Ontogenetic variation in thermal sensitivity shapes insect ecological responses to climate change

Joel G Kingsolver[1] and Lauren B Buckley[2]

Insects have distinct life stages that can differ in their responses to environmental factors. We discuss empirical evidence and theoretical models for ontogenetic variation in thermal sensitivity and performance curves (TPCs). Data on lower thermal limits for development (T_0) demonstrate variation between stages within a species that is of comparable magnitude to variation among species; we illustrate the consequences of such ontogenetic variation for developmental responses to changing temperature. Ontogenetic variation in optimal temperatures and upper thermal limits has been reported in some systems, but current data are too limited to identify general patterns. The shapes of TPCs for different fitness components such as juvenile survival, adult fecundity, and generation time differ in characteristic ways, with important consequences for understanding fitness in varying thermal environments. We highlight a theoretical framework for incorporating ontogenetic variation into process-based models of population responses to seasonal variation and climate change.

Addresses
[1] Department of Biology, University of North Carolina, Chapel Hill, NC 27599, United States
[2] Department of Biology, University of Washington, Seattle, WA 98195, United States

Corresponding author: Kingsolver, Joel G (jgking@bio.unc.edu)

Introduction

The evolution of metamorphosis in insects was key to their spectacular diversity and ecological success [1,2*]. Metamorphosis results in distinct life stages (egg or embryo, nymph and adult in hemimetabolous species; egg, larva, pupa and adult in holometabolous species) during the life cycle. In many insects, different stages utilize different habitats, resources, and microenvironments, and they may differ in sensitivity to temperature, moisture and other environmental factors.
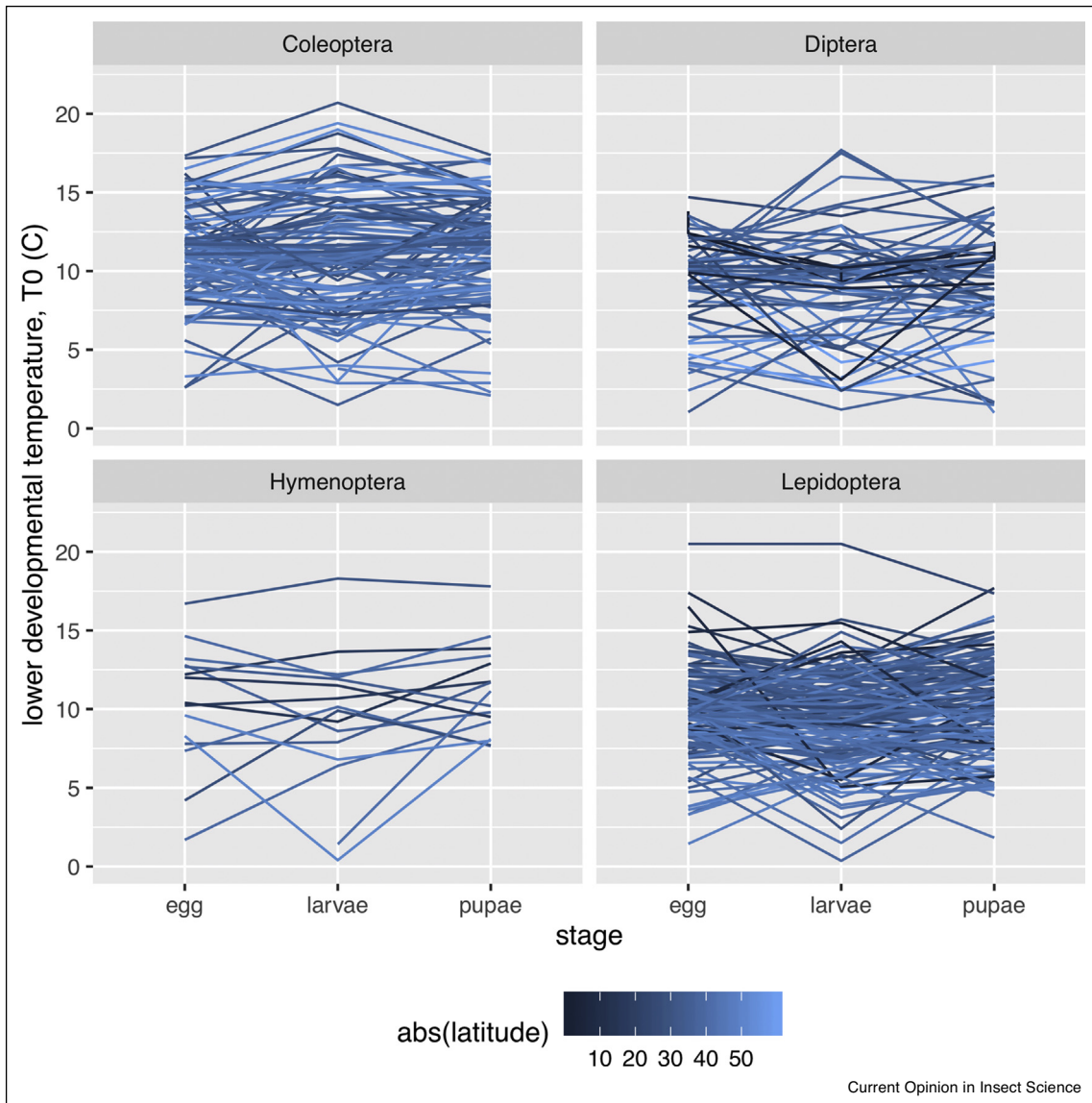
This review focuses on the importance of ontogenetic variation in thermal sensitivity for the ecological responses of insects to climate change. We do not consider effects of diapause on temperature responses [3]. We survey current data on variation in thermal sensitivity across life stages and fitness components, and we describe theoretical models that incorporate this variation. We then consider the implications of this variation for phenology and fitness in seasonal environments. We highlight some of the major gaps in current empirical evidence and modeling approaches that limit our understanding of the fitness consequences of climate change for insects and other organisms with complex life cycles.

