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Survive a Warming Climate: Insect Responses to Extreme High Temperatures

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Abstract

Global change includes a substantial increase in the frequency and intensity of extreme high temperatures (EHTs), which influence insects at almost all levels. The number of studies showing the ecological importance of EHTs has risen in recent years, but the knowledge is rather dispersed in the contemporary literature. In this article, we review the biological and ecological effects of EHTs actually experienced in the field, i.e., when coupled to fluctuating thermal regimes. First, we characterize EHTs in the field. Then, we summarize the impacts of EHTs on insects at various levels and the processes allowing insects to buffer EHTs. Finally, we argue that the mechanisms leading to positive or negative impacts of EHTs on insects can only be resolved from integrative approaches considering natural thermal regimes. Thermal extremes, perhaps more than the gradual increase in mean temperature, drive insect responses to climate change, with crucial impacts on pest management and biodiversity conservation.

1. INTRODUCTION

Temperature varies across temporal and spatial scales in terrestrial and aquatic ecosystems (66, 121). Most insect species experience thermal fluctuations that can involve sublethal or lethal extreme high temperatures (EHTs), which affect physiological processes (40) and ecological systems (35). Frequent EHTs may even lead to adaptive evolution in insects (66). For decades, however, most studies concerning thermal effects on insects concentrated on the response to mean temperature or to fluctuations within the tolerable range while ignoring variations in the characteristics of EHTs (91, 108). Recently, researchers have realized the biological and ecological importance of fluctuating temperature regimes, but little attention has been paid to the impacts of ecologically relevant EHTs (17).

Global climate change includes a substantial increase in the occurrence of EHTs (1, 61), and this increase will continue in the near future (99). By contrast, the occurrence of cold extremes (cold spells, cold nights) is largely decreasing (1, 35). Thus, in a warming world, insects will be challenged mostly by elevated body temperatures (66). Neglecting daily temperature extremes generates inaccurate predictions when modeling the impacts of climate warming on populations (91). The key role of EHTs in the response of insects to warming is now attracting more attention, and there is an urgent need to synthesize the disparate works. In this review, we provide an overview of how natural EHTs impact insect performance at individual, population, and community levels by demonstrating that EHTs are filtered by microhabitats and buffered by insects through behavioral thermoregulation, phenotypic plasticity (e.g., acclimation), ontogenetic variation, adaptive evolution, and the resilience of their network (**Figure 1**). Our synthesis complements previous works that focused on the effects of low temperatures (130), or on an increase in mean temperature (124) and fluctuation regimes (27), to finally provide a comprehensive understanding of the impact of climate change on insects. This review, together with recent work on other animal taxa (98, 131, 134), provides an integrated overview of the impacts of EHTs on the biosphere in the context of ongoing climate change.

2. HOW DO WE CHARACTERIZE THERMAL EXTREMES?

2.1. Definition and Description of Extreme High Temperatures

Until recently, no unified definition of EHTs existed in an environmental perspective. Meteorologists define EHTs as the temperatures above a given percentile (e.g., the 90th, 95th, or 99th percentile) of temperature distributions (1, 61), and similar indices are used by ecologists (17). The definition of EHTs can also be based on their societal impacts. The historical heat wave that hit Europe in 2003 is often used as a reference (9). Finally, another definition, from biology, is environmental temperature exceeding upper physiological thresholds of focal organisms (99). Overall, a hybrid definition for EHTs corresponds to an episode where temperature or temperature-driven conditions trigger a threshold-like biological response. While the impact of EHTs is often expected to be negative (6), we argue that this definition of EHTs should include the possibility for positive effects to better integrate EHTs into the whole complexity of living systems, in which species-, stage- and trait-dependent thermal responses in various seasons and geographic sites are characterized (91, 94, 151, 152, 155).

The variables used to characterize EHTs vary widely among studies, resulting in difficulties in directly comparing their results. Most studies on EHTs are opportunistic and usually lack replication (132). Controlled field experiments often simulate a single level of a given climate extreme imposed at a small spatial scale (132). The lack of a clear description of characteristics of EHTs limits our understanding of how such irregular EHTs affect biological systems (47, 89, 94, 127).

