maturation. If temperature increases over the duration of stage i, this ratio is greater than one, stage duration is shorter, and more individuals survive. If temperature decreases over the stage duration, this ratio is less than one, stage duration is longer, and fewer individuals survive. Note that survivorship ($s_i(t)$) and developmental time delays ($\tau_i(t)$) are time-varying differential equations (see Nisbet & Gurney (1983) for derivation). Appendix S3 provides more information about the DDE model developed here, and Appendix S4 and Fig. S2 discuss the results of a simplified ODE version of the model.

The third point is about environmental variability. Note that the model incorporates both direct effects of seasonal temperature variation ($T(t)$) on life-history traits and intraspecific competition, and indirect effects arising from resource variability ($Q(T)$) that affect the birth rate. Below, we explain how environmental variability is quantified in the field and incorporated into the model.

ENVIRONMENTAL VARIABILITY

We quantify seasonal temperature variation ($T(t)$) via the following sinusoidal function:

$$T(t) = m_T - a_T \cos(2\pi t/365 - \delta_T) \qquad \text{eqn 7}$$

where m_T is the mean temperature, a_T is the amplitude of seasonal temperature variation, and δ_T gives the shift in the function. We fitted this function to data from the Western Regional Climate Center (wrcc.dri.edu) from 1986 to 1987 and from 2011 to 2012, which coincide with census data (Fig. 5).

Because plant bugs mainly consume bush lupine (Booth 1990), the availability of the preferred food resource varies seasonally based on bush lupine phenology. Food availability dramatically increases at the end of January following the winter rains (Harrison, Karban & Url 1986) and remains high until the end of the flowering season in July (Kittelson & Maron 2000) when bush lupine wilts and drops its seed pods (Strong *et al.* 1995). We measured resource availability in the field as the average per cent leaf-cover of 25 marked bush lupine shrubs. Thus, leaf-cover varies from 0 to 1.

We quantify temporal variation in food availability ($Q(t)$) by fitting the following sinusoidal function to the leaf-cover data obtained in the field:

$$Q(t) = \cos(2\pi t/365 - \delta_R) \qquad \text{eqn 8}$$

where δ_R is the shift in the cosine function. Note that when eqn 8 is negative, we set $Q(t) = 0$. We find that $Q(t)$ captures the resource availability observed in the field (Fig. 5c; Table S3).

Results

HYPOTHESIS 1: ABUNDANCE PATTERNS RESULT FROM DENSITY-DEPENDENT DYNAMICS

To predict plant bug dynamics in the absence of temperature and resource variability, we analysed the stage-structured model (eqn 4) in a constant environment ($T(t) = m_T$ and $Q(t) = 1$). The model predicts a stable steady state (Fig. 6a,b), which is approached via damped oscillations. This is markedly different from the pattern of population dynamics observed in the field (Fig. 6i,j). Note that the predicted abundances are much higher than those observed in the field because adults reproduce year-round in the model, while adults reproduce only seasonally in nature.

HYPOTHESIS 2: ABUNDANCE PATTERNS RESULT FROM THE INTERPLAY BETWEEN DENSITY-DEPENDENT DYNAMICS AND ENVIRONMENTAL VARIABILITY

Seasonal temperature variation

A model with seasonal temperature forcing (eqn 7) but no variation in resource availability ($Q(t) = 1$) causes fluctuations in abundance within a year. Adult density is greatest during spring and early summer (Fig. 6c,d) when temperatures approach the optimal for reproduction. Because adult senescence is very sensitive to increasing temperature (high Arrhenius constant; Table S1), adult life span is relatively short and thus adult density declines in late summer. The density of early nymphal stages is greatest in fall following peak reproduction in late summer and is lowest in early summer when adult density declines and nymphal mortality is relatively high due to high temperatures. As a result, successive nymphal stages peak in density during winter in the model.

Comparison of the predicted time series with field census data reveals two mismatches. First, the model predicts that nymphs are present in winter, when in the field nymphs are completely absent in winter. Secondly, the predicted abundances of all life stages are much greater than are observed in the field. These mismatches are likely due to the model assumption that resources remain plentiful year-round, allowing adults to reproduce, and nymphs to survive, throughout the year. Thus, seasonal temperature variation alone does not explain the observed dynamics.

