Life cycle complexity drives variation in thermal tolerance and plasticity

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Keywords: Life history, Climate change, Metamorphosis, Developmental plasticity, Ontogeny, Microclimate, Upper thermal limits

Abstract

Accumulating evidence suggests that heat tolerance varies substantially across insect development, yet patterns of variation remain difficult to generalise across species. We discuss how the diversity of insect developmental strategies shapes both the intensity and predictability of thermal environments across ontogeny, and how this likely generates variation in heat tolerance, plasticity, and carry-over effects. We hypothesise that large developmental variation is expected in holometabolous insects, and in species undergoing pronounced microhabitat or diel activity transitions. These transitions can modify heat exposure, behavioural thermoregulatory abilities, and the physiological or genetic regulatory network underlying heat tolerance, weakening correlations among life stages. We discuss when carry-over effects are likely to be adaptive, highlighting the importance of environmental predictability, ecological similarity among stages, and the balance between heat injury and repair. We argue that an ontogenetic perspective capturing the microenvironmental conditions experienced by each life stage is essential for predicting insect vulnerability to extreme heat.

Introduction

Climate change is a dominant driver of global insect declines [1–4]. Because temperature governs nearly every aspect of insect physiology, ongoing climate warming and increasingly frequent and intense heat extremes are expected to accelerate insect declines [2,4]. Understanding why some species are more sensitive to heat stress than others, and predicting how warming will affect natural insect populations, remains a central challenge in global change biology.

Accumulating evidence indicates that heat tolerance–here defined as the likelihood that an organism approaches or exceeds its upper thermal limits–is not uniform across an insect's life cycle [5–8]. Developmental stages can differ markedly in their upper thermal limits and plasticity, reflecting stage-specific differences in morphology, physiology, mobility, and microhabitat use [9–11]. However, trends in heat tolerance variation among life stages remain difficult to generalise across insects. While some studies report higher sensitivity to heat stress in embryos or first larval instars (e.g., [12–15]), others identify heightened sensitivity during the pupal or adult stage (e.g., [15,16]). Developmental variation in heat tolerance within a species can also be comparable or greater in magnitude to differences among species [7].

Here, we provide a conceptual framework for how complex insect life cycles can result in life stages experiencing different levels of exposure to heat stress (i.e., different mean, variance and predictability) across development, and how this can lead to evolved differences in heat tolerance and plasticity within and across life stages. While some of these points have been discussed previously [5–8], we hope to highlight recent case studies that add to these discussions.

Box 1. Plasticity within and across life stages

Insects differ widely in how they experience thermal environments across their life cycle, creating variation in the opportunities for selection on heat tolerance and plasticity [17]. Plasticity—the ability of an organism to modify its phenotype in response to environmental conditions—is itself an evolvable trait and may occur within life stages (e.g., hardening, acclimation), across successive life stages (developmental acclimation), or across generations [18–20]. Carry-over effects describe the persistence of environmental effects across life stages and can lead to transgenerational effects; however, we focus here on carry-over effects across life stages.

Theoretical models predict that selection for high, canalised heat tolerance should be favoured when organisms are frequently exposed to temperatures approaching physiological limits, whereas plasticity should be favoured in environments that are variable but predictable (i.e., high temporal autocorrelation; [21,22]) and when the costs of plasticity are low [23,24]. With respect to insect life cycles, stages that are most consistently exposed to extreme heat should evolve higher heat tolerance, while stages experiencing variable, predictable thermal variation should exhibit greater within-stage plasticity. Plasticity can be reversible or irreversible, depending on the underlying physiological mechanisms and the predictability of environmental conditions. Reversible plasticity is expected to be favoured in stages experiencing short-term or fluctuating conditions, and irreversible, developmentally fixed plasticity favoured when conditions are stable and predictable across life stages [18,23,24]. When thermal environments differ substantially between stages (e.g., due to shifts in microhabitat, behaviour, or timing of exposures), developmental plasticity may be of limited value and even hamper evolutionary responses [25].

Life-cycle complexity can shape the dynamics of heat stress responses by influencing both the thermal variability experienced within stages and the continuity of conditions experienced across stages. Longer-lasting stages, or stages that are exposed to seasonal variation, often experience a broader range of temperatures, increasing opportunities for reversible acclimation. In contrast, short-lasting stages or those confined to narrow seasonal windows may experience limited thermal variation and predictability promoting canalisation of thermal traits. Phenology and voltinism is also an important driver of thermal exposure. For instance, eggs, larvae and adults may occur across distinct seasons, particularly for uni- and bi-voltine species, meaning not all life stages may be exposed to heat extremes. In contrast, in multivoltine species, all life stages may occur within the same season, effectively spreading heat stress and selection for heat tolerance across development, although different stages may nonetheless experience different microclimates.

