Forum

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The role of temperature variability on insect performance and population dynamics in a warming world

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Despite the amount of research on the consequences of global warming on ecological systems, most studies examine the impact of increases in average temperature. However, there are few studies concerning the role of thermal variability on ecological processes. Based on insect thermal and population ecology, we propose a theoretical framework for organizing the study of the role that thermal mean and variability plays in individual performance, and how it may affect population dynamics. Starting with three predictions of global warming scenarios, we develop null models of the expected changes in individual physiological performance and population dynamics. Ecological consequences in each scenario may range from simple changes in performance to drastic changes in population fluctuations and geographic ranges. In particular, our null models show that potential changes in the intrinsic population growth rate (R_m) will depend on the interaction of mean temperature and thermal variability, and that the net effect of the interaction could be synergistic or antagonistic. To evaluate these null models, we fit performance curves to compiled data from the literature on measurements of R_m at several constant and fluctuating temperatures. The fitted models showed that several of the qualitative characteristics predicted by the null model may be found in the fitted curves. We expect that this framework will be useful as a guide to study the influence of thermal changes on the dynamics of natural populations.

Synthesis

Despite the common assertion that global warming impacts depend on not only the mean temperatures but also on thermal variability, theoretical approaches to explain how the interaction of thermal mean and variability determines fitness are lacking. Here we propose a framework for studying the role of thermal mean and variability on individual performance and population dynamics. We developed null models that show how changes in the intrinsic population growth rate (R_m) will depend on the interaction of mean temperature and thermal variability, and that the net effect could be synergistic or antagonistic. We expect that this framework will be useful to study the influence of thermal changes on natural populations.

Despite the high degree of uncertainty in the predictions of global warming scenarios, there is a consensus that average temperature on a global scale will increase by 2 to 5°C during the next century, with exceptions at local scales (Solomon et al. 2008). However, and perhaps more important, there is no consensus in the expected change in thermal variability: it has been suggested that thermal variability at diel and seasonal scales will be either increased in the next century (Burroughs 2007) or reduced as a result of the expected increases in minimum daily temperatures (Solomon et al. 2008). Thus, as pointed out by Bozinovic et al. (2011a), to predict responses to climate change, ecologists must understand the patterns of thermal variation, the mechanisms by which animals cope with this variation, and the demographic and fitness consequences. Theoretically, human impact on the earth's climate will likely modify the frequency of extreme temperatures in certain regions, which would likely cause a reduction in fitness and population growth rates.

Three basic scenarios are herein proposed as a starting point to understand the ecological consequences of climate change (Meehl et al. 2000, Burroughs 2007). In the first scenario, an increase in mean temperature without changes in variability will result in fewer cold events and more hot events, with a high probability that future temperatures will exceed previously recorded maximums. In the second scenario, a change in the variance of temperature without a change in mean will result in alterations in the frequency of hot and cold events; however, we still have a high degree of uncertainty about the direction of this change. In the third scenario, both the mean and the variance of temperature change, with increased frequency and intensity of hot events. Although each scenario could have pervasive effects on life, we cannot predict these effects without understanding how the mean and variance of temperature interact to determine their effect on fitness (Calosi et al. 2008, Folguera et al. 2009, 2011, Terblanche et al. 2010).

On the other hand, it has been argued that these changes may unleash several responses at the population level, namely, latitudinal and altitudinal geographic range shifts (Parmesan et al. 1999, Estay et al. 2009a, Chown et al. 2010, Bozinovic et al. 2011b), changes in reproductive phenology (Stenseth et al. 2002, Walther et al. 2002), changes in body size (Daufresne et al. 2009, Gardner et al. 2011) or temporal variability of population abundance (May 1974, Royama 1992, Chown et al. 2010, Estay et al. 2011, 2012). Because population increase depends on physiological performance curves and how these affect developmental reaction norms on survival and fecundity, the joint study of thermal physiology and population ecology has the potential to provide a mechanistic bridge for linking individuals, demography and population dynamics under different scenarios of global warming (Crozier and Dwyer 2006, Chown et al. 2010).

Considering the susceptibility of arthropods to thermal changes (Harrison et al. 2012), special attention should be paid to the link between the ecological physiology of arthropods and their observed population dynamics (Crozier and Dwyer 2006, Chown and Terblanche 2007, Chown et al. 2010), and how physiological processes constrain their distributions and abundances (Huey and Berrigan 2001, Crozier and Dwyer 2006, Calosi et al. 2008, Bozinovic et al. 2011b). In the last few years, several authors (Chown and Nicolson 2004, Frazier et al. 2006, Martin and Huey 2008, Angilletta 2009, Chown et al. 2010, Paaijmans et al. 2010, Lambrechts et al. 2011) have explored the consequences of the nonlinear relationships between body temperature and several performance variables, such as the intrinsic rate of increase (R_m), survival, fecundity, etc., in arthropods (or another performance curve related to fitness, examples in Worner 1992, Angilletta 2009) and the consequences in individual performance. Here, and using examples from arthropods, we postulate that understanding the interaction between thermal mean and variability will help predict the ecological impacts of changes in climate. Clearly these impacts are complex and involve interactions between mechanisms and processes at different levels of ecological organization. We analyzed how performance curves may change with alterations in average temperature and, more importantly, the variability, as a starting point in linking individual and population performances under different climate change scenarios.