Seasonal resource variation

A model with seasonal variation in resource availability (eqn 8) but no seasonal temperature variation ($T(t) = m_T$) captures the gross patterns observed in the field, but greatly underestimates bug abundances (Fig. 6e,f). In the model, overwintering adults reproduce in March when resource availability increases. This initial juvenile cohort develops during the spring and adults reproduce during the summer. Reproduction ceases in August as resource availability declines. The second juvenile cohort develops during the summer/fall and matures into adults by November.

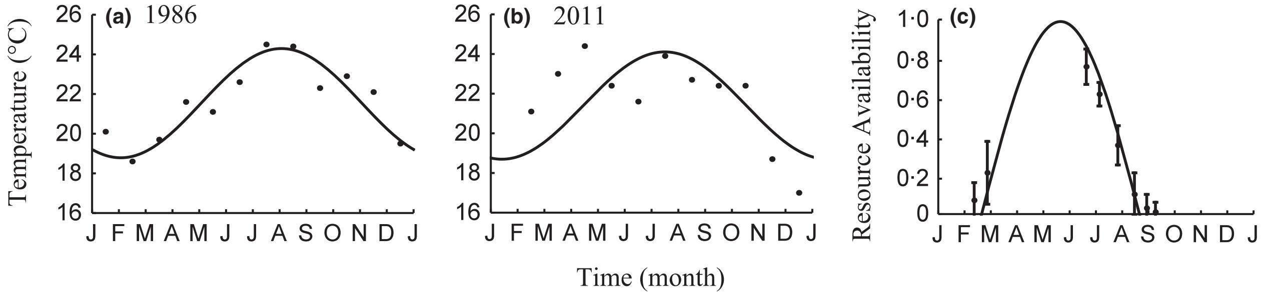

Fig. 5. Seasonal variation in temperature and resource availability is quantified by fitting functions to data on monthly temperatures in 1986 (panel a) and 2011 (panel b) and to field data on resource availability (panel c). See Table S3 for parameter estimates.