Behavioural thermoregulatory abilities also play an important role in modulating the magnitude and predictability of experienced thermal conditions across life stages. Mobile stages, such as flying adults, may have more opportunities to escape heat extremes, weakening selection for high heat tolerance and plasticity (i.e., Bogert effect [26,27]). In contrast, immobile stages, such as embryos and pupae, are forced to cope with local microenvironmental conditions, which can generate strong selection for high heat tolerance and plasticity in microsites exposed to high thermal variability.

This framework predicts that different insect life cycles, by shaping the timing, duration, variability, and predictability of heat exposure, will determine whether selection favours canalised heat tolerance, reversible within-stage plasticity, or adaptive carry-over effects across life stages (Fig. 1).

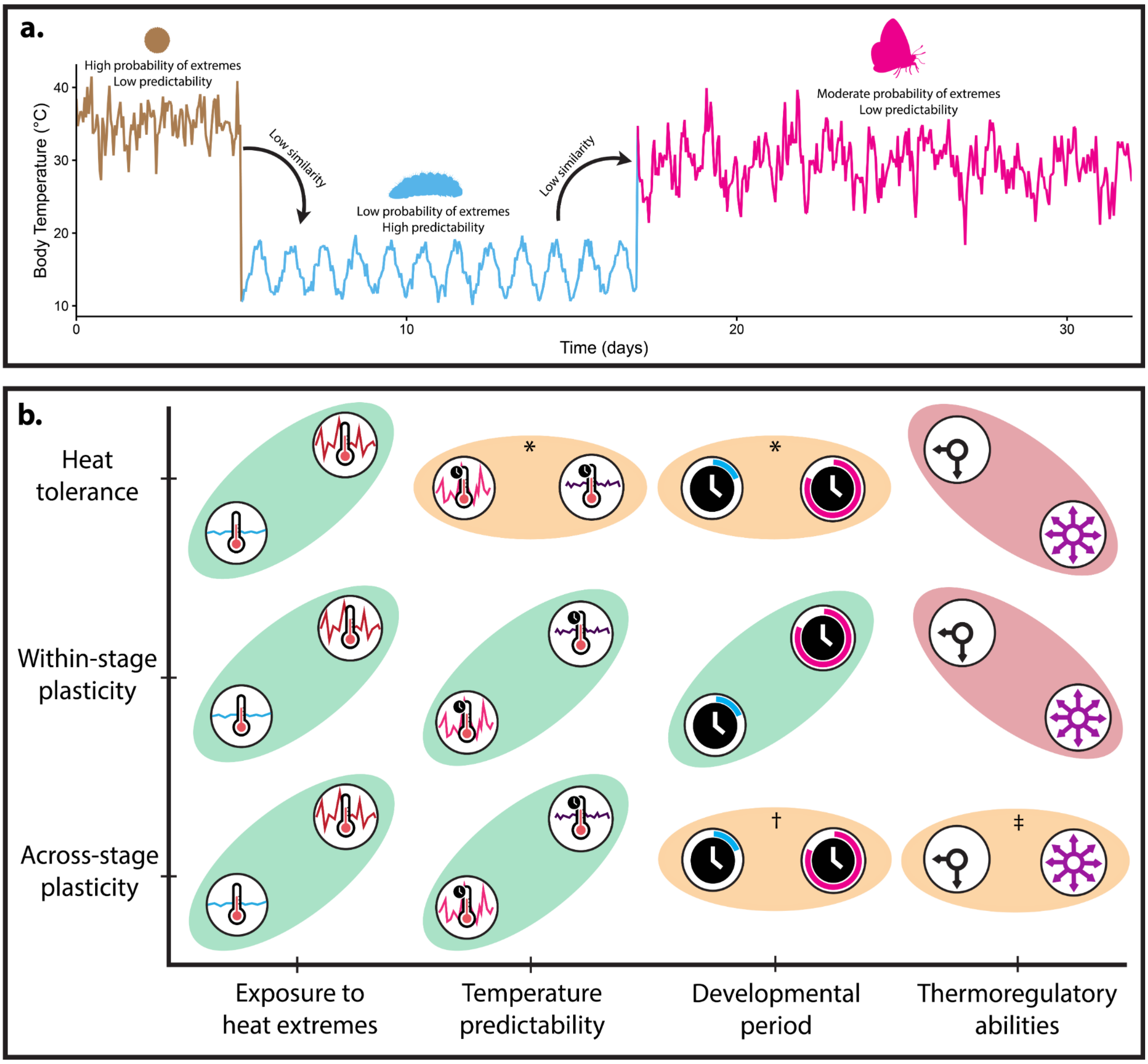

Fig. 1 | Conceptual predictions for variation in heat tolerance and plasticity within and across life stages. (a.) Example of variation in thermal exposure across the life cycle of a holometabolous insect. Displayed are simulated data varying in mean temperature, variance, and predictability among life stages, resulting in differences in ecological similarity between life stages. **(b.)** Conceptual predictions. Green ellipses indicate positive associations between factors, red ellipses indicate negative associations, and orange ellipses denote context-dependent responses. For example, high temperature predictability or short developmental windows are not necessarily associated with high heat tolerance if operative body temperatures do not approach tolerance limits (*). Similarly, whether developmental plasticity carries over across life stages depends on variation in developmental periods (†) and thermoregulatory abilities (‡) among stages, and which stages are compared.

Complex life cycles promote variation in heat tolerance and plasticity

Holometaboly and hemimetaboly

Holometabolous insects undergo complete metamorphosis, whereas hemimetabolous juveniles resemble small adults and lack a pupal stage (Fig. 2). Given that microclimatic conditions can differ substantially between life stages and be less predictable in holometabolous insects, we predict differences in heat tolerance and plasticity between life stages to be more common. There is some evidence to support this hypothesis. In the moth *Manduca sexta*, for example, larvae experience more variable temperatures and lower humidity than eggs or pupae and thus have higher heat tolerance [6]. In another study, pupae of the butterfly *Bicyclus anynana* exhibit high heat tolerance compared to eggs, consistent with their development within the humid, thermally buffered boundary layer of plant leaves [12]. In contrast, hemimetabolous insects typically maintain similar microhabitats and activity patterns across juvenile and adult stages, with the embryonic stage being the main exception. This continuity in microclimatic niche is accompanied by