A baseline null model

The relationship between arthropod ecology and climatic conditions has mainly been evaluated in terms of average conditions, and it is now well understood (Porter et al. 1991, Harrington et al. 2007, Chown et al. 2010). Most authors predict a general positive global warming effect on population density of ectotherms at high latitude (Porter et al. 1991, Crozier and Dwyer 2006, Estay et al. 2009a) and a negative effect for tropical species (Deutsch et al. 2008).

The relationship between environmental temperature and physiological performance has been described as a unimodal and asymmetric function (Fig. 1). As an extension to this curve, it is possible to describe the relationship between temperature and the intrinsic rate of population growth or fitness (R_m, Fig. 1). This type of curve will be our baseline or null model to examine the response of R_m under the

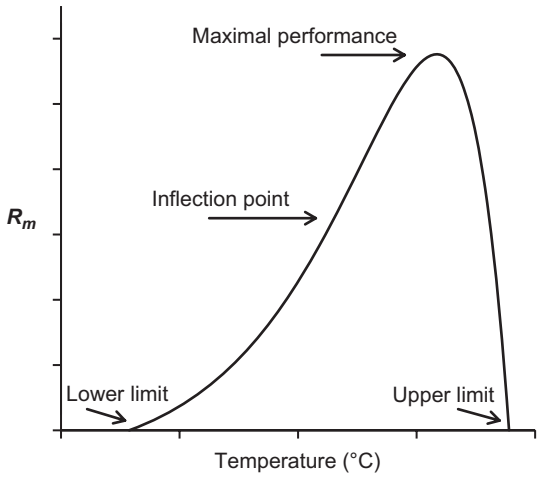

Figure 1. Prototypical performance curve for an ectothermic organism. In this case, the curve describes the relationship between temperature and the intrinsic rate of population increase (R_m).

scenarios of global warming. Several characteristics of this curve deserve special attention. First, the lower and upper limits define which can be considered the niche amplitude of the focal species in the temperature axis. These limits are the points where the curve intersects the temperature axis ($R_m = 0$). Below the lower limit and above the upper limit, R_m takes negatives values, which means the population is not viable in the long term. Second, the inflection point marks the point where the second derivative of the function is zero, or in other words, where the acceleration of performance begins to decrease. Finally, maximum performance marks the maximum R_m and the projection on the x-axis marks the optimum temperature (but see Martin and Huey 2008). This analysis may be extrapolated to any other fitness indicator, such as survival, fecundity, age-specific mortality, and so on. Due to the nonlinearity of the curve, values falling outside the thermal limits R_m become rapidly negative, so that depending on how nonlinear the function is, far from lower and upper thermal limits, even a minor exposure to these temperatures will be lethal for individuals. Particularly, our analysis will focus on sub-lethal temperatures, meaning we are interested in the range of temperatures generating low to moderate thermal stress, in the vicinity of thermal limits, and not on those generating serious damage to individuals that cause death in the short term (hours or days after exposure). However, this analysis should be cautionary when applied to physiological traits or developmental reaction norms because these operate at a different time scale. Physiological traits or developmental reaction operate at shorter time scales and the interpretation the effect of variability on these performance curves should be done at the proper time scale of the process. In the same vein, physiological traits are usually under the action of plasticity or adaptation, which makes the performance curves associated to these traits show a higher flexibility than R_m – temperature curves. As previously shown, plasticity/adaptation could induce not only changes in the form of the curve, but also complete displacement in the temperature axis, contractions, expansions and/or changes in maximum without changes in limits (Angilleta 2006, Frazier et al. 2006).

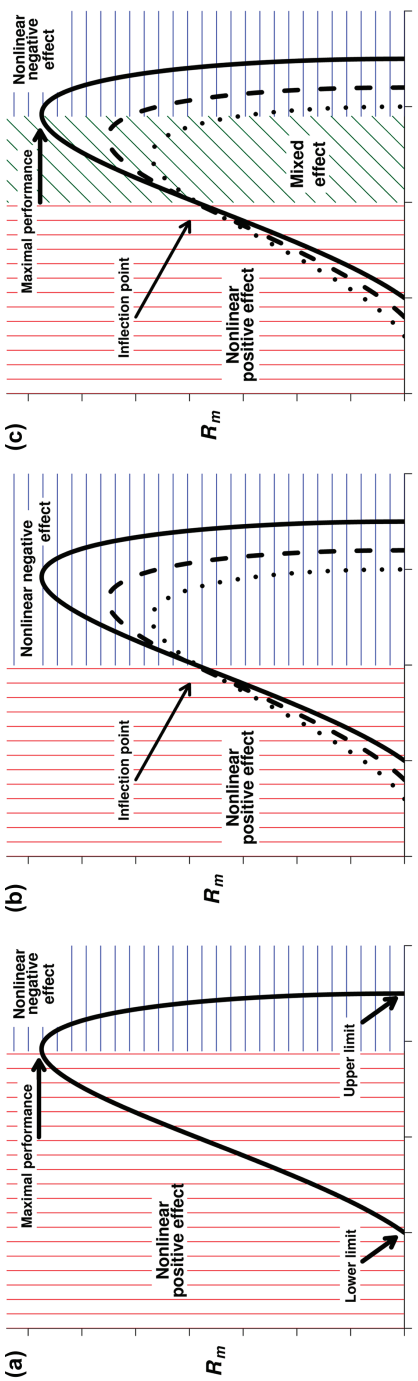

Figure 2. Expected responses of R_m under scenarios 1, 2 and 3. (a) An increase in the average temperature without change in variance would have a positive nonlinear effect on populations located between the lower limit and the maximum performance point (red area), but a negative one between this last point and the upper limit (blue area). (b) An increase in thermal variability without change in average temperature would have a positive nonlinear effect on populations located between the lower limit and the inflection point (red area), but a negative one between this last point and the upper limit (blue area). (c) An increase in thermal variability and average temperature would have a positive nonlinear effect on populations located between the lower limit and the inflection point (red area), but a negative one between the point of maximum performance and the upper limit (blue area). Between the inflection point and maximum performance point (green area), the net effect depends on the relative magnitude of the increments of average temperature and variability. Solid (low), dashed and dotted (high) lines show a sequence of increased variability.