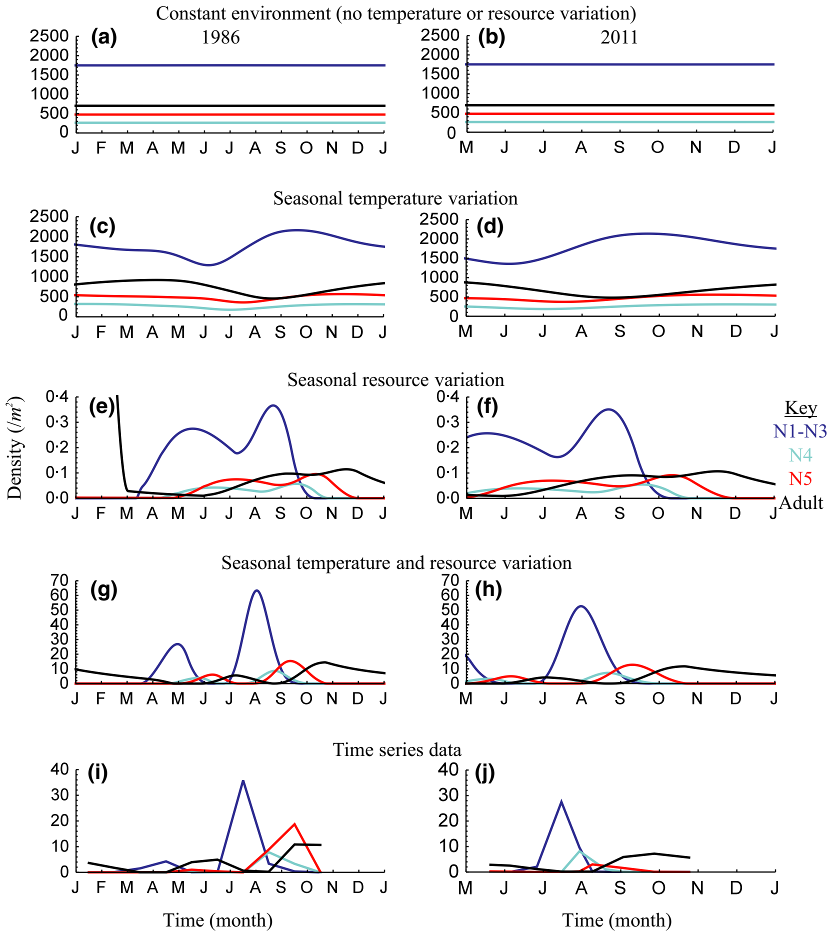

Fig. 6. Plant bug population dynamics predicted by stage-structured DDE models (eqn 4). Left panels show model predictions for the 1986 census period and right panels show model predictions for the 2011 census period: panels (a,b): constant environment (no temperature or resource variation), panels (c,d): seasonal temperature variation, panels (e,f): seasonal resource variation, panels (g,h): seasonal temperature *and* resource variation, panels (h,i): census data.

While this version of the model captures the overall trend in plant bug dynamics, it greatly underestimates abundances, as a result of which the population goes extinct within a few years. Extinction likely occurs because mean annual temperatures are suboptimal for reproduction (recall that reproduction is optimal near the maximum, not mean, field temperatures). This perhaps signifies an important role for seasonal temperature variation. The crucial significance of this model version is the prediction that seasonal variation in resource availability determines the period of the year during which reproduction occurs and hence when nymphal stages are present. Resource variation alone, however, is insufficient to explain the observed time-series data.

Seasonal variation in temperature and resource availability

The full model with seasonal variation in temperature (eqn 7) and resource availability (eqn 8) captures both the qualitative pattern of population dynamics and the magnitude of bug abundances observed in the field (Fig. 6g,h). Adults cannot reproduce during the fall or winter due to insufficient resource availability; thus, nymphs are absent in the winter. Overwintering adults have a relatively long life span due to reduced mortality as a result of low temperatures. Thus, adults survive long enough to reproduce when resource availability increases in February before senescing by April. The initial juvenile cohort develops fairly slowly in the spring when development rates are low due to low temperatures and matures into adults by July. Reproduction ceases in August as resource availability declines and adults senesce by September as a result of increased mortality due to elevated summer temperatures. The second juvenile cohort develops relatively quickly in late summer when development rates are faster due to higher temperatures and matures into adults by October. Bug abundances are greater in the second cohort because reproduction is greatest in the summer as temperatures approach the optimum for reproduction. Model dynamics lag slightly behind field census data, perhaps due to uncertainty around the fit of seasonal resource variability (eqn 8) to the start of the growing season (Fig. 4c). This lag is slightly greater in 2011 than in 1986, likely due greater uncertainty around the fit of season temperature variation (eqn 7) to temperature data in 2011 (Fig. 4b).

The full model yields two key findings. First, density is driven by both resource availability (via its effects on reproduction) and temperature (via its effects on reproduction, development and mortality). Secondly, density-dependent population dynamics are influenced by both resource availability (which determines when reproduction occurs) and temperature (which determines stage duration). These findings suggest that plant bug population dynamics result from the interplay between development-driven time delays in the operation of density dependence and life-history traits' responses to seasonal variation in both temperature and resource availability.

Discussion

In species with complex life cycles, juvenile development leads to time delays in the operation of negative feedback processes (e.g. intraspecific competition), leading to population cycles (Murdoch, Briggs & Nisbet 2003). Environmental variability can interact with such delays, leading to patterns of population dynamics that deviate from those expected under density-dependent processes alone. Understanding how environmental variability interacts with density-dependent processes is important for predicting population dynamics not only under typical environmental regimes, but also under perturbations, natural or anthropogenic, to the typical environment. Here, we investigate this issue using the bordered plant bug (*Largus californicus*) as a model system.

We report two key results. The first result pertains to the joint effects of temperature and intraspecific competition on fecundity. We find that competition is strongest at temperatures optimal for reproduction and declines at higher and lower temperatures. This is an important finding because theory predicts that, in such a case, the effects of temperature and competition interact antagonistically, resulting in more complex dynamics than when the strength of competition increases monotonically with temperature (Amarasekare & Coutinho 2014).