more gradual changes in body size across development compared with holometabolous insects. Because surface area-to-volume ratio strongly influences rates of water loss and heat exchange, these smaller size transitions are expected to generate more modest shifts in heat tolerance across life stages. Nevertheless, body size can also shape heat tolerance within holometabolous insects even when microclimatic niches remain similar, such as across larval instars, due to variation in body size [12].

A recent meta-analysis has also found greater plasticity early in life, and in hemimetabolous insects relative to holometabolous insects [28]. These patterns are consistent with the idea that environmental cues are more predictable in hemimetabolous taxa, potentially favouring the adaptive value of developmental carry-over effects (Fig. 2). These patterns are also likely explained by the strong asymmetry in life-stage developmental periods in holometabolous insects. Short stages, such as eggs and pupae, are likely to experience a narrower range of operative temperatures than the longer larval stage, which can contribute to differences in plasticity across stages. Nonetheless, developmental carry-over effects have been documented in holometabolous insects [29–31], suggesting that metamorphosis does not universally preclude their occurrence. Evidence for greater plasticity in thermal limits early in life [28] is also consistent with stronger selection for within-stage plasticity in stages with limited opportunities for behavioural thermoregulation. However, empirical evidence for the Bogert effect remains mixed (e.g., [27,32,33]), potentially because microclimatic variation at biologically relevant scales for each life stage is difficult to quantify [34]. For instance, cryptic thermal variation at the scale of a single leaf can strongly influence the thermal limits of herbivorous insects [35], and mothers may oviposit in microhabitats that are buffered from large environmental fluctuations [36]. Ultimately, predicting variation in heat tolerance and plasticity requires an understanding of the operative body temperatures experienced by each life stage.

Crucially, physiological or genetic regulatory networks underlying heat tolerance and plasticity can also be decoupled among life stages, especially in holometabolous insects [5,37,38]. Experimental evolution studies have demonstrated that selection on heat tolerance in one life stage does not often result in correlated increases in tolerance in other stages, suggesting partial independence in the underlying physiological or genetic regulatory network [39]. This decoupling likely reflects the extensive metamorphic reorganisation characteristic of holometabolous development, as well as systematic differences in thermal exposure and selective pressures across life stages. These findings call for an ontogenetic perspective in comparative and evolutionary studies of insect sensitivity to heat stress, particularly in holometabolous taxa where life-stage transitions are most pronounced.