Thus, using this theoretical nonlinear curve ($R_m = f(T)$) we can predict that, in our first scenario (increase in the mean temperature without changes in variability), populations located between the lower limit and the point of maximum performance will react in a positive nonlinear way as a response to the increase in average temperature. On the other hand, populations between the point of maximum performance and the upper limit will react in a negative nonlinear way to the increase in temperature (Fig. 2a). In this case, assuming that the average temperatures at time 1 and 2 are μ_{T1} and μ_{T2}, the net effect of a change in average temperature on R_m is simply:

$$\Delta R_m = f(\mu_{T2}) - f(\mu_{T1}) \quad (1)$$

In the second scenario, average temperature does not change, but variability could increase or decrease. In this case, the effect of thermal variability on performance may be understood by analyzing the mathematical properties of the performance curve. Considering the asymmetric curve of performance, the effect of variability under no other forces can be derived from Jensen's inequality (Jensen 1906, Ruel and Ayres 1999). This inequality states that for a sample of the variable x with average $\bar{x}$ and $y = f(x)$ being a nonlinear function of x, then $\overline{f(x)} > f(\bar{x})$ if $f(x)$ is accelerating (2nd derivative is positive), and $\overline{f(x)} < f(\bar{x})$ if $f(x)$ is decelerating (2nd derivative is negative). According to this mathematical law and the dome-shaped relationship between temperature and R_m (Huey and Berrigan 2001, Frazier et al. 2006, Martin and Huey 2008, Fig. 1), it is possible to infer that along the accelerating portion of the curve (between the lower limit and the inflection point), a greater variability in temperature will result in a higher R_m. On the other hand, in the decelerating part of the function (between the inflection point and the upper limit) a greater variability in temperature will result in a lower R_m. This phenomenon is termed the Kaufmann effect when applied to insect physiology (Worner 1992) and it has been observed in arthropods growing under different conditions of daily thermal variability (Bozinovic et al. 2011a, Estay et al. 2011). Jensen's inequality was also used to explain the differences between predicted and observed values of optimal performance (Martin and Huey 2008) and to explain the differences in transmission rates of malaria (Paaijmans et al. 2010) and dengue (Lambrechts et al. 2011) estimated at constant temperatures and at field temperatures (variable). We believe that the consequences of Jensen's inequality establish the null model to test the effect of thermal variability. Any deviation from this model implies the action of a different mechanism. Considering a scenario of increased variability (Burroughs 2007), populations to the left of the inflection point would increase their performance, or in this case they would have a higher R_m value compared to less variable conditions. The opposite would occur for populations to the right side of the inflection point. In this case, any increment in variability would be detrimental to the performance of the population (lower R_m value than in less variable conditions as predicted by Solomon et al. 2008). Another interesting consequence of the effect of variability is the change in the thermal limits. In particular, increments in variability imply that lower and

upper limits shift to the left (towards the origin in the graph of Fig. 2b), and a decrease in variability pulls the limits to the right. In this situation some temperatures below the lower limit at less variable conditions ($R_m < 0$) turns into suitable conditions ($R_m > 0$), and some temperatures below the upper limit at less variable conditions ($R_m > 0$) turns into unsuitable conditions ($R_m < 0$). The relative change of these limits is not the same. It is expected that the lower limit changes proportionately less in comparison to the upper limit. This means that a change in variability has greater impact on the upper limit than on the lower limit, but the exact magnitude depends on the slope of the curve close to these limits.

Another important consequence is that at any level of thermal variability, the maximum value of R_m will always be lower than expected under constant optimal temperature. This last result, along with the asymmetric change in thermal limits explained in the previous paragraph, leads us to the corollary that the area under the performance curve (AUC) will always decrease with thermal variability. If the AUC is considered to be a measure of the total performance or fitness of the population inside the thermal niche, then the total performance would be negatively related to thermal variability.

The magnitude of the effect of thermal variability may be approximated through the δ-method (Rice 2006). Considering that T is a random variable with mean μ_T and variance σ^2_T, we can then approximate $E(R_m)$ using a Taylor expansion of $f(T) = Rm$ around μ_T.

The second-order Taylor expansion of $f(T)$ is:

$$R_m \approx f(\mu_T) + (T-\mu_T) f'(\mu_T) + \tfrac{1}{2}(T-\mu_T)^2 f''(\mu_T) \quad (2)$$

Taking the expectation on both sides we have

$$E(R_m) \approx f(\mu_T) + \tfrac{1}{2}\sigma^2_T f''(\mu_T), \quad (3)$$

since $E(T-\mu_T) = 0$ and $E(T-\mu_T)^2$ is the second moment around the mean which is the variance (σ^2_T). How reliable such approximations are depends on how nonlinear $f(T)$ is in the neighborhood of μ_T and on the size of σ^2_T (Rice 2006).