Ontogenetic variation in thermal sensitivity

The relationship between temperature and the rate of some important biological process—for example, the rate of survival, development, growth, movement or reproduction—can be represented by a thermal performance curve (TPC) [4,5]. The shape and position of TPCs can be characterized in terms of lower and upper thermal limits, optimal temperature, thermal breadth and other metrics [6,7]. There is now an abundant empirical literature documenting widespread and systematic variation in TPCs among organisms and among traits [8–10].

What do these data tell us about ontogenetic variation in thermal sensitivity among life stages? By far the most extensive information for insects is for development rate for temperatures below the optimal temperature, as characterized by the classic 'degree-day' model. This model assumes that development rate increases linearly with temperature above some lower (minimum) developmental temperature (T_0), and characterizes thermal sensitivity in terms of T_0 and G, where G is the cumulative degrees-days (above T_0) required to complete development of a particular life stage. A recent complication of data that incorporates earlier datasets [11–13] includes estimates of T_0 and G for multiple life stages for both hemi-metabolous (101 populations in 80 species) and holo-metabolous (406 populations in 317 species) groups (data available at Ref. [13]). For example there are data on T_0 and G at the egg, larval and pupal stages for more than 200 populations in four holometabolous orders, that reveal substantial variation in T_0 across life stages within species (Figure 1). (Data for T_0 at each larval or nymphal instar are also reported for more than 70 populations: [13]; see also Ref. [14,15]). To quantify this variation, we used a linear mixed-effects model, with life stage and taxonomic order (and their interaction) as fixed effects, and
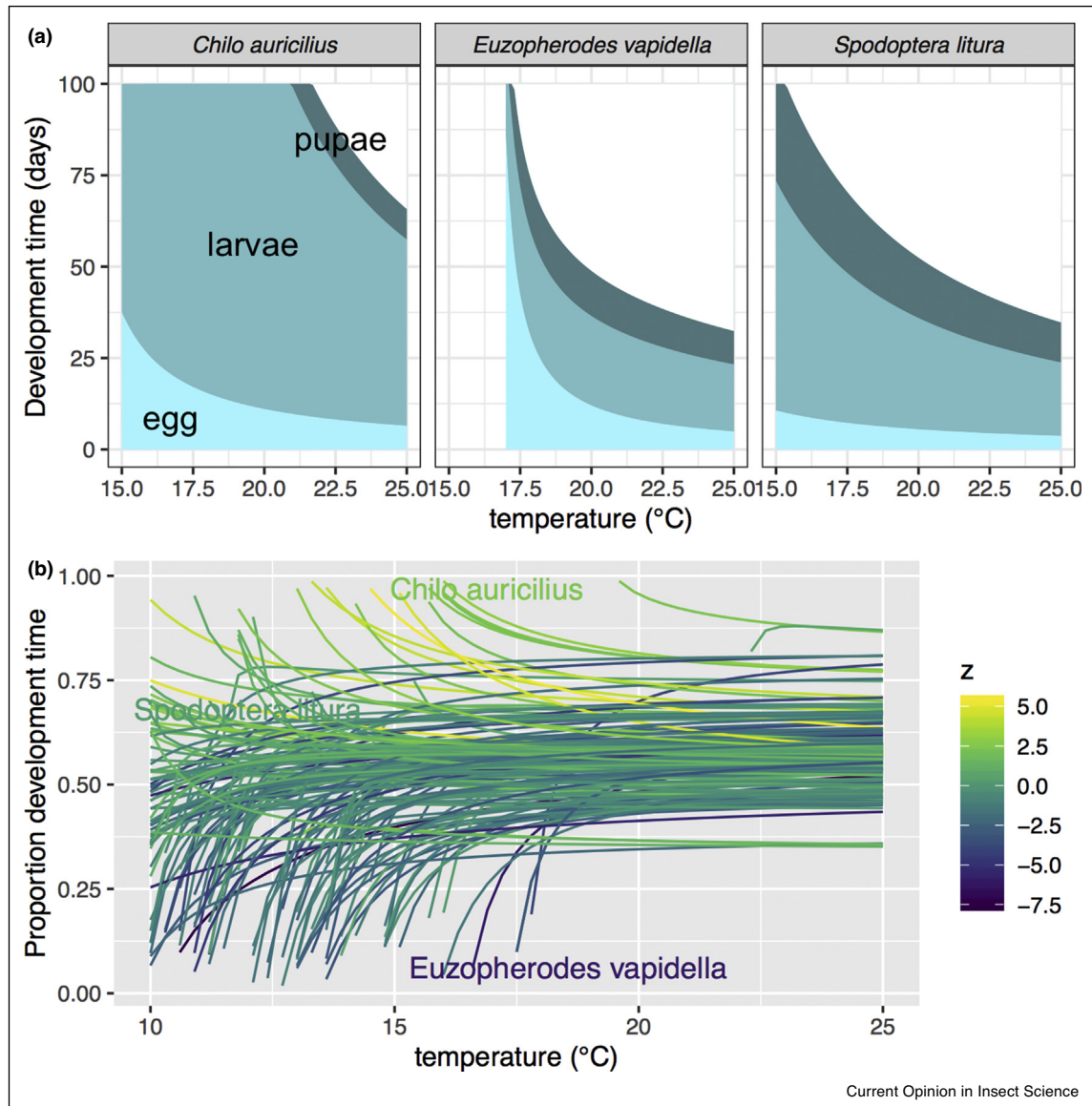
Figure 1

Lower developmental temperatures, T_0 (°C) vary across developmental stages for four insect orders. Population latitudes are indicated by color.