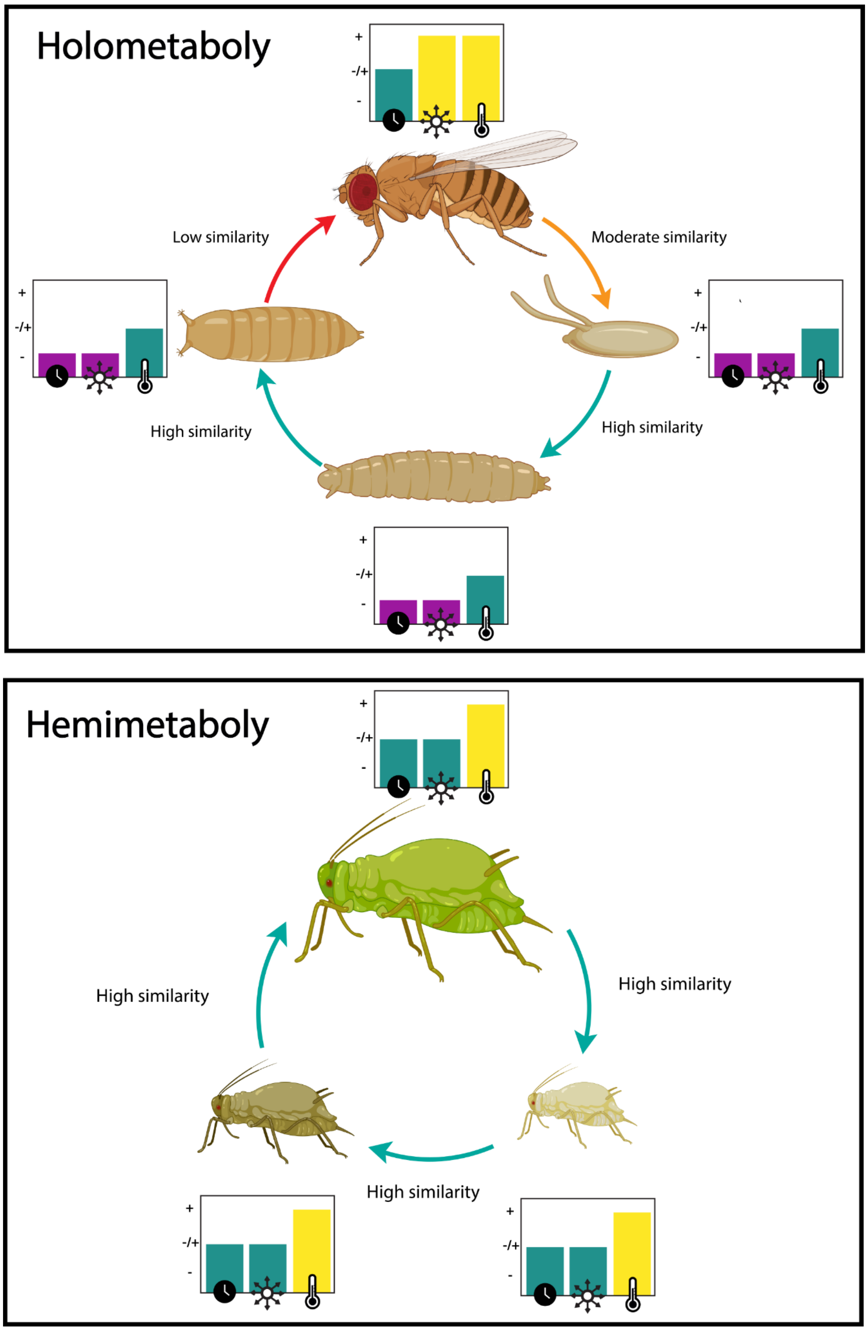

Fig. 2 | Example of variation in heat stress exposure among life stages in holometabolous and hemimetabolous insects. Vinegar flies (*Drosophila melanogaster*) and green peach aphids (*Myzus persicae*) are used as examples of holometabolous and hemimetabolous insects, respectively. Note that only the summer cycle of the green peach aphid is presented here. Variation in developmental periods, thermoregulatory abilities, and exposure to heat extremes (left to right) is presented relative to other life stages with three values: low (-), moderate (+/-), and high (+). Arrows connecting different life stages represent the degree of ecological similarity among life stages, which is expected to generate developmental variation in heat tolerance and plasticity. Species icons were taken from BioRender.

Microhabitat transitions

Many insects experience pronounced microhabitat transitions across their life cycle, generating substantial differences in thermal exposure across life stages (Fig. 3). Aquatic–terrestrial transitions are a clear example of developmental habitat transitions. In dragonflies and damselflies, for instance, early-life stages develop in aquatic habitats, while adults emerge into far more variable terrestrial conditions. Similarly, many insects develop as larvae in thermally stable microhabitats, such as soil (e.g., cicadas, ground beetles) or plant tissues (e.g., leaf miners, borers), before emerging as adults into microhabitats with larger environmental heterogeneity [40]. In addition, transitions to flying adult stages can also have a pronounced influence on thermal exposure. Apterous or weakly mobile larvae are often constrained to local thermal conditions, whereas flying adults can behaviourally thermoregulate by selecting favourable microclimates.