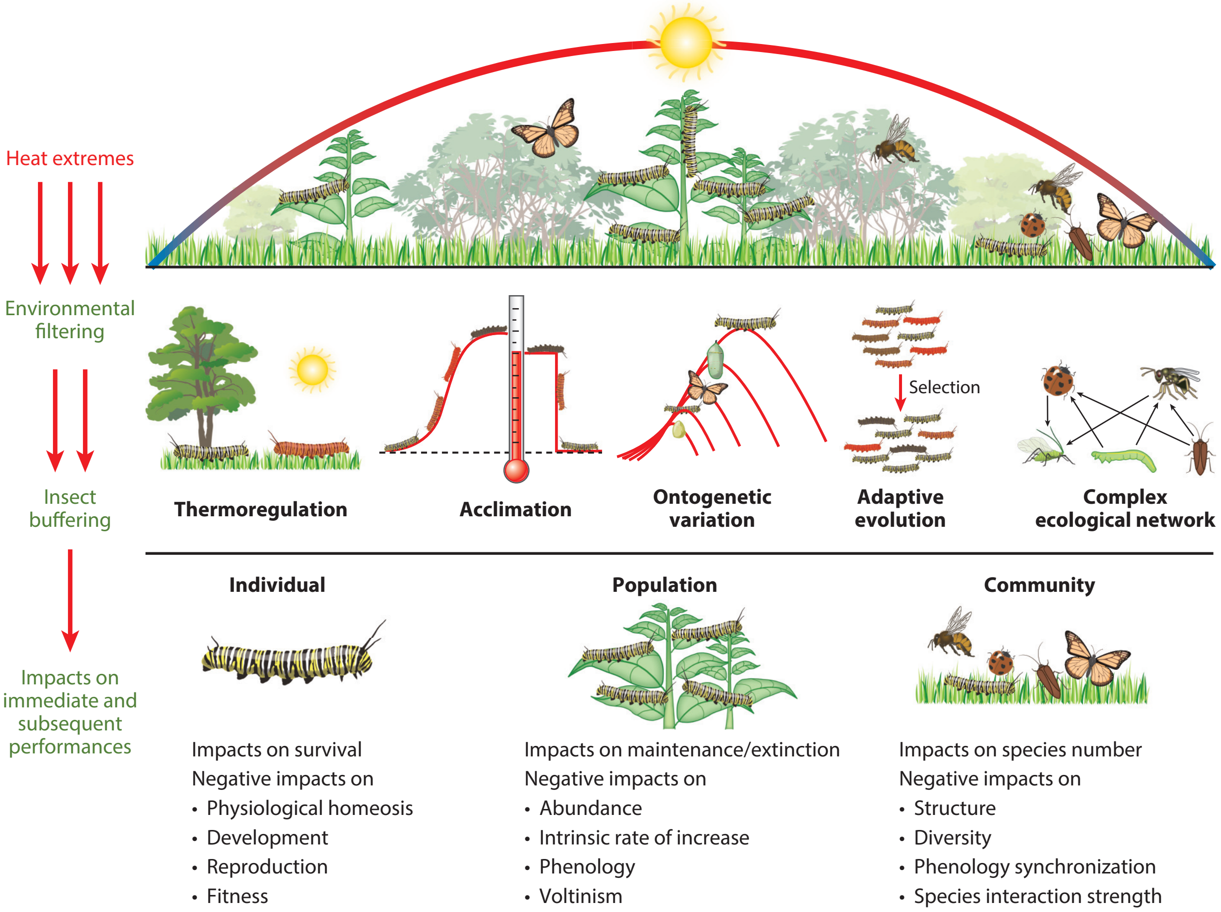

Figure 1

Diagram illustrating how natural thermal extremes are filtered (intensity is often lowered) by microhabitats and buffered by insects through behavioral thermoregulation, phenotypic plasticity, ontogenetic variations, and adaptive evolution to ultimately increase survival in response to heat. Even after filtering and buffering, thermal extremes still impact insect performance at the individual, population, and community levels within and across generations.

Thus, resolving the main components of EHTs becomes more meaningful than providing a general definition for ecological research (**Figure 2**). Based on field temperature data including EHTs (89), several important characteristics can be identified: daily maximum and minimum temperatures, which define the daily amplitude during the EHT events; the frequency of EHT events over long temporal scales (typically the number of hot days during a given period); and the time elapsed between each subsequent EHT event, defining the temporal variance of extreme events. By manipulating values of each variable and their combinations, experimental designs in the laboratory, in mesocosms, or in the field can quantify the impacts of EHTs with varying intensity, frequency, duration, and temporal variance on fitness-related life history traits and demography (**Figure 2**).

In the field, insects experience temperature cycles with a single or several successive hot days alternating with a few mild days (89, 156). Diurnal cycles also alternate several hot hours around midday with mild hours (91, 155). Thus, the effects of EHTs depend largely on characteristics that