species and life stage within population as random effects. There are significant fixed effects of both life stage ($F_{6,643} = 8.1$, $p < 0.001$) and order ($F_{3,320} = 8.7$, $p < 0.0001$); in particular mean T_0 was greater for the pupal than the egg or larval stage, though the magnitude of these mean differences was quite small (<1°C.) The estimated magnitudes (standard deviation, SD) of the random effects were greater than these fixed effects, for both variation among species (SD = 3.2°C) and variation among life stages within species (2.7–3.0°C). Mean T_0 declines with increasing (absolute) latitude [13,16], but our analyses do not detect latitudinal patterns in ontogenetic variation in T_0 (Figure 1). These results show that the differences in thermal sensitivity of development

between life stages within a species are comparable in magnitude to the differences between species (Figure 1).

Variation in T_0 and G among life stages has important consequences for insect life cycles (Figure 2). Note that if T_0 does not vary among life stages, the proportion of total development time spent in each life stage is independent of temperature. By contrast if T_0 is higher for the larval than egg stage, then larval development time will increase more rapidly than egg development time as the temperature declines (Figure 2a: left panel). As a consequence of ontogenetic variation in T_0, the proportion of total development time spent as a larva varies dramatically among species—and is highly temperature-dependent—at lower

Figure 2

(a) The duration of development for each stage varies depending on the lower developmental temperature (T_0, °C) and degree days required for development (G, °C-day) of each stage. We list developmental traits for eggs, larvae, and pupae, respectively, for (from left to right) three Lepidoptera: *Chilo auricilius* (T_0 = 12.9, 15.7, 14.1; G = 78.8, 473.5, 90.6), *Euzopherodes vapidella* (T_0 = 16.5, 5.1, 5.7; G = 42.2, 364.9, 176.0), *Spodoptera litura* (T_0 = 9.6, 10.3, 10.2; G = 57.7, 295.1, 161.8). **(b)** We depict how the proportion of development time spent as larvae varies as a function of temperature (°C). Each line represents a Lepidopteran population. The proportion of development time spent as larvae can either decrease or increase at low temperatures depending on the lower developmental temperature (T_0, °C) and degree days required for development (G) for each stage and population. The z value (color) indicates the deviation of larval T_0 from the T_0s for other stages [°, $z = T0_L - (T0_E + T0_P)/2$].

