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Temperature-sensitive development shapes insect phenological responses to climate change

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Phenological shifts vary within and among insect species and locations based on exposure and sensitivity to climate change. Shifts in environmental conditions and seasonal constraints along elevation and latitudinal gradients can select for differences in temperature sensitivity that generate differential phenological shifts. I examine the phenological implications of observed variation in developmental traits. Coupling physiological and ecological insight to link the environmental sensitivity of development to phenology and fitness offers promise in understanding variable phenological response to climate change and their community and ecosystem implications. A key challenge in establishing these linkages is extrapolating controlled, laboratory experiments to temporally variable, natural environments. New lab and field experiments that incorporate realistic environmental variation are needed to test the extrapolations. Establishing the linkages can aid understanding and anticipating impacts of climate change on insects.

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Introduction

Butterfly monitoring data linking dramatic population declines in the Western US to late-season warming suggest the importance of considering how climate change alters phenology [1••]. Warming late-season temperatures can alter development rates and diapause energetics and induce physiological stress [1••,2]. Amidst the deluge of phenological observations addressing responses to climate change [3], studies of insects have the distinct advantage of their development and growth being highly temperature sensitive and well documented. Much of this owes to the relative ease of rearing insects in controlled laboratory conditions. The physiological and genetic mechanisms underlying temperature-sensitive development have recently been reviewed [4]. Although most populations and species advance phenology in response to climate warming, they exhibit considerable variability in advancements and some populations and species delay phenology with warming [5]. Here I review the potential to apply understanding of the temperature-sensitivity of insect development to account for variable phenological responses. I consider how interactions with microclimate and topography also contribute to the heterogenous responses [6].

I focus on life history differences across elevations and latitudes associated with season length. I explore the ramifications of the life history differences, including differential phenological shifts and altered community interactions. I aim to encourage both more consideration of the ecological implications of development and growth rates and the physiological mechanisms underlying phenology.

Several aspects of insect life history contribute to the variable phenological shifts. Many species undergo diapause, a physiologically controlled state of dormancy. Photoperiod (daylength) often interacts with temperature to cue development including the induction and termination of diapause [7]. Cues for diapause timing and other aspects of seasonal regulation can become suboptimal with climate warming [5]. Whether insects complete only a single generation each active season (univoltine) or have the potential to complete a variable number of generations (e.g. multivoltine) shapes the fitness consequences of phenology. While many multivoltine insect populations have been able to complete additional generations with advanced phenology [8], others face a developmental trap whereby they attempt but fail to complete additional generations [9]. Diapause, voltinism, and the thermal sensitivity of development interact, as has been demonstrated for Australian grasshoppers [10].

Insects shift phenology in response to both how much climate warming they experience and how sensitive they are to the warming. Both these factors interact with seasonal timing [11]. Phenological shifts can be more pronounced for species that develop more slowly and mature later in the season since they are exposed to a greater duration of warming. However, earlier season species can exhibit greater thermal plasticity in development, which allows responsiveness to variable early

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season conditions [12]. Early season species, which may also overwinter in more advanced developmental stages, often exhibit more pronounced phenological shifts [13]. However, a compilation of observations for univoltine butterflies suggests early season species delayed flight phenology and later-season species advanced flight phenology at high, northern latitudes [14]. Developmental plasticity tends to be particularly pronounced at high elevations and latitudes to ensure the completion of a generation within a short, temperature-limited growing season. Although warming generally accelerates development, developmental relaxation can occur for univoltine species in these systems as the duration of thermal opportunity expands with warming [15]. A study of mountain butterfly communities found that the phenological delay with cooler temperatures at higher elevation was less than expected for the majority of species, suggesting physiological differences between populations along the elevation gradient [16•]. The study also documented greater temperature sensitivity of development rate among early season species.

Another complication with interpreting phenological shifts is their potential to interact with range shifts in tracking environmental niches. Although 40% of butterfly and moth species in Finland shifted neither phenology nor distribution over 20–25 years of surveys, the 15% of species that exhibited both advanced flight phenology and a northern range shift were more likely to exhibit positive population growth [17••].

Characterizing the thermal sensitivity of development

A common and long-employed method for predicting insect phenology is estimating the accumulation of heat units (degree-days) [18]. The method assumes a constant development response to a heat unit, but can readily account for variability in heat unit accumulation over time. Linear regressions of developmental durations at several constant temperatures are used to estimate a lower thermal limit for development ($T_{0,}$ sometimes called lower developmental temperature, LDT) as well as to estimate the number of heat units required to complete development (G) [19,20]. Upper thermal limits on development are less often assessed. Developmental traits are available for thousands of insect populations and species [21] and some studies account for variation across developmental stages [22]. Insects tend to respond to limited thermal opportunity (e.g. at high latitude or altitudes) through reduced T_0. Sometimes G increases as well, reflecting a physiological tradeoff of more heat units required to complete development if development initiates at lower temperatures [23]. Development often occurs at cool, early season temperatures where thermal responses are typically linear, but increasingly developmental rate summations use thermal performance curves (TPCs) to account for non-linear thermal responses [18,24].