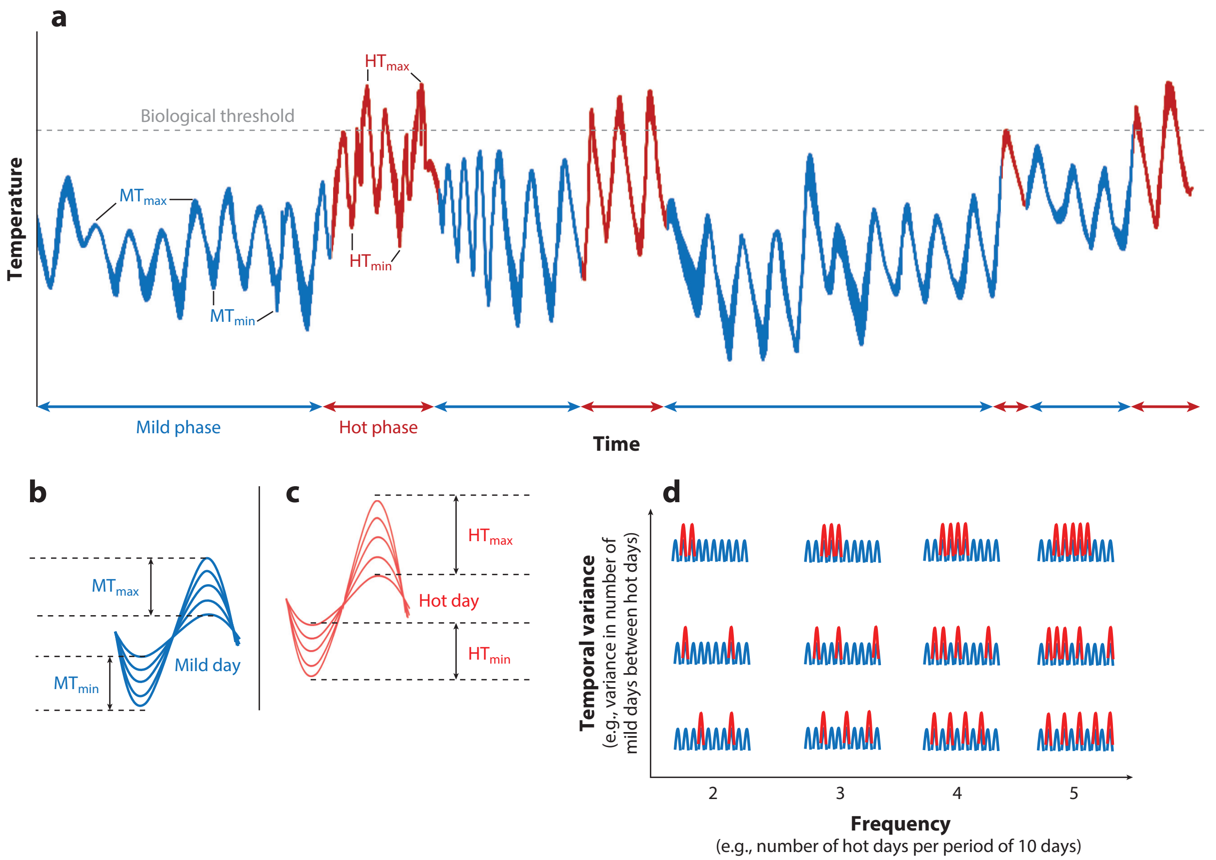

Figure 2

Characterizing extreme high temperatures (EHTs) in the field. (*a*) A temporal series of microclimatic temperature for a theoretical insect illustrates the different metrics used to describe the occurrence of EHTs (*red*) and mild periods (*blue*): their intensity [maximal and minimal temperatures of hot days (HT$_{max}$ and HT$_{min}$) and mild days (MT$_{max}$ and MT$_{min}$)], frequency (the number of consecutive hot days and the frequency at which hot periods occur), temporal variance (the timing of occurrence of hot and mild phases), and the biological threshold (temperature inducing thermal stress in a given organism, or CT$_{max}$). The dichotomy between hot and mild events hides a large range of possibilities when designing experiments to simulate natural thermal extremes. (*b–c*) In particular, the maximum and minimum temperatures of mild and hot days vary within their own range. (*d*) These complex thermal extremes with a daily subunit are embedded in naturally fluctuating temperature regimes that can be described by their temporal variance of EHT occurrence and their frequency (e.g., the number of consecutive hot or mild days). In this case, the temporal arrangement of hot and mild days varies across two axes defined by the number of hot days during a period of 10 days (frequency) and the variance in the number of mild days between each hot day (temporal variance). Note that the global mean and variance of temperature remain the same across all configurations at a given frequency of hot days.

are complex to describe and to simulate in the lab or mesocosms due to the stochastic nature of EHTs.

Intensity, duration, and frequency are often used to link ecological performance and EHTs (47, 94, 127), despite the high uncertainty in these metrics. Simple statistical characteristics describing EHTs were designed to explore the impact of different temperatures during daytime (91) and nighttime (155), different frequencies of hot days (88, 153), and different amplitudes of fluctuation (148). During hot events, insects can be injured by EHTs approaching their physiological thresholds, but the mild temperatures between hot events allow insects to repair (5, 89). The temporal sequence of hot and mild phases is therefore an important characteristic of EHTs (89, 156). The impact of EHTs should be a subtle balance between heat injury and recovery (5, 89, 156).

2.2. Thermal Extreme Versus Mean Temperature

Thermal performance curves (TPCs) are often used to describe the response of biological performance to temperature based on constant temperature treatments (129). TPCs are asymmetrical and nonlinear, thereby generating Jensen's inequality (125), which is used to describe the biological effects of environmental variability (31). TPCs, combined with Jensen's inequality, are frequently used to compute insect performance under fluctuating or changing temperatures, contributing to predictions of climate change impacts (15, 74, 108, 129, 142). Based on Jensen's inequality, the effects of temperature variation would be positive, small, and dramatically negative at low, intermediate, and high temperatures, respectively (31, 78). The left-skewed TPCs show that the thermal optimum (T_{opt}) is close to the critical thermal maximum (CT_{max}), meaning that even a small variation in mean temperature above T_{opt} can push insects over CT_{max}, leading to dramatic declines in performance and fitness (108).