Our second result illustrates the complex interplay between environmental variability and delays in density-dependent feedback in driving population dynamics. While either temperature or resource availability can interact with density-dependent processes to induce population fluctuations, it is the interplay between density dependence and seasonal variation in temperature *and* resource availability that generates the distinctive abundance patterns observed in the field. Specifically, density-dependent dynamics are modified by seasonal variation in resource availability (which determines the timing and magnitude of reproduction) and temperature (which affects life-history traits both directly and indirectly via its effects on competition).

At a more conceptual level, we develop a theoretical framework for simultaneously considering the direct and indirect effects of abiotic variation on ectotherm population dynamics. There is growing emphasis on the importance of indirect effects of environmental variation on species' phenology and population dynamics (Araújo & Luoto 2007). Quantifying and modelling these indirect effects, however, can be challenging. This framework provides a natural way to incorporate both direct and indirect effects of abiotic variation. The direct effects of abiotic variation (here, in temperature) are quantified via the responses of life-history and competitive traits. In the case of the bordered plant bug, indirect effects of abiotic factors such as temperature and rainfall are likely manifested via the effects of resource phenology on fecundity (which is the only trait that exhibits density dependence; Fig. S1). Thus, incorporating temperature-dependent parameters and the effects of resource availability on fecundity allows the simultaneous consideration of direct and indirect effects of abiotic factors on plant bug dynamics.

It is important to discuss our results in the light of previous studies investigating the joint effects of temperature and resource variation on population dynamics. We discuss three studies. Ritchie (1996) studied the effects of temperature and resource limitation on the grasshopper *Melanoplus sanguinipes*. He used a non-delay model in which a fixed supply of resources is allocated to maintenance or growth at temperature-dependent rates. The model predicts greater mortality and lower density under elevated temperatures. Our model also predicts that mortality increases with increasing temperatures; however, temperature effects on population density are more complex as the underlying life-history and competitive traits are also temperature-dependent.

Reigada and Godoy (2006) studied the effects of larval density on the dynamics of the fly *Chrysomya megacephala* at two temperatures in a laboratory environment and found that fecundity declines with increasing density and temperature, which may lead to a transition from a two-point limit cycle to a stable equilibrium. While plant bug fecundity also declines with increasing density, fecundity exhibits a unimodal temperature response. While we consider temperature variation, not increasing temperature, it predicts more complex dynamics when temperature is considered.

Finally, Laws and Belovsky (2010) studied the effects of density and temperature on the dynamics of the grasshopper *Camnula pellucida* in the field. They found that peak survival in low-density treatments occurs at higher temperatures than for high-density treatments, indicating that the strength of intraspecific competition varies with temperature; however, the temperature response of competition was not quantified. Our model explicitly incorporates the temperature response of intraspecific competition, which likely leads to more complex population dynamics.

In summary, previous studies often incorporate only a few (2–3) temperatures, do not quantify the temperature responses of both life-history and competitive traits and fail to explicitly consider temperature effects on the developmental delays that characterize ectotherm life cycles. Our framework differs from these previous studies in that it incorporates measurable temperature response functions for all parameters, explicitly considers variability in developmental delays due to temperature variation, and is well-linked with independent field census data.

The work presented here suggests several future directions. First, our study underscores the importance of considering the role of abiotic factors on bottom-up processes such as resource availability. It does not, however, consider the effects of abiotic factors on top-down processes such as natural enemies, which are likely important to gain a full understanding of how abiotic factors affect species' population dynamics. Indeed, natural enemies can interact with intrinsic delays in density dependence to drive more complex dynamics (Murdoch *et al.* 1987; Murdoch & Walde 1989; Nisbet 1997; Gurney & Nisbet 1998; Murdoch, Briggs & Nisbet 2003). A key question for future research is how direct and indirect effects of abiotic variation influence consumer-resource dynamics. This framework provides a theoretical foundation for investigating these issues because it incorporates mechanistic descriptions of trait responses to abiotic variation.