Physiological metrics of temperature sensitivity are often applied to investigate growth and development rates. Q10 indicates the ratio by which a 10-degree temperature increase shifts physiological rates [12]. A related approach, which accounts for non-linear thermal responses, uses the activation energies required for biochemical reactions and thermodynamics to estimate rates [25]. Insects in warmer, temporally constant environments generally mature faster and at smaller size than do those grown in cooler, constant environments. One prominent explanation for this temperature-size rule (TSR) is that increasing temperatures accelerate ectotherm development rate more than growth rate due to the thermal response of development rate having either a greater slope or temperature intercept [26]. In some insects, particularly univoltine insects in season-limited environments, the TSR is reversed [27]. The warm adaptation of physiological processes related to feeding in some insects may lead to greater increases in growth than development at warm temperatures [28].

Are development models relevant for variable, natural environments?

Fluctuating temperatures tend to accelerate development unless the fluctuations result in stressful temperatures [29]. The occurrence of warm temperatures in variable environments can accelerate development in cool environments but decelerate development in warm environments [30]. This observation is aligned with Jensen's Inequality, which points out that rates at mean temperatures deviate from mean rates at a sequence of temperatures due to non-linearities in temperature dependence [31]. Some studies suggest that integrating over temperature variation is sufficient to predict developmental rates [32•], but others suggest the need to consider carry-over effects (e.g. acclimation, stress) and other impacts of temporally variable temperatures. Fluctuating rearing temperatures can, for example, elevate optimal temperatures and maximal growth rate [30].

A field study across microhabitats for the butterfly *Pieris napi* indicated that development rates could be accurately predicted using data from constant temperature laboratory experiments, but suggests the importance of accounting for non-linearities [32•]. Another rearing experiment with sepsid flies suggest that TPCs from fixed temperatures accurately predicted development rates in variable conditions as long as temperatures never got below the critical minimum temperature [33]. But flies exposed to cold temperatures developed faster than predicted because they were able to continue growing or to accelerate development when temperatures warmed.

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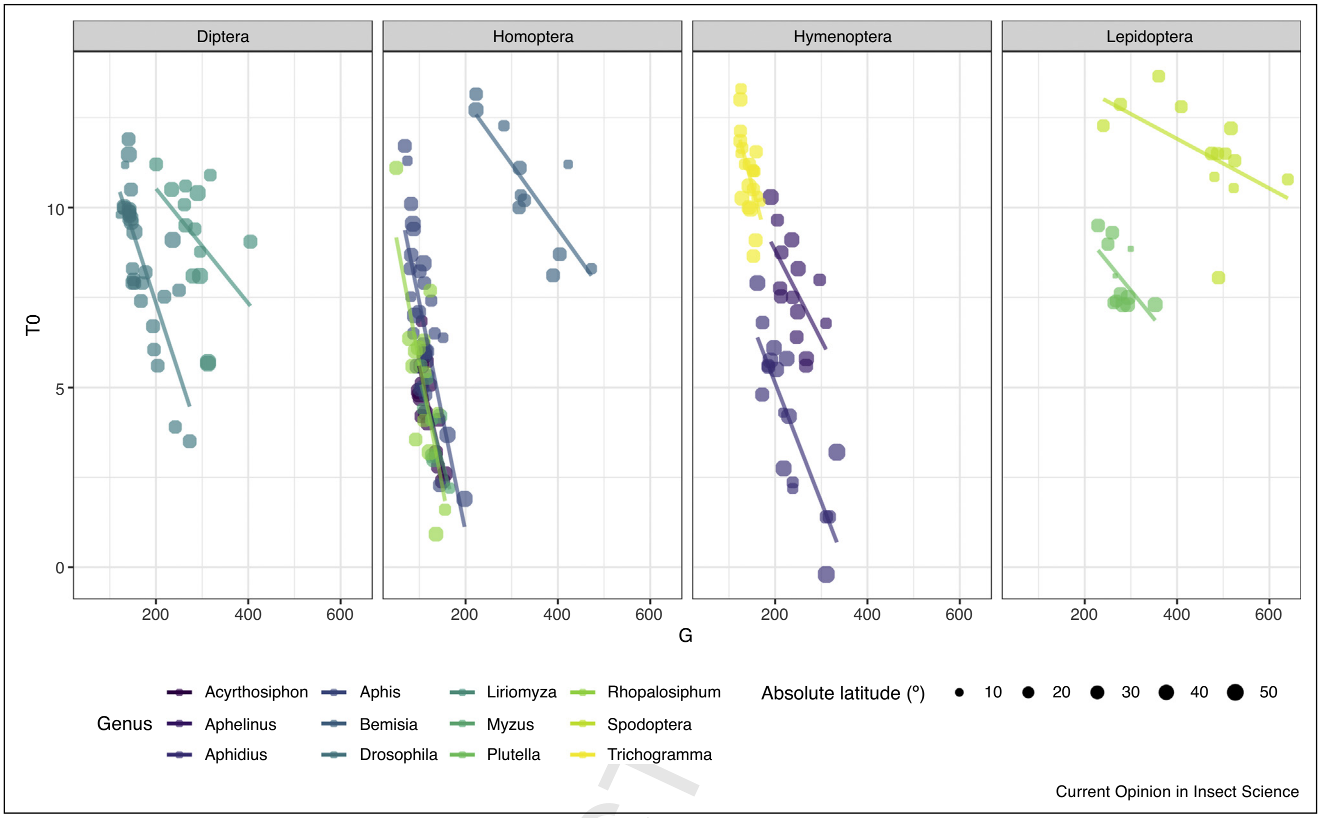
Figure 1