By causing increases in thermal variance and in the strength of the Jensen's inequality, EHTs negatively impact insect fitness even if mean temperature remains near the optimal range (89, 91, 108). Indeed, the impact of increasing variance on key traits related to fitness can be larger than the impact of an increase in mean temperature (91, 108, 148). Greater variance caused by EHTs can lead to decreased maximum performance, truncated thermal performance breadth, and narrow thermal safety margins (108, 142). However, ambient temperature fluctuates, usually with reasonable amplitude up to sublethal daily maxima. Near-optimal temperatures may occur during some parts of the day (e.g., morning, night), thus providing an opportunity for insects to recover from heat injuries occurring around midday (89, 156). Better performance is therefore expected under variable regimes than under constant high temperatures. For example, temperature variation can improve rather than depress the development of aphids when mean temperature is higher than the T_{opt} for development, thereby challenging the Kaufmann effect (155). Importantly, the use of TPCs derived from constant temperatures to predict insect fitness in field conditions requires the unrealistic assumption that performance is independent of thermal history, rates of temperature change, and exposure times (129). More work on the thermal responses to EHT characteristics will certainly help to design novel approaches to draw TPCs that could incorporate the influence of EHTs on insect performance and fitness.

Thermal performance curve: describes the effect of temperature on any measurement of biological traits, such as development or fecundity

Jensen's inequality: a mathematical property of nonlinear functions, $f(x)$, and a set of x values with a mean of x, in which the average result of the function does not equal the result of the function of the mean x; it is widely used to account for effects of environmental variance on organisms and implies that environmental variance may have important biological consequences that cannot be inferred from average environmental conditions

Thermal optimum (T_{opt}): the optimal temperature at which organisms have the best performance in a given trait

Critical thermal maximum: the upper temperature at which animals stop motor activity and lose their coordination

2.3. The Seasonal and Diurnal Patterns of Extreme High Temperatures

The amplitude of warming, including more frequent and intense extremes, is higher in spring, autumn, and winter than in summer (1, 61). However, the biological impacts of EHTs in these seasons are relatively overlooked. EHTs in spring affect the phenological synchronization between plants and herbivore insects (79, 119) and parasitoids (38). EHTs in autumn may affect diapause induction, subsequent overwintering survival, and spring population growth (140). EHTs in winter may influence survival during diapause and postdiapause development (11, 135). Individuals of univoltine species can experience EHTs across different seasons (123).

However, we have little information on seasonal stage-specific responses and their consequences at the population level. Moreover, the amplitude of nighttime warming is higher than that of daytime warming (1, 61). Nighttime warming leads to contrasting effects on thermal performance and fitness, contradicting the predictions based on constant temperatures (155) or daytime warming (8, 91). To date, however, few studies have explored the specific effects of diurnal versus nocturnal patterns of EHTs on insects (5, 8, 91, 155).

3. HOW DO INSECTS RESPOND TO THERMAL EXTREMES?

3.1. Physiological, Biochemical, and Symbiont Responses

Kaufmann effect: a specific form of Jensen's inequality for temperature-dependent development, stating that the effects of temperature variation on development rate will tend to be positive at low temperatures, minimal at intermediate temperatures, and negative at high temperatures

EHTs can lead to heat injury, as well as to a series of changes at the molecular, biochemical, and physiological levels. Moreover, the endosymbionts of insects can also respond to EHTs.

3.1.1. Mechanisms underlying heat damage. Heat damage in insects involves a series of disorders at the molecular, biochemical, and physiological levels (13, 25). Extreme heat causes protein denaturation (72). Heat-induced changes in the fluidity of phospholipidic membranes and cellular homeostasis initiate heat damage (13). The oxygen and capacity limitation of the thermal tolerance (OCLTT) hypothesis proposes that performance is constrained by the capacity for oxygen delivery relative to oxygen demand. The delivery of oxygen is the limiting factor during EHTs (36, 118). This hypothesis was confirmed in several aquatic species (143). However, it is not generally applicable to terrestrial insects since they are unlikely to become oxygen limited (13, 81) unless they live in closed microenvironments such as plant galls (112). Finally, EHTs can disrupt the cellular ion balance (hyperkalemia), thereby impairing neurophysiological functions (106) and damaging mitochondria (13). EHTs can also generate damage indirectly by driving an increase in water loss and causing death by desiccation (26).

3.1.2. Physiological and molecular responses. Insects can produce and accumulate particular molecules to prevent protein denaturation or cell inactivation during EHTs. Polyols, e.g., mannitol in *Aphis gossypii* and sorbitol in *Bemisia argentifolii*, are accumulated to cope with daytime EHTs (55). Mannitol and sorbitol quantities were higher at noon than during early morning. Heat-shock proteins (Hsps) (40, 87) and cuticle proteins (105) are induced and/or accumulated to deal with EHTs. Apple maggots express Hsp increasingly from midday to a peak in late afternoon, paralleling the dynamics of air and fruit temperature in summer (87). Locusts are more heat tolerant at low than at high latitudes as a result of their expression pattern of Hsp70 and Hsp90 (22). The potato aphid increases concentration of several exoskeletal proteins during heat stress (105).