Taken together, differences in microhabitats across life stages can substantially dampen or exacerbate exposure to thermal extremes and thermoregulatory abilities, which is likely to influence selection on heat tolerance and plasticity (Fig. 3). There is evidence for lower heat tolerance in thermally buffered (wood-boring or subterranean) larvae relative to flying adults, resulting in lower thermal safety margins [41,42]. However, broad-scale analyses report heterogeneous results regarding differences in thermal plasticity between aquatic and terrestrial insects, suggesting greater plasticity in heat tolerance in aquatic invertebrates [32,43], or little difference between habitats across insects [28]. Nevertheless, within-species comparisons across life stages transitioning to different microhabitats remain largely untested, and it is an interesting avenue for future comparative research. While it will be challenging for some species, we need more studies that characterise the microclimates experienced by different life stages to determine if variation in plastic responses and heat tolerance match theoretical expectations (Fig. 1).

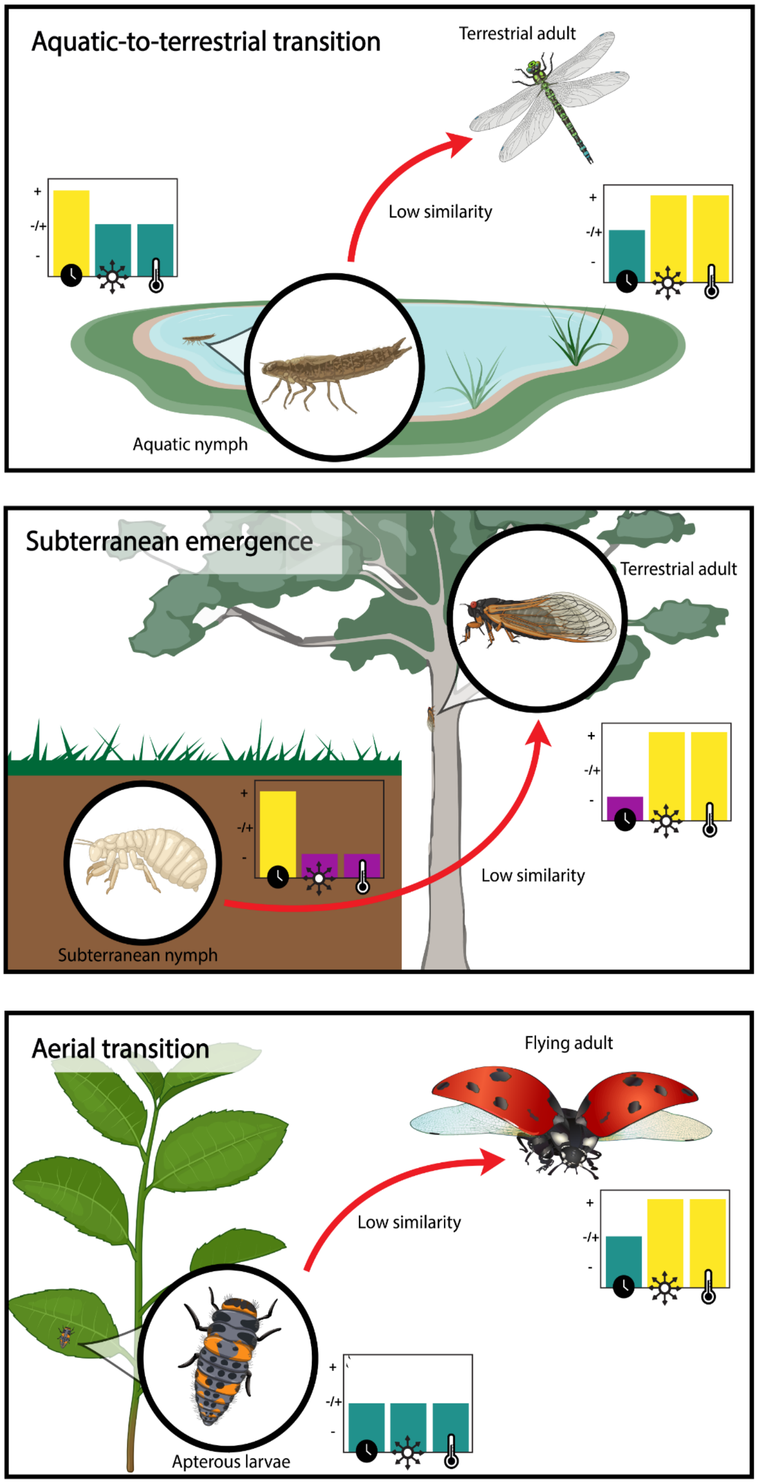

Fig. 3 | Example of variation in heat stress exposure among life stages of insects with major microhabitat transitions. Mosaic darner dragonflies (*Aeshna sp.*), periodical cicadas (*Magicicada sp.*), and harlequin ladybirds (*Harmonia sp.*) are used as examples of insects experiencing aquatic-to-terrestrial transitions, subterranean emergence, and aerial transitions across their life cycle, respectively. Variation in developmental periods, thermoregulatory abilities, and exposure to heat extremes (left to right) is presented relative to other life stages with three values: low (-), moderate (+/-), and high (+). Red arrows connecting different life stages represent a low degree of ecological similarity among life stages, which is expected to generate developmental variation in heat tolerance and plasticity. Species icons were taken from BioRender.

Shifts in diel activity