(but not higher) temperatures (Figure 2b). These onto-genetic differences can strongly impact seasonal life history patterns. For example in the tropical sugarcane stemborer, *Chilo auricilius* (Figure 2, left panel) [17], which has multiple generations per year, larval development times are 8–10 fold longer in the winter than in summer months, with important consequences for seasonal patterns of crop damage [13,15,18,19].

What about ontogenetic variation for other metrics of development rate and for other aspects of performance? The available databases on thermal sensitivity provide surprisingly limited information about variation across life stages [8,9,20]. For example, insect adult body sizes respond strongly to developmental temperature [21], but how life stages contribute to size differences has scarcely been considered. In comprehensive compilations

of data on insect upper thermal limits, less than 2% of species included estimates for both adult and juvenile stages [20,22]. A recent meta-analysis of lethal temperature thresholds for marine invertebrates documented that upper thermal limits increased during ontogeny, from embryos and larvae to juveniles and adults [23••], but comparable data and analyses are unavailable for insects or other terrestrial arthropods (see Ref. [24] for an excellent older review).

Fortunately, an increasing number of studies during the past decade explore this empirical issue [14,15,19, 23••,25–28,29••,30•,31,32•,33,34•,35•]. Multiple studies report differences in thermal tolerance between adults and embryos or larvae [31,32•,34•,35•]. However, ontogenetic changes in thermal sensitivity can be idiosyncratic. For example heat tolerance in the butterfly *Bicyclus anynana* increases with body size across life stages, with pupae and adults having greater tolerance than larvae, hatchlings, or eggs [32•]. In contrast heat tolerance in widow spiders decreases with body size, with adults having lower tolerance than juveniles or spiderlings [25]. Clearly more data will be required to identify general patterns of ontogenetic differences in thermal tolerance and sensitivity.

The mechanisms underlying ontogenetic variation in thermal tolerance also remain poorly understood [24]. In marine invertebrates, decreasing heat tolerance with increasing body size across life stages supports the hypothesis that oxygen limits heat tolerance of larger aquatic organisms [23••], and such effects also occur in aquatic insects [36]. However, oxygen availability is unlikely to play a similar role for heat tolerance in most terrestrial insects [37]. Klockmann *et al.* [32•,38] propose that heat tolerance will increase with increasing size as a result of allometric scaling, but this pattern does not appear to be general for insects. Several recent QTL studies with *Drosophila* show that heat tolerance and cold hardiness are polygenic traits in both larvae and adult with no significant genetic correlation across stages, supporting the hypothesis that thermal sensitivity is genetically decoupled across metamorphosis [28,29••]. Physiological and functional genetic analyses of thermal tolerance across insect life stages are sorely needed.