3.1.3. Symbiont-mediated responses. Bacterial endosymbionts provide essential nutrients to their insect host. EHTs depress the diversity, abundance, and activity of endosymbionts, decreasing heat tolerance and fitness of the host insect (39, 71). For example, EHTs decrease the quantity of symbiotic bacteria, lowering heat tolerance in ants (39) and aphid species (150) and altering fitness-related traits in stinkbugs (71). Nevertheless, endosymbiosis may assist insect hosts to adapt to natural EHTs. In aphids, clones with heat-tolerant symbionts develop faster than clones without under EHTs (53). Mutants of the symbiont *Buchnera aphidicola* with lower expression of the heat-shock gene *ibpA* decrease heat tolerance of pea aphids (150). In addition, facultative symbionts, e.g., *Serratia symbiotica* and *Acetobacter*, can protect *B. aphidicola* from short-term heat shock, improving aphid fecundity and offspring survival under EHTs (103).

3.1.4. Morphological responses. EHTs can induce changes in the body size of insects. High developmental temperature generally produces small individuals due to enhanced metabolism and fast development (4, 20, 139). This temperature–size rule arises due to phenotypic plasticity or selection for smaller body sizes (4, 42), although smaller individuals are more vulnerable to dehydration and overheating (45). However, small body size may facilitate heat damage in the insect gut or gut symbionts, thus depriving the insect of nutrients and water (71). Nevertheless, we know little about growth trajectories under repeated EHTs and the underlying physiological mechanisms. For example, frequent heat exposure sometimes produces large individuals (128, 148). The selective advantage of smaller size might become disadvantageous under repeated EHTs (45).

3.2. Fitness-Related Life History Traits and Demography

EHTs alter fitness-related life history traits such as survival, development, and reproduction. Generally, the effect size depends on the thermal conditions previously experienced, focal traits, stage-specific thermal responses, and immediate or subsequent consequences. Collectively, these effects translate into demographic changes.

3.2.1. Stage-specific responses. All stages of insects may experience EHTs. Meanwhile, different stages or instars often have different thermal sensitivities (14, 76, 154). Therefore, EHTs may produce stage-specific thermal responses. Generally, thermal responses relating to development, survival, reproduction, and longevity vary with life stage (152), and adults are often more vulnerable to EHTs. For example, EHTs reduced reproduction to a greater extent when they occurred closer to adulthood (149, 151). The early and reproductive stages of *Sitobion avenae* (154) and *Plutella xylostella* (151) are more sensitive to EHTs than the mature larval stage. Thus, the stage at which the insects are exposed to EHTs is an important component in determining the impact of EHTs. Three hypothesized mechanisms may be involved in ontogenetic variations of thermal tolerance. (*a*) First, the microclimate selection hypothesis states that different stages live in (and thus adapt to) different thermal environments (76, 111, 146). (*b*) Second, the body size hypothesis (77) explains why larger larvae are more heat tolerant than the smaller early life stages (88, 152, 154), which are subject to faster increases in body temperature (3) and water loss (46). However, the body size hypothesis fails to explain the decreased tolerance at the adult stage. (*c*) The Bogert effect hypothesis suggests that the immobile stages (egg and pupa) should be more heat tolerant than mobile adult and larval stages due to their lower ability to behaviorally thermoregulate (59). The Bogert effect hypothesis, however, has been frequently rejected (77).

Life cycle modularity hypothesis: states that modular life cycles may allow insects to mitigate the consequences of temperature by uncoupling its physiological effects from one life stage to the next

Adaptive decoupling hypothesis: proposes that metamorphosis is an adaptation for optimizing expression of traits across life stages that experience opposing selection pressures

3.2.2. Trait-dependent responses. Different life history traits differ in their thermal sensitivity (69). Among the main life history traits, reproduction has the narrowest thermal range, followed by development, while survival has the widest. Reproductive potential is expected to be the fitness-related life history trait that is most vulnerable to EHTs (144, 151). For example, a single hot event of a few hours does not affect survival but does decrease reproduction in the moths *Plutella xylostella* (153) and *Grapholita molesta* (82). The optimal temperature for reproduction is lower than that for development (91, 155), while the optimal temperatures for immature survival often compose a relatively wide range. When temperature increases continuously and surpasses the optimum, development is restricted, and mortality soon occurs (47, 64, 91), indicating that there are slightly higher temperature thresholds for survival than for development. Thus, the critical upper thermal limits for reproduction are lower than those for development, which are lower than those for survival (91, 155).