Given a specific model for $f(T)$ and using Eq. 2 we can approximate the value of R_m under different scenarios of variability. Considering that μ_T does not change between times 1 and 2, and that the variances of each period are σ^2_{T1} and σ^2_{T2}, then the net effect of the change of variance on R_m is:

$$\Delta R_m \approx [f(\mu_T) + \tfrac{1}{2}\sigma^2_{T2} f''(\mu_T)] - [f(\mu_T) + \tfrac{1}{2}\sigma^2_{T1} f''(\mu_T)] = \tfrac{1}{2} f''(\mu_T)\,[\sigma^2_{T2} - \sigma^2_{T1}] \quad (4)$$

Finally, the last scenario predicts changes in average temperature and in thermal variability. In this scenario we combine the predictions of the two previous ones. Results show that the area of positive nonlinear effects of a simultaneous change in mean and variance would be between the lower limit and the inflection point. In this area, the effect of changes in average temperature and variability is positive. In other words, increments in thermal average and variability generate an increase in performance. The area of negative nonlinear effects would be between the point of maximum performance and the upper limit. In this area, increments in average and variance generate a reduction in performance. The area between the inflection point and the maximum is an area where there are mixed and opposing effects of average and variability. In this area, an increment in average temperature causes an increment in performance; however, the opposite is true for variance. Therefore, the net effect of a change in average and variance would depend of the relative magnitude of their respective changes (Fig. 2c). Finally, thermal limits change in the same way as in scenario 2.

To calculate the net effect of the changes in average and variance we can use Eq. 2. If the averages and variances of temperatures at time 1 and 2 are μ_{T1}, μ_{T2}, σ^2_{T1} and σ^2_{T2}, then in this section of the curve the value of R_m will be:

$$\begin{aligned}\Delta R_m \approx\ & [f(\mu_{T2}) + \tfrac{1}{2}\sigma^2_{T2} f''(\mu_{T2})] - [f(\mu_{T1}) \\ & + \tfrac{1}{2}\sigma^2_{T1} f''(\mu_{T1})] \\ =\ & [f(\mu_{T2}) - f(\mu_{T1})] + \tfrac{1}{2}[\sigma^2_{T2} f''(\mu_{T2}) \\ & - \sigma^2_{T1} f''(\mu_{T1})] \end{aligned} \quad (5)$$

A summary diagram of the joint effect of thermal mean and variability on R_m is shown in Fig. 3.

Some consequences for population dynamics

To illustrate how the effects of thermal mean and variability on individual performance may propagate to the population level, we analyzed two classic population models (one unstructured and one structured) and described how temperature-dependent individual performance could modify the dynamic behavior of this system.

Unstructured populations: the case of the Ricker model

May (1974) showed how an increase in R_m leads to higher variances in the logistic model, and, if the change is significant, it could even modify the dynamic behavior of the system. Sudden changes in the variability of natural populations can increase the likelihood of extinction (Royama 1992, Schreiber 2001) or increase the frequency and/or intensity of pest outbreaks (Berryman and Millstein 1989, Desharnais et al. 2001).

In the first case, a non-linear version of the Ricker model of population dynamics (Ricker 1958) was used as a baseline for our analysis. This simple model, based on a difference equation, has been used successfully in the modeling of insect species (Saldaña et al. 2007, Lima et al. 2008, Estay et al. 2009b), and it has been extensively studied, simplifying our analytical approach. Despite this, any population dynamics model, structured or unstructured, may be used to achieve our objective following the reasoning below.

The increase in the maximum per capita growth rate is related to changes in the intrinsic birth (increase) or death (decrease) rates of a population. This parameter is also linked to the equilibrium density (or carrying capacity) of the population (Pastor 2008), which means that if R_m changes, then it is expected that long-term average abundance will also change. From these assertions, we can now infer that changes in the current patterns of thermal variability can impact stability and long-term abundance in natural populations (Estay et al. 2011).

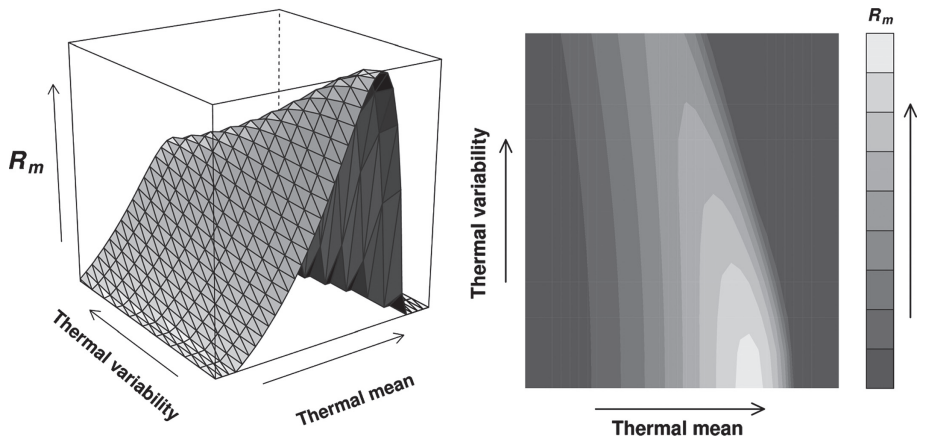

Figure 3. Diagram of the joint effect of thermal mean and variability on R_m. On the left side is the 3D graph and on right side is the contour graph of the response curve corresponding to a simulation using the model by Lactin et al. (Lactin et al. 1995). Values under different levels of variability were obtained by simulation considering a specific variance values for each temperature level.