The bordered plant bug offers an intriguing case study for investigating the effects of abiotic variation on bottom-up and top-down processes as we have documented variation in resource availability due to bush lupine phenology (bottom-up effects) and plant bugs are attacked by multiple ectothermic natural enemies (top-down effects). Our model suggests that, in this system at least, bottom-up processes are important in driving the observed abundance pattern. Intriguingly, while the full model captures the overall patterns observed in nature, it tends to overestimate bug density, perhaps signifying a key role for natural enemies in suppressing bug density. Future work should therefore incorporate natural enemies within the mathematical framework described here.

The second future direction involves predicting how ectotherms respond to perturbations in their typical thermal environment, such as climate warming (Bale *et al.* 2002; Walther *et al.* 2002; Root *et al.* 2003; Parmesan 2006; Deutsch *et al.* 2008; Tewksbury, Huey & Deutsch 2008; Kingsolver 2009; Kingsolver *et al.* 2011; Sheldon, Yang & Tewksbury 2013). The framework we have developed here is particularly amenable to investigating the effects of climate change on ectotherm population dynamics because the temperature responses of life-history traits can be empirically quantified and climate change scenarios can be easily incorporated into the model.

In conclusion, this study serves as a first step towards a mechanistic understanding of how the interplay between density-dependent processes and abiotic variation affects ectotherm population dynamics. It also provides a case study of a variable delay model with mechanistic descriptions of trait responses to temperature. The model is readily amenable to incorporating empirically derived temperature response functions and yields predictions about abundance patterns that can be tested with census data. We have shown that this framework, parameterized with empirical data on life-history traits, can capture very complex dynamics observed in the field. This is a key development as mechanisms underlying patterns of population dynamics cannot be elucidated from time-series analysis alone (Knape & de Valpine 2010). Thus, our framework offers the conceptual foundation and mathematical tools to investigate ectotherm population dynamics under climate warming.

Acknowledgements

We thank S. Hubbell, J. Lloyd-Smith, V. Savage, S. Bewick, and an anonymous reviewer for helpful comments that substantially improved the manuscript. A special thanks to Julie Himes for the beautiful illustration of a bordered plant bug. The authors have no conflicts to declare. Support was provided by Science Foundation Arizona Grant BSP 0528-13 to C.A.J. and NSF grant DEB-0717350 and a Complex Systems Scholar Grant from the James S. McDonnell Foundation to P.A.

Data accessibility

The python script for the DDE models (Variable DDE.py) and all data used to parameterize and validate models in this manuscript (Plant Bug Data.xlxs) are uploaded as supporting information.

References

Amarasekare, P. & Coutinho, R. (2014) Effects of temperature on intraspecific competition in ectotherms. *The American Naturalist*, **184**, E50–E65.

Amarasekare, P. & Sifuentes, R. (2012) Elucidating the temperature response of survivorship in insects. *Functional Ecology*, **26**, 959–968.

Araújo, M.B. & Luoto, M. (2007) The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*, **16**, 743–753.

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K. *et al.* (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology*, **8**, 1–16.

Begon, M., Harper, J. & Townsend, C. (2005) *Individuals, Populations and Communities*. Blackwell Science, Oxford, UK.

Bommiredyy, P.L., Parajulee, M.N. & Porter, D.O. (2004) Influence of constant temperatures on life history of immature *Lygus elisus* (Hemiptera: Miridae). *Environmental Entomology*, **33**, 1549–1553.

Booth, C.L. (1990) Biology of *Largus californicus* (Hemiptera: Largidae). *Southwestern Association of Naturalists*, **35**, 15–22.

Brown, J., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.

Castillo, J., Jacas, J.A., Peña, J.E., Ulmer, B.J. & Hall, D.G. (2006) Effect of temperature on life history of *Quadrastichus haitiensis* (Hymenoptera: Eulophidae), an endoparasitoid of *Diaprepes abbreviatus* (Coleoptera: Curculionidae). *Biological Control*, **36**, 189–196.

Crozier, L. (2004) Warmer winters drive butterfly range expansion by increasing survivorship. *Ecology*, **85**, 231–241.

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

De Conti, B., Bueno, V.H.P., Sampaio, M.V. & Sidney, L.A. (2010) Reproduction and fertility life table of three aphid species (*Macrosiphini*) at different temperatures. *Revista Brasileira de Entomologia*, **54**, 654–660.