Lower thermal limits (T_0) are inversely related to the number of heat units required (G) for development across genera within four insect orders. Developmental traits are variable across latitude (symbol size).

Accurate predictions of development can require consideration of additional cues beyond just temperature. Photoperiod can cue acceleration or deceleration of development to ensure the completion of a seasonal generation or capitalization on permissive conditions, respectively. For example, damselfly populations accelerate development when reared under photoperiods indicative of seasonal-time constraints [34•].

Intra-specific and inter-specific patterns of thermal sensitivity

An analysis of developmental traits for 1037 populations of 678 insect species concentrated in six orders [21] indicated that T_0 decreases and G increases with increasing absolute latitude [23, see also Refs. 19,20]. An inverse relationship between T_0 and G, indicating more heat units required to complete development if development initiates at lower temperatures, was weak across the full data but apparent within orders. Here, I further explore how developmental traits vary among related species, and assess their capacity to account for phenological variation, by subsetting the database [23] to genera with data for at least 10 populations [methods follow 23 and are summarized in Appendix S1 (Supplementary material)]. T_0 strongly declines with increasing G within genera (Figure 1). Shifts in T_0 and G across absolute latitude are variable, but there is a significant interaction between G and latitude such that the decline in T_0 with increasing G is steeper for higher-latitude populations (Figure 2a, linear mixed effect model with genera as a random effect, ANOVA: G standardized coefficient = -0.54 ± 0.14 SE, $\chi^2 = 14.2$, $p < 0.001$; latitude standardized coefficient $= 0.09 \pm 0.08$ SE, $\chi^2 = 1.3$, $p = 0.25$; G × latitude standardized coefficient $= -0.29 \pm 0.13$ SE, $\chi^2 = 4.5$, $p = 0.03$). This is consistent with a stronger physiological tradeoff in cool, high-latitude environments.

Virtual 'reciprocal transplants' explore how intragenus variation in developmental traits influences phenology (Figure 2). I apply the model described above to estimate T_0 for populations at three northern latitudes (20, 35, 50°) requiring 150 and 350 heat units to complete development (G). The G range was selected to bound most data. I estimate T_0s varying from 6.0° to 5.8°C for $G = 150$ and 2.1° to 0.6°C for $G = 350$ at 20° and 50°, respectively (Figure 2a). Hourly interpolations of weather station data were used to estimate the accumulation of heat units and first-generation phenology based on T_0 and G (Appendix

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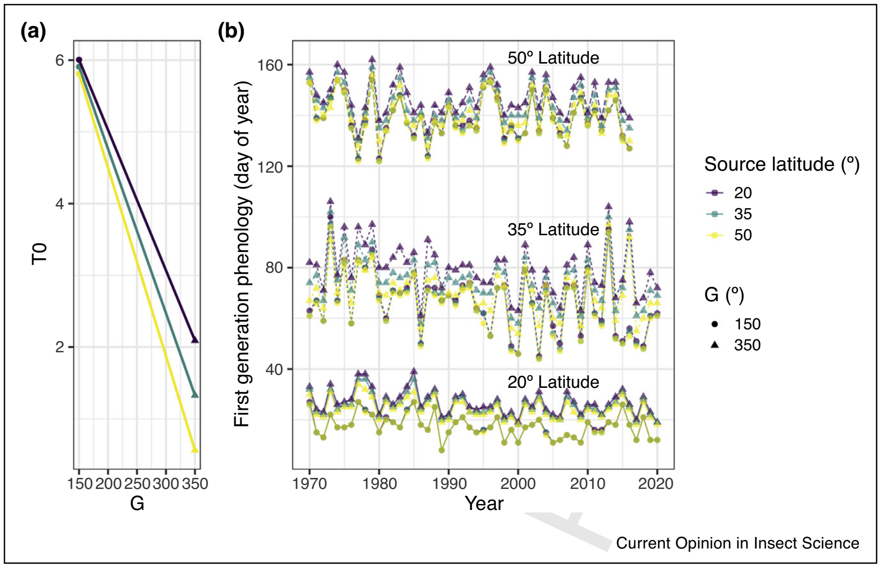
Figure 2