The nonlinear time-discrete version of the logistic model (Ricker model) is:

$$R = R_m\left(1-\left(\frac{N_{t-d}}{K}\right)^Q\right) \quad (7)$$

Where N_{t-d} is the abundance at time $t - d$; R is the realized per capita growth rate $R = ln(N_t/N_{t-1})$; R_m is the intrinsic growth rate estimated for a particular species; K is the equilibrium density, and Q is a nonlinearity factor.

The linear version of this model,

$$R = R_m\left(1-\frac{N_{t-d}}{K}\right) \quad (8)$$

was analyzed in detail by May (1974). The dynamic behavior of the linear version at equilibrium depends on one parameter, R_m. May (1974) demonstrated that when $0 < R_m < 1$, the system approaches equilibrium (K) monotonically; if $1 < R_m < 2$, then the system approaches equilibrium with damped oscillations; if $2 < R_m < 2.526$, the system has a two-point cycle, and so on (see the threshold values in May 1974).

In the non-linear version, the dynamic behavior at equilibrium depends on two parameters, R_m and Q.

The R-function,

$$R = \ln\left(\frac{N_t}{N_{t-1}}\right) = R_m\left(1-\left(\frac{N_{t-1}}{K}\right)^Q\right) \quad (9)$$

evaluated at equilibrium, depends on the function $Q \times R_m$ (slope, Estay et al. 2012). The function $Q \times R_m$ is assumed to be equal to every threshold value of the linear version of the model, $Q \times R_m = a$, where a is the threshold of the linear case (1, 2, 2.526,..., etc.). Then, the functions describing the limits of areas of monotonic damping, damped oscillations and two-point cycles in the $Q - R_m$ parameter space are: $R_m = 1/Q$, $R_m = 2/Q$ and $R_m = 2.526/Q$, respectively (Fig. 4). Therefore, all functions describing thresholds have the general form $R_m = a/Q$ (Fig. 4, Estay et al. 2012).

Combining performance curves with the stability properties of the logistic model, we can make some generalizations about the expected change in population dynamics under each scenario of climate change. In the first scenario of global warming, the effect of the increment in mean temperature on R_m could have a destabilizing effect on populations located to the left of the maximum performance point, but a stabilizing effect on populations located to the right (Fig. 5a).

In the second scenario, the effect of an increase in thermal variability on R_m could have a destabilizing effect on populations located to the left of the inflection point, but a stabilizing effect on populations located to the right (Fig. 5b). The reduction on the AUC due to increased variability could have important consequences at the population level, such as modifying the pattern of coexistence between species (if the reduction in AUC is different between competitors) or modifying the cyclicity pattern of predator–prey interactions

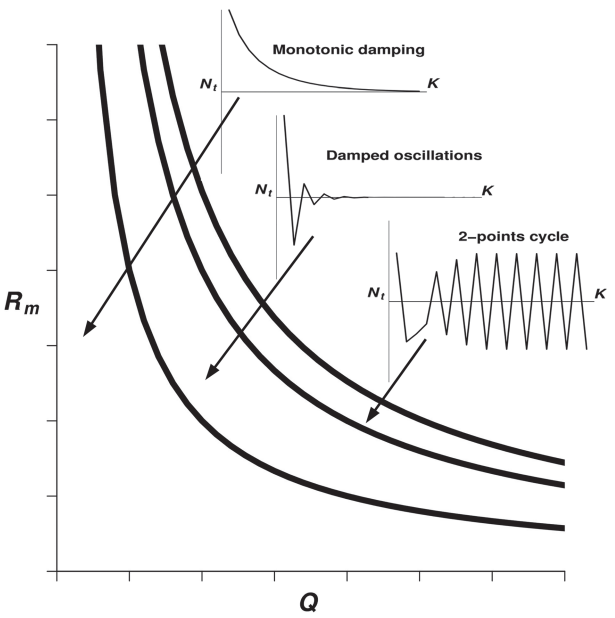

Figure 4. $Q - R_m$ parameter space and thresholds for the Ricker model. The first three regimes are shown. Each curve represents a threshold with the form a/Q.