Deutsch, C.J., Tewksbury, J., Huey, R.B., Sheldon, K., Ghalambor, C., Haak, D. *et al.* (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 6668–6672.

Dreyer, H. & Baumgartner, J. (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.

Englund, G., Öhlund, G., Hein, C. & Diehl, S. (2011) Temperature dependence of the functional response. *Ecology Letters*, **14**, 914–921.

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

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

Gurney, W. & Nisbet, R. (1998) *Ecological Dynamics*. Oxford University Press, Oxford, UK.

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

Harrison, S., Karban, R. & Url, S. (1986) Folivorous moth on the success of a later-season species, mediated by a change in the quality of the shared host, *Lupinus arboreus sims*. *Oecologia*, **69**, 354–359.

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

Huang, Z., Ren, S. & Musa, P.D. (2008) Effects of temperature on development, survival, longevity, and fecundity of the *Bemisia tabaci gennadius* (Homoptera: Aleyrodidae) predator, *Axinoscymnus cardilobus* (Coleoptera: Coccinellidae). *Biological Control*, **46**, 209–215.

Huey, R. & Berrigan, D. (2001) Temperature, demography, and ectotherm fitness. *American Naturalist*, **158**, 204–210.

Jandricic, S.E., Wraight, S.P., Bennett, K.C. & Sanderson, J.P. (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.

Kingsolver, J. (1989) Weather and the population dynamics of insects: integrating physiological and population ecology. *Physiological Zoology*, **62**, 314–334.

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

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

Kittelson, P.M. & Maron, J.L. (2000) Outcrossing rate and inbreeding depression in the perennial yellow bush lupine, *Lupinus arboreus* (Fabaceae). *American Journal of Botany*, **87**, 652–660.

Knape, J. & de Valpine, P. (2010) Effects of weather and climate on the dynamics of animal population time series. *Proceedings of the Royal Society B*, **278**, 985–992.

Lang, B., Rall, B., Brose, Y. & Rall, B. (2011) Warming effects on consumption and intraspecific interference competition depend on predator metabolism. *Journal of Animal Ecology*, **81**, 516–523.

Laws, A.N. & Belovsky, G.E. (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.

Liu, Y.H. & Tsai, J.H. (2000) Effects of temperature on biology and life table parameters of the Asian citrus psyllid, *Diaphorina citri kuwayama* (Homoptera: Psyllidae). *Annals of Applied Biology*, **137**, 201–206.

Matadha, D., Hamilton, G.C. & Lashomb, J.H. (2004) Effect of temperature on development, fecundity, and life table parameters of *Encarsia citrina* Craw (Hymenoptera: Aphelinidae), a parasitoid of euonymous scale, *Unaspis euonymi* (Comstock), and *Quadraspidiotus perniciosus* (Comstock) (Homoptera: Diaspididae). *Environmental Entomology*, **33**, 1185–1191.

McMahon, S.M., Harrison, S.P., Armbruster, W.S., Bartlein, P.J., Beale, C.M., Edwards, M.E. *et al.* (2011) Improving assessment and modelling of climate change impacts on global terrestrial biodiversity. *Trends in Ecology & Evolution*, **26**, 249–259.

Medeiros, R.S., Ramalho, F.S., Zanuncio, J.C. & Serrao, J.E. (2003) Effect of temperature on life table parameters of *Podisus nigrispinus* (Heteroptera, Pentatomidae) fed with *Alabama argillacea* (Lepidoptera, Noctuidae) larvae. *Journal of Applied Entomology*, **127**, 209–213.

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

Murdoch, W., Briggs, C.J. & Nisbet, R. (2003) *Consumer-Resource Dynamics*. Princeton University Press, Princeton, NJ.

Murdoch, A.W.W. & Walde, S.J. (1989) Analysis of insect population dynamics. *Towards a more exact ecology* (eds P.J. Grubb & J.B. Whittaker), pp. 113–140. Blackwell Science, Oxford, UK.

Murdoch, A.W.W., Nisbet, R.M., Blythe, S.P., Gurney, W.S.C. & Reeve, J.D. (1987) An invulnerable age class and stability in delay-differential parasitoid-host models. *The American Naturalist*, **129**, 263–282.