3.2.3. Immediate, cross-stage, and transgenerational responses. The impacts of EHTs occur at various temporal scales across insect life cycles, leading to immediate impacts at the exposed stage (24, 88, 120, 148), permanent damage at later stages through carry-over effects (24, 77, 149, 152, 154), and transgenerational responses via parental effects (153). The immediate impacts involve all of the molecular, physiological, and morphological mechanisms developed above and are reflected in heat death or delayed development during the events. EHTs in early life stages can influence performance of later stages (151) or of the next generation (82, 153) depending on the intensity of the EHTs, although this is still a matter of debate. The life cycle modularity hypothesis and adaptive decoupling hypothesis (120) state that early life stress has no effects on adult performance, probably because the stressful temperatures are not extreme enough. However, there is evidence that extreme temperatures occurring in egg, larval, or pupal stages can decrease survival (152) and fecundity (24, 77, 149, 154) of adults through carry-over effects or even result in decreased offspring survival via transgenerational effects (153). Nevertheless, we still know little about the mechanisms underlying carry-over and transgenerational effects of extremes.

3.3. Population Dynamics

Increased occurrence of EHTs is concomitant to increases in seasonal and annual average temperature, as well as to longer growing seasons, for insect activity, thereby causing changes in insect phenology and the temperature-dependent population dynamics.

3.3.1. Phenology and voltinism. Frequent EHTs increase overall mean temperature, advancing spring, postponing autumn, and causing shorter winters and longer growing seasons (102). For nondiapausing insects, frequent EHTs may advance phenology in spring and postpone phenology in autumn, thereby increasing the number of annual generations (2, 102). However, for insects with obligate diapause, the combination of longer summers and shorter or warmer winters delays adult emergence due to insufficient winter chilling for diapause termination and to the reduced ability to regulate the onset and termination of diapause (20). For insects with facultative diapause, winter warming leads to earlier diapause termination (135). Nevertheless, EHTs do not always significantly increase overall mean temperature, and their effects on phenology and voltinism remain largely unknown for most insects. A few consecutive hot days occurring in autumn or spring would potentially disturb diapause induction or postdiapause development, thereby altering the phenology of insects.

3.3.2. Abundance. Repeated EHTs generally depress insect fecundity, survival and abundance (20, 89, 91, 104, 127, 155). For example, an increase in daily maximum temperature dramatically reduces arthropod biomass in a rainforest (84). However, the effects of EHTs on insect abundance are complex due to variations in the characteristics of EHTs, local baseline climates and habitat uses, species-specific thermal sensitivity of insects, and the biotic interactions with other species. For instance, frequent EHTs depress abundance of the heat-sensitive species *Sitobion avenae* and *Schizaphis graminum*, whereas they have null or even positive impacts on the heat-tolerant species *Rhopalosiphum padi* (94). Frequent EHTs reduce the abundance of *S. avenae* at the southern margin but not in the north (94). EHTs may also favor soil insects by enhancing their reproduction and abundance (83). Extremely warm winters occurring at high latitudes can increase insect abundance (49). However, EHTs in the Arctic winter also accelerate snowmelt, indirectly decreasing insect abundance (11).

3.4. Biotic Interactions and Community Structure

The species-specific responses of insects to EHTs may alter interspecific competition at the same trophic level, as well as trophic cascades across multitrophic levels, leading to changes in community composition, structure, and ecosystem functioning.

3.4.1. Changes in community composition and structure. Differences in the thermal tolerance of insects at the same trophic level can alter the relative dominance and interspecific competition among species (11, 21, 47, 94), leading to EHT-driven changes in the composition of communities (138). For example, more frequent EHTs alter the structure of cereal aphid communities across large temporal and geographical scales (94). In this case, EHTs alter the dominant pest species in winter wheat crops (94). EHTs during summer affect interspecific competition in

Mediterranean ant communities by changing the circadian rhythm of foraging in subdominant ants but not that of dominant species (21). An aphid-borne plant virus increases the thermal limit of a cereal aphid but not other aphids, facilitating coexistence by weakening competition among these aphids during extreme heat (117). Insects are usually at the intermediate or lower trophic levels in communities and ecosystems. The EHT-induced changes in the composition and structure of insect communities could potentially influence top-down and bottom-up processes in plant–insect herbivore–predator systems.

3.4.2. Cascading effects across multitrophic systems. Increasing the frequency and intensity of EHTs enhances the vulnerability of species at higher trophic levels in simple trophic cascades (23, 104). Thus, EHTs are likely to reduce predator diversity and disrupt ecosystem services such as natural biological control (7). Nevertheless, biodiverse multitrophic assemblages are more resilient to EHTs (47, 62, 127). For simplified food chains including only two trophic levels, such as plant–insect herbivore (47), prey–predator (104, 127), or parasitoid–hyperparasitoid systems (23), the species at higher trophic levels are more susceptible to EHTs. However, the overall effects of EHTs on tritrophic systems such as plant–insect herbivore–predator/parasitoid are much less dramatic and often similar to patterns under normal climates (47, 127). Studies on the relationships between EHTs and the responses of each trophic level are helpful to clarify the resilience of ecological communities to changes in climate extremes.