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(a) I use the model characterizing the data in Figure 1 to estimate T_0 at three source latitudes for insects that require $G = 150$ and 350° heat units. T_0 declines with increasing absolute latitude, with the decline more pronounced for larger G. **(b)** I conduct virtual 'reciprocal transplants' to predict the first generation phenology for insects with developmental traits corresponding to each point in (a) at each latitude. Fewer required heat units (symbols) and lower latitude thermal conditions (line types) accelerate projected phenology. Lower T_0s also accelerate phenology, with the variance being particularly apparent at $G = 350°$ given the substantial predicted variation in T_0.

S1 in Supplementary material). Lower G requirements accelerate development (Figure 2b). For higher G values and 'transplant' latitudes, lower T_0s associated with higher source latitudes accelerate development and the predicted phenology of the first generation (Figure 2b).

Although the phenology projections are for geographically disparate populations, differences in developmental traits that occur for populations along elevation gradients and between species within communities can produce divergent phenologies [12,35]. The significance of development trait differences for phenology depends on climate context (e.g. compare 'transplant' sites in Figure 2b). Developmental traits vary with seasonal timing, which can help explain variable phenological responses to warming among species with different seasonal timing [11,12].

Community implications of developmental differences

Species traits such as voltinism and diet specialization can influence whether species advance/delay or prolong/shorten activity periods, which can restructure communities and alter interactions [36]. Negative fitness impacts are anticipated when phenological mismatches occur among interacting species but evidence for such fitness detriments are mixed [37]. Differential shifts in the phenology of plants and their herbivores or pollinators have been prominently studied [38]. For example, bee emergence advances with warmer temperatures and earlier snowmelt whereas peak abundance and senescence was more influenced by functional traits including overwintering stage [39•]. Warmer season thus extended bee flight periods but flower phenology shifted less, indicating that climate warming may erode the synchrony of flowers and pollinators [39•] and thus ecosystem function.

Phenological shifts within communities tend to reduce synchrony, but dynamics including longer active periods can increase synchrony. For example, herbivory can induce early leafing phenology, but warming can counteract this strategy by advancing insect phenology [40]. Broader abundance distributions coupled with phenological advancements of later-season species increases phenological overlap among grasshopper species [41]. Increased phenological overlap corresponds to decreased abundance, particularly of later-season species, consistent with altered interactions such as resource competition [41]. Such examples highlight the need to consider full phenological distributions—not just emergence dates—when assessing shifts in phenological overlap with warming [42].

Conclusions

The pronounced temperature sensitivity of insect development and growth drive phenological shifts with climate warming. Well-established means of describing and measuring the temperature sensitivity of insect development

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and growth along with abundant existing measurements offer promise in understanding and predicting phenological responses to climate change. In particular, differences in environmental conditions and seasonal constraints along elevation and latitudinal gradients can be linked to differences in temperature sensitivity and development plasticity. These differences (along with variation in life history including seasonal timing, voltinism, overwintering stage, and diet breadth) often shape intra-specific and inter-specific variance in phenology and phenological shifts with implications for species interactions and community and ecosystem function. A crucially important, and oft omitted, step is linking shifts in phenology and phenological synchrony to changes in the vital rates that shape population dynamics [43••]. Establishing these linkages is central for understanding and anticipating ongoing, dramatic insect declines. Indeed, observations such as insect population declines being most pronounced in areas with substantial fall warming [1••] point to the importance of linking underlying physiological mechanisms, phenology, and demographic consequences.

Fully realizing this potential will require coupling physiological and ecological insight to determine how lab experiments can best be applied to variable, natural environments and to design new lab and field experiments that incorporate realistic environmental variation, including the interaction of multiple environmental drivers. Field experiments that examine fitness consequences are essential to understanding the implications of phenological shifts. For example, experimentally accelerating bee phenology increased fitness with survival increases outweighing a trade-off of decreased reproduction [44]. Incorporating realistic environmental variability and employing integrative approaches is increasingly important given increases in the incidence and severity of environmental extremes, which can substantially alter insect phenology with community and ecosystem consequences [45].

Conflict of interest statement

Nothing declared.

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[46,47].

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.cois.2022.100897.

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