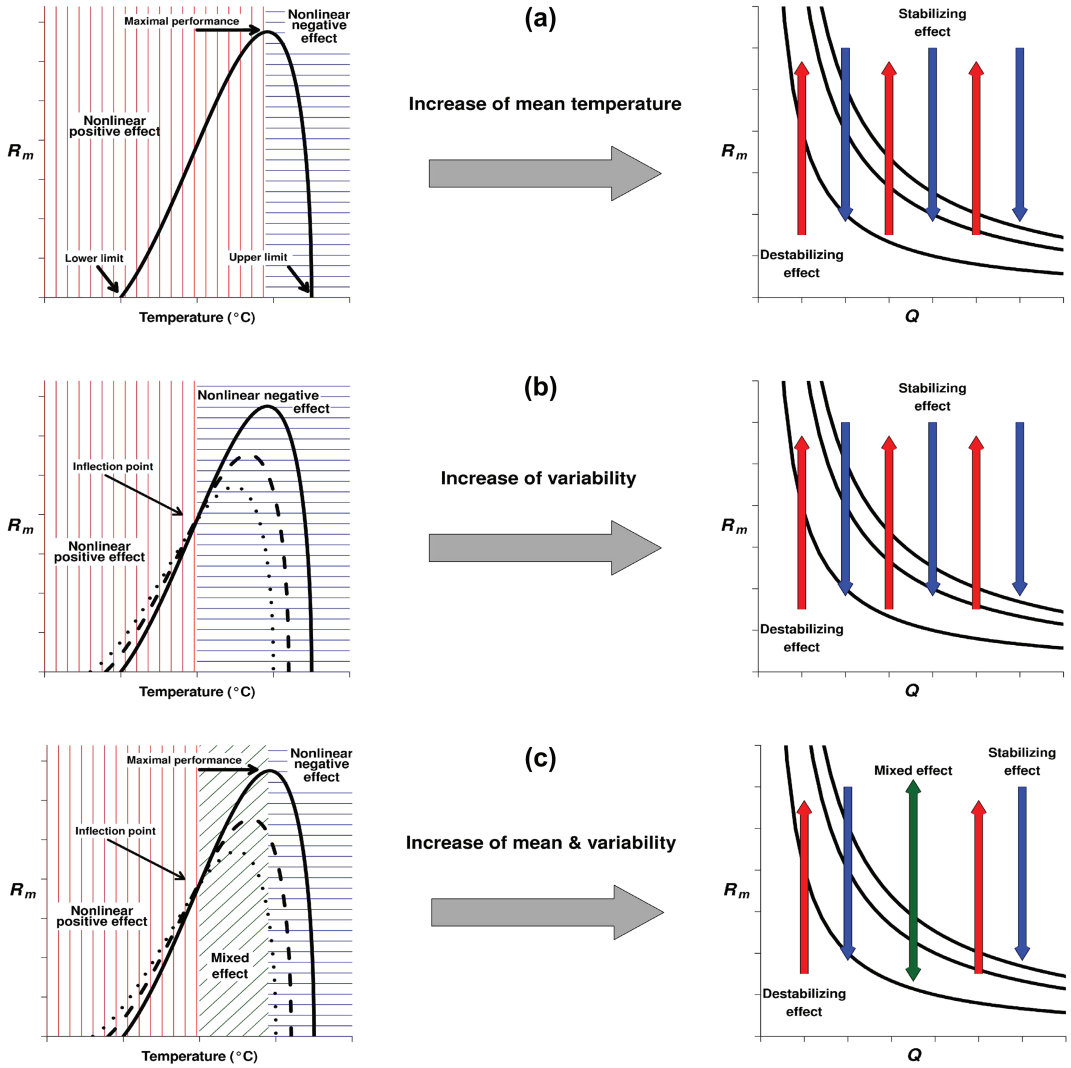

Figure 5. Diagram of the theoretical effects of an increase in thermal mean and/or variability on the dynamics of a population. The left side is similar to Fig. 2. The right side shows the expected change in R_m and the type of effect. (a) An increase in mean temperature on the left side of the point of maximum performance (red area) implies a destabilizing effect on population dynamics due to the increase in R_m (red arrows). The opposite effect is seen on the right side of the point of maximum performance (blue area). (b) Increase in variability on the left side of the inflection point (red area) implies a destabilizing effect on population dynamics due to an increase in R_m (red arrows). The opposite is seen on the right side of the inflection point (blue area). (c) Increase in variability on the left side of the inflection point (red area) implies a destabilizing effect on population dynamics due to an increase in R_m (red arrows). The opposite effect is seen on the right side of the point of maximum performance (blue area). Between these two areas (green area), the net effect will depend on the relative magnitude of the change in average and variance.

(If the reduction on prey or predator R_m changes the relative mortality caused by the predator).

Finally, in the third scenario, the effect of an increase in average temperature and variability on R_m could have a destabilizing effect on populations located to the left side of the inflection point, a stabilizing effect on populations located between the maximum performance point and the upper limit, and a mixed effect between the inflection and maximum performance points, where the net effect will depend on the relative magnitude of the changes in average and variance (Fig. 5c). All these results assume that the parameter Q remains constant. However, this parameter could change in the same or opposite direction as R_m. The consequences of each alternative are interesting. If Q follows the change of R_m, then the effect (stabilizing or destabilizing) will be amplified in its magnitude or perhaps in the velocity at which the change in the dynamic regime occurs. In contrast, if the change in Q is opposite to the change in R_m, then Q will act as a stabilizer, avoiding change in the dynamic regime of the population. However, the biological meaning of Q is still unclear. Despite the fact that adaptation to new environments could avoid the instability in population dynamics in the long term (Berryman and Millstein 1989), Estay et al. (2012) showed that within ecological time frames, it is possible to observe some degree of increased instability as a consequence of an increase in R_m in populations of aphids in the UK. In the same vein, Paaijmans and collaborators (Paaijmans et al. 2010, Lambrechts et al. 2011) have shown how parasite infection, the rate of parasite development, and some other biological parameters of mosquito vectors, that

determine malaria and dengue transmission rate, are drastically modified by temperature variability.