Transitions between diurnal, crepuscular, and nocturnal activity are common across insect life cycles and can substantially alter thermal exposure across development (Fig. 4). For example, larvae of many insect species are predominantly nocturnal (e.g., butterflies) or remain concealed during the day within soil (e.g., cicadas), plant (e.g., seed beetles), or host tissues (e.g., parasitoids), whereas adults are often active during the day. In other cases, larvae can develop under cathemeral (i.e., day and night activity) thermal regimes, while adults shift their activity to crepuscular or nocturnal periods (e.g., moths, mosquitoes), reducing exposure to daytime heat extremes. Such shifts can modify not only the mean temperatures experienced, but also the amplitude and predictability of thermal variation across life stages (Fig. 4). Therefore, transitions in diel activity are expected to influence selection on heat tolerance and plasticity.

Diurnal stages are more likely to experience frequent exposure to high and variable temperatures, potentially favouring increased heat tolerance, whereas nocturnal stages typically encounter cooler and more stable thermal conditions, suggesting lower heat tolerance and plasticity in tolerance. As with microhabitat transitions (see section above), diel shifts are associated with unreliable environmental cues across development and may generate stage-specific heat tolerances that are only weakly correlated. This is evidenced in the fall armyworm, for instance, where 45 °C kills the majority (>80%) of nocturnal adults but does not influence the survival of cathemeral larvae [44]. In addition, adults have an ~ 4°C lower CT_{max} than first-instar larvae [45]. Similar conclusions have been reached when comparing nocturnal and diurnal bee species [46]. Despite their potential importance, diel activity patterns are not always incorporated into comparative analyses of heat tolerance (but see [47–49]), and may represent an underexplored axis through which life-history complexity shapes insect responses to climate change.