Nisbet, R. (1997) *Delay-Differential Equations for Structured Populations*. Chapman and Hall, New York, NY, USA.

Nisbet, R.M. & Gurney, W. (1983) The systematic formulation of population-models for insects with dynamically varying instar duration. *Theoretical Population Biology*, **23**, 114–135.

Nishikawa, H., Shimada, T., Nakahira, K. & Arakawa, R. (2010) Thermal effect on the development and reproduction of an indigenous mirid bug, *Pilophorus typicus* distant (Heteroptera: Miridae), a potential biological control agent in japan. *Applied Entomology and Zoology*, **45**, 313–318.

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

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.

Ragland, G.J. & Kingsolver, J.G. (2008) The effect of fluctuating temperatures on ectotherm life-history traits: comparisons among geographic populations of *Wyeomyia smithii*. *Evolutionary Ecology Research*, **10**, 29–44.

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

Ritchie, M.E. (1996) *Interaction of Temperature and Resources in Population Dynamics: An Experimental Test of Theory*, pp. 79–91. Frontiers of Population Ecology. CSIRO Publishing, Melbourne, Australia.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.

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

Sheldon, K.S., Yang, S. & Tewksbury, J.J. (2013) Climate change and community disassembly: impacts of warming on tropical and temperate montane community structure. *Integrative and Comparative Biology*, **14**, 1191–1200.

Strong, A.D.R., Maron, J.L., Connors, P.G., Whipple, A., Harrison, S., Jefferies, R.L. *et al.* (1995) High mortality, fluctuation in numbers, and heavy subterranean insect herbivory in bush lupine, *Lupinus arboreus*. *Oecologia*, **104**, 85–92.

Tewksbury, J.J., Huey, R.B. & Deutsch, C. (2008) Climate warming puts the heat on tropical ectotherms. *Science*, **320**, 1296–1297.

Ulmer, B.J., Jacas, J.A., Pena, J.E., Duncan, R.E. & Castillo, J. (2006) Effect of temperature on life history of *Aprostocetus vaquitarum* (Hymenoptera: Eulophidae), an egg parasitoid of *Diaprepes abbreviatus* (coleoptera: Curculionidae). *Biological Control*, **39**, 19–25.

Urbaneja, A., Llacer, E., Tomas, O., Garrido, A. & Jacas, J.A. (1999) Effect of temperature on development and survivorship of *Cirrospilus* sp. near *lyncus* (hymenoptera: Eulophidae), a parasitoid of *Phyllocnistis citrella* (Lepidoptera: Gracillariidae). *Environmental Entomology*, **28**, 339–344.

Urbaneja, A., Llacer, E., Garrido, A. & Jacas, J.A. (2001) Effect of temperature on the life history of *Cirrospilus* sp. near *lyncus* (Hymenoptera: Eulophidae), a parasitoid of *Phyllocnistis citrella* (Lepidoptera: Gracillariidae). *Applied Entomology and Zoology*, **45**, 313–318.

Walther, G.R., Post, E., Convery, P., Menzel, A., Parmesan, C., Beebee, T.J.C. *et al.* (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

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

Zamani, A., Talebi, A., Fathipour, Y. & Baniameri, V. (2006b) Temperature-dependent functional response of two aphid parasitoids, *Aphidius colemani* and *Aphidius matricariae* (Hymenoptera: Aphidiidae), on the cotton aphid. *Journal of Pest Science*, **79**, 183–188.

Received 8 April 2015; accepted 24 September 2015
Handling Editor: Scott Carroll

Supporting Information

Additional Supporting information may be found in the online version of this article:

Appendix S1. Census protocols.
Appendix S2. Experiment methods.
Appendix S3. Effects of density on life history traits.
Appendix S4. DDE model description.
Appendix S5. Non-delay ODE model.
Figure S1. Density-dependence of life history traits.
Figure S2. Population dynamics predicted by ODE model.
Table S1. Parameter estimates for temperature responses.
Table S2. Effects of density on development and mortality.
Table S3. Parameter estimates for temperature and resource availability functions.
Data S1. Data used to parameterize DDE model.