3.5. Geographical Distributions

Heat tolerance is weakly linked to latitude in insects, but tolerant species often live in warm microhabitats, while heat-vulnerable species remain mostly in cooler microhabitats (43, 113). The thermal safety margin, defined as the difference between the CT_{max} of insects and the ambient maximum temperature of the hottest month (67, 142), is frequently used to predict insect distribution following EHTs. Thermal extremes exceeding CT_{max} restrict the thermal performance range and influence the distribution across latitudes and altitudes and in heterogeneous landscapes (74, 107, 142), thereby shaping the distribution of insects worldwide (67, 96). EHTs can shift distributions through local extinction induced by mass mortality due to fitness decline, to mismatch in the phenology of insects and host plants (20, 100), or to interaction with landscape fragmentation (109). However, EHTs in winter or at nighttime may release the constraint of low temperatures, leading to positive effects such as increased winter survival and dispersal abilities in insects (9, 10), resulting in range expansion. Prolonged heat waves lead to an increase in the number of nights above the flight threshold temperature, promoting take-off behavior in *Thaumetopoea pityocampa* and causing a rapid distribution shift to higher altitudes in the Alps (9). Some species with higher adaptive potential for heat tolerance can expand their range to lower latitudes (57).

4. HOW DO INSECTS BUFFER AGAINST THERMAL EXTREMES?

4.1. Microhabitats as Filters of Thermal Extremes

Insects can exploit the thermal diversity of their microhabitats as a buffering strategy to avoid overheating when they encounter EHTs. However, the extent to which insects can buffer the impacts of EHTs largely depends on the physical structure of their microhabitats, the severity of heat stress, and their complex interactions.

4.1.1. Mosaic of microclimates. Forecasting the biological impacts of EHTs requires a general understanding of how microhabitats filter environmental fluctuations and whether the heterogeneity will allow insects to escape heat extremes (66, 116, 137). Living and nonliving objects in the environment produce a complex mosaic of microclimates that depends on the nature of the objects and how the microhabitat transfers atmospheric variations (147). Little is known, however, about the dynamics of these microclimatic mosaics during thermal extremes (114). In the apple tentiform leaf miner, the location within the tree canopy mosaic of optimal, suboptimal, and lethal microenvironments can be totally reversed during EHTs (115). The temperature gradient at the microscale matters for arthropods' escape of EHTs. For example, the ground a few centimeters below hot rocks in the Australian desert can be up to 9°C lower in temperature (110), and the temperature heterogeneity on the surface of apple leaves can be 6–12°C (126). Spider mites can fully exploit this leaf surface heterogeneity by moving over a few centimeters, but this possibility is restricted during EHTs (19). Aphids need to remain near the main veins to feed on phloem, and therefore they cannot really exploit this heterogeneity (18). EHTs are expected to alter these fine-scale temperature gradients (19), depending on the baseline buffering property of the microhabitat (147).

4.1.2. Buffering ability of microhabitats. EHTs are transmitted through the microhabitat before they reach insects. Different microhabitats filter atmospheric conditions differently. For example, differences of >5°C in the maximal microclimate temperature were observed when comparing different habitats, e.g., grassland, heathland, and deciduous woodland (136). The understory of forests is probably the strongest buffer of EHTs (29), almost independently of the dominant tree species and of latitude (30). Insects could benefit from moving to these microhabitats during EHTs, although a direct effect remains to be demonstrated. Nevertheless, some insect species are specialized to microhabitats at the top canopy, and the potential for vertical zonation of herbivore insects across forest canopies is important (80). The temperature of leaves hit by solar radiation is higher than ambient air temperature for most species within a moderate transpiration rate range in temperate and boreal latitudes (116); thus, the leaf surface magnifies the amplitude of thermal extremes (147), but the stomatal behavior of the plant may ameliorate the thermal conditions at the leaf surface by increasing evapotranspiration (113). The thermal limit of small herbivore arthropods living at the leaf surface is related to leaf temperature during EHTs, especially when the specific effect of the herbivore insect on the leaf transpiration rate is included (113). Therefore, these herbivores are already vulnerable to contemporary thermal extremes. Similarly, endophagous insects such as leaf miners and gall-inducing organisms live in structures (mines, galls) where the temperature increases more than that of ambient air during thermal extremes (111, 112). By contrast, aquatic systems buffer atmospheric temperature variations due to the thermal inertia of water bodies and geophysical processes (147). In general, we lack enough data on the temperature of most microhabitats to provide an exhaustive ranking from the best to the worst buffer of EHTs.

4.2. Thermoregulation

Behavioral thermoregulation across the mosaic of microclimates plays an important role in avoiding EHTs (97). Thermoregulatory behavior can directly increase survival during EHTs (12, 66, 147). Nevertheless, the availability of suitable microclimates affects thermoregulation (147), determining the efficacy of insect buffering against climate warming (19, 66). However, it is predicted that warming will reduce seasonal and diurnal temperature ranges (61), causing decreases in temperature heterogeneity across temporal and spatial scales (66), including in microhabitats (19). Thus, behavioral thermoregulation alone may not be sufficient to buffer ongoing climate warming (19). Physiological thermoregulation including evaporative cooling (during water loss by transpiration) can be significant in insects of relatively large body size (122). Nevertheless, the amplitude of change in insect body temperature during evaporative cooling remains much lower than during behavioral thermoregulation (133).