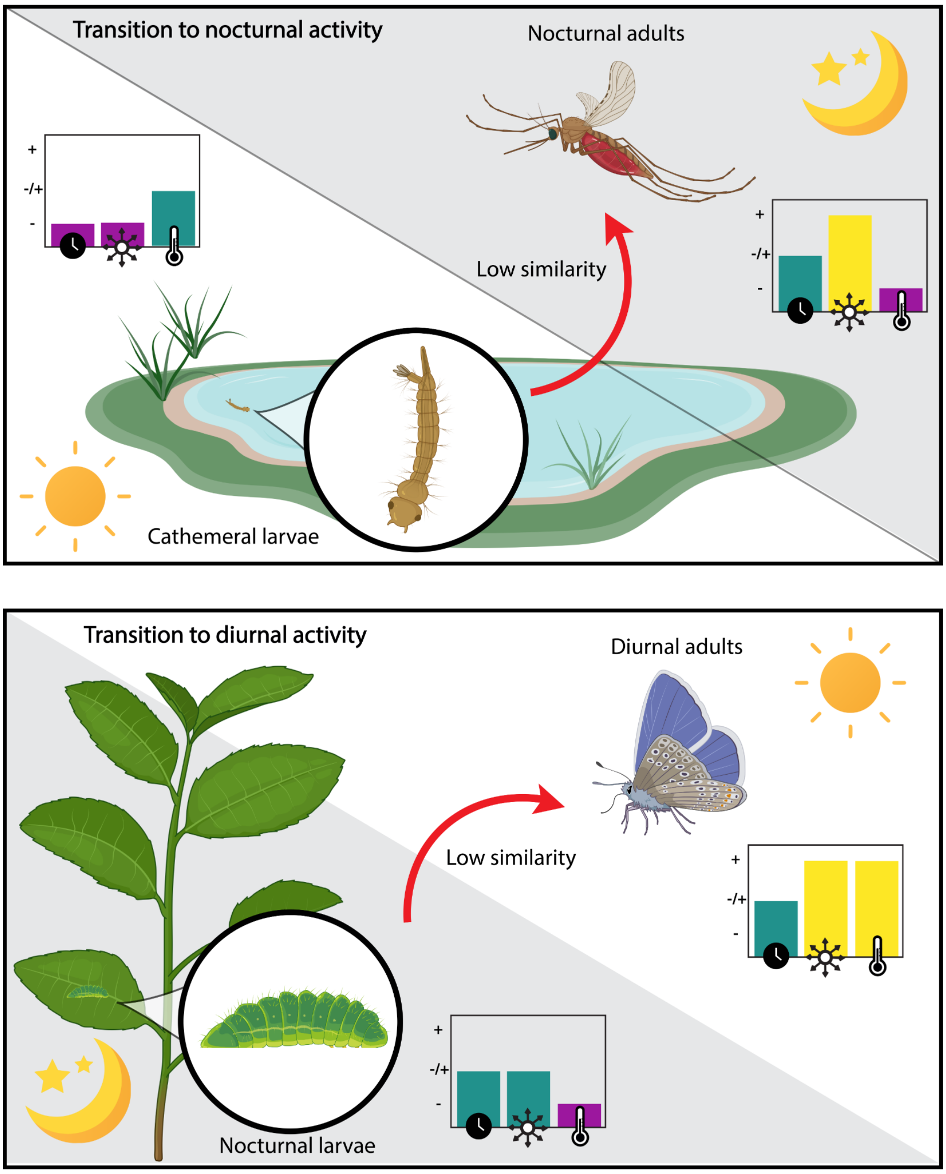

Fig. 4 | Example of variation in heat stress exposure among life stages of insects with diel activity transitions. Anopheles mosquitoes (*Anopheles sp.*) and common blue butterflies (*Polyommatus sp.*) are used as examples of insects experiencing shifts to nocturnal and diurnal activity across their life cycle, respectively. Variation in developmental periods, thermoregulatory abilities, and exposure to heat extremes (left to right) is presented relative to other life stages with three values: low (-), moderate (+/-), and high (+). Red arrows connecting different life stages represent a low degree of ecological similarity among life stages, which is expected to generate developmental variation in heat tolerance and plasticity. Species icons were taken from BioRender.

Complex life cycles

The developmental strategies highlighted above are not mutually exclusive, and some insects exhibit multiple key transitions across their life cycle. Mosquitoes, for example, experience complete metamorphosis with pronounced shifts in both microhabitat (aquatic larvae vs. terrestrial flying adults) and diel activity (cathemeral larvae vs. crepuscular or nocturnal adults). Such combinations are expected to amplify ontogenetic differences in heat tolerance and potentially weaken the adaptive benefits of carry-over effects across life stages. For example, Orlinick and colleagues [50], recently showed that *Aedes albopictus* diurnal and aquatic larvae have a much higher CTmax than nocturnal, flying adults (ΔCTmax ranging from 5.6 to 8.4°C). In contrast, a recent study in three hemimetabolous aphid species found a much smaller range of CTmax variation across life stages (ΔCTmax = 0.49-0.79°C)[51]. Heat tolerance in adult *Culex pipiens* is also influenced primarily by adult thermal acclimation, with comparatively weak effects of larval conditions [52]. This pattern is consistent with the idea that temperatures experienced during the aquatic larval stage provide an unreliable cue of the thermal conditions encountered by flying adults, limiting the adaptive value of carry-over effects across life stages. Therefore, the degree of ecological similarity among life stages is predicted to be a key determinant of heat tolerance (de)coupling across development.

Future directions

Although an increasing number of studies demonstrate that insects vary in their heat tolerance and plasticity across life stages, most comparative datasets remain heavily biased towards a single or a few life stages. For example, fewer than 2% of species included in large thermal tolerance compilations, such as GlobTherm [53], have data for both juvenile and adult stages [7]. Embryonic stages are particularly underrepresented, accounting for less than 10% of empirical studies in conservation physiology [54], which likely reflects the logistical challenges of working with small, fragile, and rapidly developing eggs. Predicting population-level responses to climate warming will require addressing these gaps through within-species comparisons of heat tolerance and plasticity across life stages.