Another very interesting result of our analysis is the potential role played by variance in the population dynamics of arthropods. From the point of view of the theory of population dynamics, all these changes in R_m belong to the vertical type of effects (sensu Royama 1992). In this type of effect, the change in R_m induces changes in both the pattern of variability of population dynamics and the long-term abundance of organisms. According to our analysis, variability, especially diel or seasonal, could be by itself a factor inducing vertical effects on the reproductive curve, and has not received any attention in the literature as far as we know. Considering the Ricker model, variability (σ^2_T) could be incorporated as an additive function in the equation:

$$R = R_m\left(1-\left(\frac{N_{t-d}}{K}\right)^Q\right)+f\left(\sigma^{2_r}\right) \quad (10)$$

Structured populations: the case of the LPA model

The LPA model, developed for populations of flour beetles of the genus *Tribolium* (Dennis et al. 1995), consists of three difference equations, each one related to the larvae, pupae and adult stages. The model includes density-dependent egg cannibalism by larvae and adults, density-dependent pupae cannibalism by adults, and density-independent fecundity, and larval and adult mortality rates (Dennis et al. 1995). The model is represented in the next three equations:

$$L_t = bA_{t-1}e^{\left(-c_{ea}A_{t-1}-c_{el}L_{t-1}\right)} \quad (11)$$

$$P_t = L_{t-1}\left(1-\mu_l\right) \quad (12)$$

$$A_t = P_{t-1}e^{\left(-c_{pa}A_{t-1}\right)}+A_{t-1}\left(1-\mu_a\right) \quad (13)$$

where L_t, P_t and A_t are the abundances of larvae, pupae and adults at time t. b is the larvae recruited per adult per unit of time in the absence of egg cannibalism. μ_l and μ_a are the larval and adult probabilities of dying from causes other than cannibalism. The fractions $exp(-c_{ea}A_t)$ and $exp(-c_{el}L_t)$ are the probabilities that an egg laid between $t-1$ and t is not eaten in the presence of A_t adults and L_t larvae. Finally, the fraction $exp(-c_{pa}A_t)$ is the survival probability of a pupa in the presence of A_t adults (Dennis et al. 1995).

The dynamic behavior of this model has been previously described (Dennis et al. 1995, 1997, Cushing 2003). It has been reported that changes in per-adult recruitment rate (b), adult mortality rate (μ_a) and/or rates of cannibalism induce changes in the dynamic behavior of the system (Dennis et al. 1995, 1997). For instance, using the scenario where cannibalism of eggs by larvae is negligible (see Dennis et al. 1995 for other parameter configurations), parameter b modifies the dynamics from stable equilibrium to two-point cycle (Dennis et al. 1995) when its value is above the function

$$b_2\left(\mu_a\right) = \frac{\mu_a}{1-\mu_l}e^{\frac{2}{\mu_a}} \quad (14)$$

Another interesting transition occurs when adult mortality (μ_a) changes in the model parameterized to a sensitive genetic strain. Below $\mu_a \approx 0.4$, the dynamics of larval stage show a two-point cycle; if $0.4 < \mu_a < 0.75$, there is a stable equilibrium, and if $\mu_a > 0.75$ the dynamic exhibits quasiperiodicity (Dennis et al. 1997).

As with any ectothermic organism, parameters b and μ_a are strongly temperature-dependent (Park 1954, Howe 1956, White 1987), and both show a unimodal and asymmetric response to temperature (White 1987). The maximum observed fecundity in *Tribolium castaneum* occurs at around 32.5°C and decay is greater at higher temperatures than at lower temperatures, similar to R_m behavior (Howe 1962, White 1987). On the other hand, adult survival ($1-\mu_a$) also shows a unimodal response to temperature with a maximum survival at around 25°C (White 1987).

Regarding the evidence from mathematical models and experiments, it is clear that temperature mean and variability could affect the dynamic behavior of the LPA model in a slightly more complex way than in the Ricker model. If cannibalism of eggs by larvae is zero, then in the first scenario the LPA model could be destabilized for populations located to the left side of the maximum b value (from stable equilibrium to two-point cycle), but have a stabilizing effect on populations located to the right side. In the second scenario, the effect of an increase in thermal variability on b could have a destabilizing effect on populations located to the left side of the inflection point, but a stabilizing effect on populations located to the right side. In the third scenario, the effect of an increase in average temperature and variability on b could have a destabilizing effect on populations located to the left side of the inflection point, a stabilizing effect on populations located between the maximum b value and the upper limit, and a mixed effect between the inflection point and the maximum b value, where the net effect will depend on the relative magnitude of the changes in average and variance. In the case of adult survival ($1-\mu_a$), the situation is more complex and each particular scenario depends on the specific configurations of the temperature scenario, on the position of the target population on the performance curve, and on the specific value of μ_a. Potential results are too numerous to be described here. As an example, in the first scenario to the left side of the maximum 1-μ_a value,

Table 1. References of the origin of thermal performance data. Species and temperatures used in each experiment are shown.