Temperature sensitivity of fitness components

For most insects, the duration of the juvenile (pre-adult) stages are much longer than the period of adult reproduction (some parthenogenetic and social insects are notable exceptions). Consequently it is often useful to define the key components of fitness in terms of the probability of survival to adulthood (S); adult fecundity or reproductive rate (F); and generation time (G), which primarily reflects the development time to the adult stage. The thermal sensitivity of different fitness components [39,40]
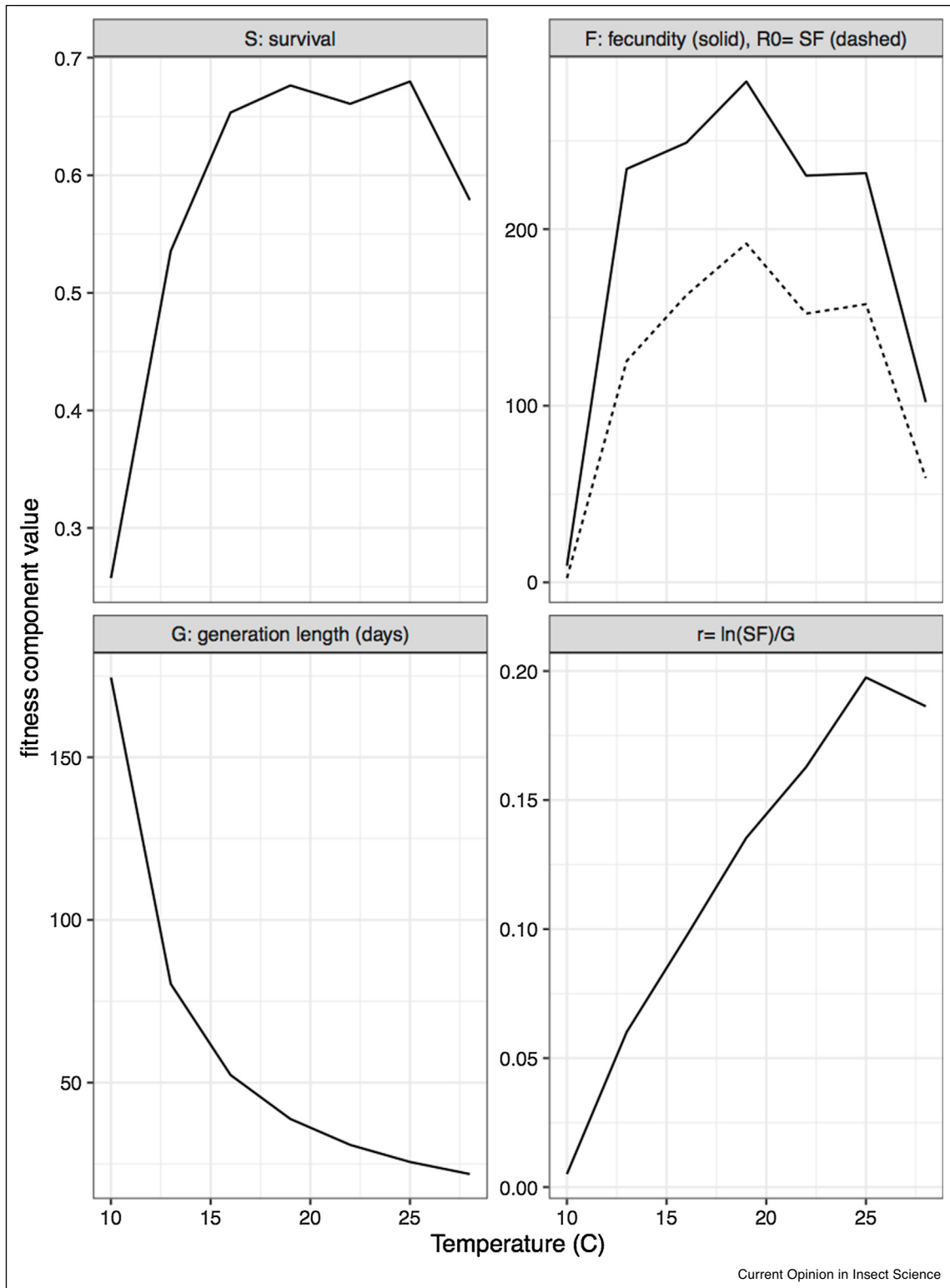
typically vary in characteristic ways (Figure 3) [41]. Survival to adulthood is high and relatively constant over a range of temperatures, and declines rapidly at lower and higher temperatures. Fecundity is highest at some intermediate optimal temperature, and declines at temperatures above and below the optimum. Generation time declines rapidly with increasing temperature, and approaches some minimum generation time at higher temperatures (and may also increase at stressfully high temperatures).

These fitness components combine to determine the thermal sensitivity (the TPC) for fitness. Two widely used metrics of fitness are the net reproductive rate, R_0 = SF; and the intrinsic rate of increase, $r = \ln(SF)/G$. R_0 is most appropriate for the case of distinct (non-overlapping) generations in discrete time, whereas r is most appropriate for the case of overlapping generations in continuous time [42]. The shapes of TPCs for R_0 and r differ markedly: the optimal temperature for R_0 occurs at intermediate temperatures and the performance curve is generally symmetric, whereas the optimal temperature for r occurs at higher temperatures and the curve is strongly skewed to the right (Figure 3) [40,42,43]. The thermal sensitivity of generation time determines the changes in skew and optimal temperature in r [44]. As a result the thermal sensitivity of fitness, and the relative importance of the thermal sensitivities of juvenile and adult fitness components, depends critically on whether the population has overlapping or non-overlapping generations (see next section).