Predicting the impacts of changing temperatures will also require knowledge of the interplay between thermal damage and repair across all life stages [55,56]. When temperatures fall within the “stressful range” (*sensu* [57]), where damage accumulates faster than repair mechanisms can compensate, developmental exposure may impair heat tolerance, reduce plasticity, or generate latent fitness costs across life stages. This was elegantly shown in flour beetles, where effects on male fertility were most pronounced when heat waves were experienced during the pupal or juvenile stages [16]. Similarly, cold temperatures experienced during the larval stage are most detrimental to female fecundity in seed beetles [58]. In contrast, adult heat stress has more pronounced impacts on fertility than developmental warming in *Drosophila melanogaster*, because different life stages may also vary in their ability to tolerate different durations of heat stress or repair physiological damage [59]. However, these apparent “carry-over effects” may instead reflect stage-specific heat sensitivity of reproductive processes. For example, in many insects, spermatogenesis begins during larval or pupal stages, which may be more heat-sensitive than mature sperm, generating delayed impacts on fertility even when stress exposure precedes adulthood [60]. Understanding the physiological mechanisms driving variation in heat tolerance and plasticity across life stages is an important avenue for future research.

Characterising the microenvironments experienced by different life stages, and how these will change in the future, should also be a research priority. Microclimates can vary dramatically at fine spatial scales–even within a single leaf [35]–and these differences can translate into substantial variation in thermal exposure across development [34,61]. In addition, microclimate exposure is expected to vary with insect phenology and life-history traits [62]. Notably, winter warming during diapause can induce strong carry-over effects depending on the life stage overwintering, though this remains rarely studied [63,64]. How voltinism influences variation in heat tolerance across life-stages is not well explored. Although studies in univoltine butterflies suggest that voltinism, through its effects on the timing of thermal exposure during development, is critical in shaping body size, timing of emergence, and range shifts [65,66]. The dynamics of thermal acclimation and hardening are also important to consider at fine temporal resolutions. Changes in thermal tolerance can occur within hours in the wild and should be considered [67]. Fine temporal and spatial measurements of the microclimates experienced by each life stage, and how to quantify their influence on phenotypes (e.g., intensity, predictability [22]) will therefore be critical for linking observed heat tolerance, plasticity, and climate vulnerability [34].

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This systematic review demonstrates a pronounced bias in research towards adult life stages with embryos, larvae and juveniles being underrepresented (embryos 8-9% and juveniles 29% of studies), with insects making up 19% of studies reviewed.

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This review paper describes how to model thermal load sensitivity across animals and plants. It emphasises the need to incorporate an understanding of thermal exposure and the differing sensitivities of organisms and tissues to predict lethal and sub-lethal impacts of temperature. It describes how thermal load is a balance between damage and repair to physiological processes and presents an updated thermal load sensitivity model with repair incorporated.

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This study uses aphids to show that rates of damage and repair in response to heat stress impact fecundity and development through time. Experiments demonstrate that temperatures above Topt, with limited opportunities for recovery, decrease fitness. Models incorporating recovery better match experimental results and findings largely support other studies showing that increased nighttime temperatures above Topt compromise fitness by limiting opportunities for recovery.

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This study develops a quantitative model to explain diapause and uses the butterfly, *Pieris napi*, to validate the model. They show that diapause termination and post-diapause development in *P. napi* are directly sequential with different thermal maxima – diapause has maximal rates at low temperatures, whereas post diapause maxima are higher temperatures – allowing predictions of when diapause ends and how fast development proceeds post-diapause.

** **64. Nufio CR, Sheffer MM, Smith JM, Troutman MT, Bawa SJ, Taylor ED, Schoville SD, Williams CM, Buckley LB: Insect size responses to climate change vary across elevations according to seasonal timing. *PLOS Biol* 2025, 23:e3002805.**

This study leverages long-term data for six montane grasshoppers species along an altitudinal gradient to show: 1) size shifts have occurred based on elevation and species seasonal timing of development since the 1960s; 2) Size shifts have been greater for species at low elevations with early emerging species (overwintering as juveniles) increasing in size whereas the opposite is true for late emerging species and 3) interannual variation in temperature accounts for size shifts. Results suggest early season species can take advantage of warming conditions to accelerate growth whereas late emerging species experience sub-optimal temperatures which slow growth.

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This study highlights the importance of rapid plastic responses in thermal tolerance in an Arctic insect (the seed bug). Notably, recent thermal exposure, within just a few hours, affected both heat and cold tolerance in the field. Transcriptional responses were also highly sensitive to daily temperature fluctuations, with warmer conditions driving the largest shifts in gene expression and overall transcriptomic profiles.

Acknowledgements

PP was supported by a Wenner-Gren Stiftelserna postdoctoral fellowship (UPD2024-0239). During the preparation of this manuscript, PP used ChatGPT 5.2 to improve the clarity and grammar of some sentences. The authors reviewed and edited the content as needed and take full responsibility for the content of the published article. We thank Carmen Da Silva, Sarah Diamond, Ryan Martin, and Mike Moore for the invitation to contribute this manuscript.

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Conceptualization: All authors

Visualization: PP

Writing – Original Draft: PP

Writing – Review & Editing: All authors

Project administration: PP