		Variable temp. (°C)		
Species	Constant temp. (°C)	Mean	Variability	Reference
Acyrtosiphon pisum	15, 17.5, 20, 22.5, 25	15, 17.5, 20, 25	± 10	Siddiqui 1973
Drosophila melanogaster	20, 22.5, 25, 26, 27.5	20, 22.5, 23.5, 25	± 5	Siddiqui and Barlow 1972
Helicoverpa armigera	20, 25, 27.5, 30, 32.5	17.5, 22.5, 25, 27.5	± 15	Mironidis and Savopoulou-Soultani 2008

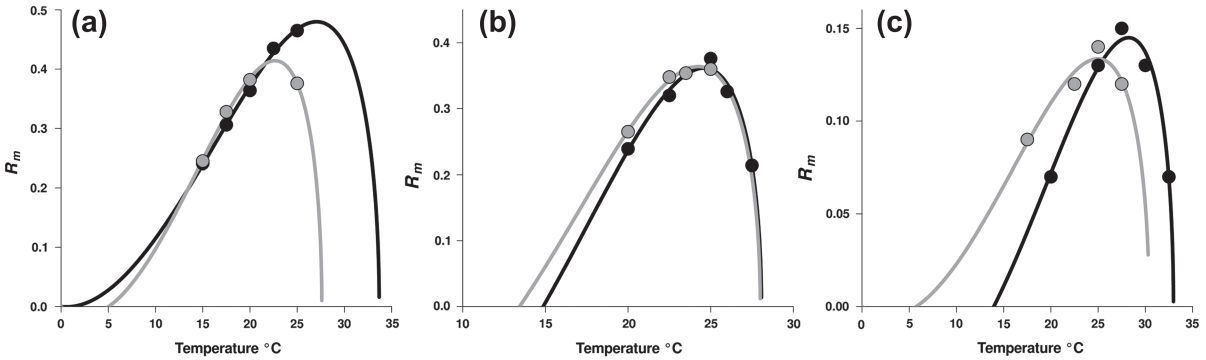

Figure 6. Performance curves for three different insects under constant and variable thermal conditions: (a) *Acyrtosiphon pisum*. Black line represents constant temperatures. Grey line represents treatments with 5°C thermal amplitude (data from Siddiqui 1973). (b) *Drosophila melanogaster*. Black line represents constant temperatures. Grey line represents treatments with 10°C thermal amplitude (data from Siddiqui and Barlow 1972). (c) *Helicoverpa armigera*. Black line represents constant temperatures. Grey line represents treatments with 15°C thermal amplitude (data from Mironidis and Savopoulou-Soultani 2008).

populations could be destabilized if $0.4 < \mu_a < 0.75$ before the increase in temperature, but stabilized if $0.75 < \mu_a < 1$. To the right side of the maximum $1 - \mu_a$ value, populations could be stabilized if $0.4 < \mu_a < 0$ before the increase in temperature, but destabilized if $0.4 < \mu_a < 0.75$.

Preliminary evaluation

Using some of the very scarce data from the literature on measurements of R_m at several constant and fluctuating temperatures, we fit some performance curves. To perform our analysis, we compiled data from laboratory studies of our focal insect pests following the same criteria used by Frazier et al. (2006). We searched data sets for which R_m was measured at five or more constant and variable temperatures, and for which an optimum temperature was evident. The data sets compiled and used in this study, as well as the time scale at which R_m was measured, are shown in Table 1.

Data sets were fitted to the three-parameter Briere model (Briere et al. 1999) for simplicity. This model has three parameters, whereas all other models have four or five. Data sets normally consist of four to seven points, which reduce degrees of freedom and turns the fitting of the models very difficult.

Overall, three characteristics of the null model may be compared with the fitted curves. First, the reduction in the point of maximal performance is especially clear for *Acyrtosiphon pisum* and *Helicoverpa armigera* (Fig. 6a and 6c). Second, the lower limit decreased in two of the observed curves, that of *Drosophila melanogaster* and *H. armigera*. The performance curve of *A. pisum* did not show the expected decrease in the thermal limit (Fig. 6b–c). Finally, upper thermal limit also decreased in the three examples, but it is most evident in the case of *A.pisum* and *H. armigera* (Fig. 6a and 6c).

The low number of data sets (and points in each data set) impedes an exhaustive and formal comparison between the observed performance curves and the prediction of the null model; we observed that several of the qualitative characteristics predicted by the null model may be found in the fitted curves. This fact suggests an important degree of matching between the assumptions of the null model and the responses of these simple, but real examples.

Contrasting these simple predictions against real data could be useful in the identification (or rejection) of a biological mechanism responsible for the observed and expected future dynamics of natural populations under climate change scenarios.

Conclusions

1) The limits of thermal niche will be different to those predicted under constant temperature. It is expected that the lower limit will be slightly reduced, and the upper limit will be much lower than predictions made at constant temperature.
2) Maximum R_m will always be lower than expected under constant temperatures, and total performance (measured as the area under the curve, AUC) is negatively related to variability.
3) Specifically, for species whose niche space is limited to some degree by thermal conditions, we can predict that, as suggested by Solomon et al. (2008), a reduction in daily thermal variability could ameliorate the stress of individuals living close to the upper thermal limit. On the other hand, under an scenario of increased variability the predicted expansion to new habitats will be greater than the expansion without considering thermal variability, since the lower limit will always be lower than the limit under constant temperatures. On the other hand, the losses of current habitat will be more dramatic than those predicted under constant conditions, since the upper limit will always be lower than the limit under constant temperatures.
4) There is a paradoxical increase in population variability under a decrease in thermal variability due to the increase in R_m (for mean temperatures between the inflection point and the upper limit). This last prediction has serious consequences for outbreak frequency of some pest species, as well as for assessing the impact of extreme climatic events and its variability on the ecological systems.
5) Finally, our analysis emphasized the importance of the link between ecophysiologist and population ecologist to

link individuals, demography and population dynamics under different scenarios of global warming.

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