Differences in TPCs among fitness components may result in part from differences in the timing and duration of temperature exposure during their measurement. For example, TPCs for *Manduca sexta* larval growth rates vary depending on the duration of exposure (developmental versus acute TPCs) and whether temperatures fluctuated [45]. Fitness components both respond to and are measured at different time scales: survival tends to be an acute response whereas development and fecundity are integrated responses over time [46]. The temporal dynamics of acclimation responses and performance detriments in response to thermal stress also differ across fitness components [26]. The timescale at which TPCs were measured accounted for more variation than that observed among fitness components for *Drosophila* [47••]. Models that account for different temporal dynamics may help resolve temporal issues in the application of TPCs [48] and will be essential to applying TPCs to accurately project fitness responses to variable and changing environments [49].

A well-known but ongoing challenge in characterizing TPCs is that the data for estimating such curves are often incomplete, especially at higher temperatures [7,40]. Even in exemplary studies—such as that illustrated in

Figure 3

Fitness components and fitness measures differentially vary across temperature for the artichoke moth, *Platyptilia carduidactyla*. Data from Ref. [41].

Figure 3 [41]—there is limited information to estimate how rapidly fitness declines toward zero at temperatures above the optimum, and which fitness components contribute to this decline. Experimental designs that concentrate measurements at higher temperatures, rather than evenly spaced temperatures across the temperature range as in most studies, may be more efficient at quantifying high temperature responses [50]. Such data are crucial for predicting how insects will respond to heat waves and other extreme climatic events.

Numerous studies have used TPCs to predict the population consequences of climate change for ectotherms [51–54], but a general theoretical framework to guide these efforts is generally lacking. The efforts of Amarasekare and collaborators are a notable exception [44]. Amarasekare and Savage [44] modeled age-structured population dynamics using the classic Euler-Lotka equation, incorporating the thermal sensitivity of each fitness component—rates of juvenile and adult mortality, of juvenile development, and of reproduction—to predict the TPC for fitness (r, the maximum rate of population increase). This approach provides a flexible and tractable framework for modeling the effects of temperature on fitness, and demonstrates how different features of the TPC emerge from the thermal sensitivities of the underlying fitness components. A similar approach can be used to explore how ontogenetic changes in thermal tolerance determine overall survival. For example, differences in the TPCs for stage-specific survival can generate complex and asymmetric TPCs for cumulative (egg-to-adult) survival [55]. These models have been extended to incorporate interspecific resource competition and thermal niche partitioning [56•], and phenological shifts and seasonal abundance of insects in response to climate change [57,58,59••]. We believe these studies provide a promising start towards a more general theoretical framework for understanding the ecological and evolutionary responses of ectotherms to thermal variation and climate change, and deserve further application and development.

Life cycles and the thermal sensitivity of fitness in seasonal environments

Most insects in temperate and higher latitude regions overwinter in a diapause or dormant state that occurs in a specific life stage, and many tropical and subtropical insects have an analogous aestivation or dormancy during the dry season. Diapause and aestivation reset the stage structure of insect populations at the return of the growing season each year. The effects of weather variation and climate change for seasonal phenology, and for phenological mismatches of insects with their resources and natural enemies, have been widely documented [53••,54]. For univoltine (one generation per year) populations, life stage and seasonal climate are predictably related, but this is not the case for multivoltine populations. For example, it is unclear how much of the ontogenetic

variation in T_0 (Figure 1) is associated with overwintering stage or voltinism; this warrants further study.

Seasonal climatic variation also has important implications for the thermal sensitivity of fitness in insect life cycles. The two most widely used metrics of fitness—net reproductive rate R_0 and intrinsic rate of increase r—differ strongly in their TPCs, particularly at higher temperatures (Figure 3). For univoltine populations R_0 is clearly appropriate, but multivoltine populations in seasonal environments rarely approach a stable age-distribution or stage-distribution—the key assumption in using r as a metric of fitness [60]. As a result, the appropriate metric of fitness, and the relative contributions of different components to overall fitness, will vary across seasons for many insects [61,62]. Individual-based models have been used to simulate seasonal population dynamics in particular study systems, but we believe that process-based population models that incorporate temperature dependence provide a promising framework for understanding and predicting phenology, population dynamics and fitness of insects [7,63••,64]. How best to incorporate demographic stochasticity (including partial generations) and environmental variation into such models remains an important challenge.

Conflict of interest statement
Nothing declared.

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