Behavioral thermoregulation can also bring costs and lead to ecological consequences. More frequent EHTs increase the occurrence of thermoregulatory behaviors (92, 145) and maintenance energy costs (66) and, in turn, decrease foraging activity, energy efficiency, and reproduction (66, 89). For example, aphids leave their host plants by dropping off or walking downward to seek cooler microhabitats to escape EHTs (88, 92, 93, 105). Therefore, they may have to endure food and water deprivation and spend time and energy to find another suitable feeding site, thereby reducing reproduction opportunities (90). Moreover, behavioral thermoregulation may also alter the microhabitat use of insects (7, 90). Differences in behavioral regulation and microhabitat use between species can change the interspecific interaction and food web structure (7). Furthermore, thermoregulatory behavior may limit evolutionary adaptation by reducing or even eliminating the selection pressure of EHTs (59).

4.3. Ontogenetic Variations and Tradeoffs Among Different Traits

Insects have evolved complex life cycles with multiple developmental stages differing in thermal sensitivity (14). However, the role of ontogenetic variation of thermal sensitivity in buffering EHTs has received little attention. Different stages or age cohorts can overlap in field populations, resulting in the coexistence of multiple life stages or age cohorts during a growth season. When the mixed-stage population experiences EHTs, the most sensitive stages would be injured or die, whereas the most tolerant may survive and develop to the adult stage for reproduction during the following mild phases, thereby contributing to population recovery. Compared to the pupal and adult stages, medium and late larval stages can better resist heat stress in both immediate survival and subsequent reproduction (153). Larval stages may acquire sufficient nutrients and water to both resist EHTs and recover from heat injury, thereby reducing the carry-over effects of EHTs on adult reproduction.

The intrinsic rate of increase, a metric for fitness, integrates survival, development time, and reproduction (89, 91). Different responses to EHTs and even tradeoffs among these traits may also help buffer impacts of EHTs. Temperatures above the optimum for reproduction reduce fecundity (e.g., number of offspring) but can also accelerate maturation and reproduction processes (151, 155). When temperature surpasses the optimum for development, insects tend to invest more energy in heat tolerance to improve survival, generating costs that reduce reproduction output (154) and delay development, at least temporally (120, 148). Thus, variations in thermal sensitivity of different traits may contribute to buffering heat stress in insects.

4.4. Phenotypic Plasticity

Phenotypic plasticity is a nongenetic strategy to cope with environmental variation, including thermal extremes (50, 58, 141). Most of the insect responses detailed above relate to phenotypic plasticity. Four types of plasticity in heat tolerance were identified based on the timescale and temperature intensity. Rapid hardening or heat shock corresponds to a short and harsh exposure to high temperatures for a few minutes or hours (70, 141). The other types of thermal plasticity are all generated by exposure to moderately high temperatures for several hours to days for acclimation (laboratory) or acclimatization (field) (63, 70), days to weeks for development acclimation or plasticity (68, 70, 141), and weeks to months for transgenerational acclimation (63). In general, previous exposure to elevated temperatures increases heat tolerance both within and across generations.

Nevertheless, the potential to buffer against EHTs through plasticity may be limited. Quantitatively, there is limited scope for plasticity to increase heat tolerance significantly in many arthropod taxa (50, 58, 68, 141). For instance, the increases in CT_{max} of some *Drosophila* species and the moth *Manduca sexta* are limited to only approximately 0.6–1.0°C (68, 141) and 1–2°C (75), respectively, via hardening and developmental acclimation processes. In addition, increased heat tolerance brings a series of concurrent costs in other plastic traits that are related to fitness (37, 85, 141). These costs can generate considerable transgenerational consequences such as declines in offspring size and survival (95).

4.5. Evolutionary Adaptation

Frequent EHTs could induce evolution of thermal tolerance to buffer against high temperature impacts (16, 58). Thermal evolution occurs in small insects during artificial selection (41, 52). Long-term thermal selection is commonly found in local adaption, e.g., *Drosophila* and ants at different latitudes (33, 107) or beetles and butterflies at different altitudes (44, 56). Urban heat islands also trigger thermal adaptation. Urban worker ants evolved a CT_{max} that is 1°C higher than that of rural populations (33). Local adaptation often results from a subtle interaction among generation time, heritability, covariance between phenotypes, phylogenetic inertia, and the strength of selection (67).

However, rapid evolution of thermal traits hardly ever occurs under natural selection in insects. Higher feeding rates in nature evolved only after decades under more frequent EHTs in *Colias eurytheme* (56). EHTs embedded in fluctuating patterns may constrain the evolution of thermal traits due to lower heritability under ramping temperature than under artificial static temperature (101), slowing down the speed at which insects can track climate warming (52). Thermal selection can also modify fitness-related life history traits (60, 73). Thermal tolerance often incurs fitness costs due to antagonistic genetic interactions between traits (86). Thermal tolerance could also be shaped by phylogenetic inertia, rather than by thermal selection in nature (67). To some extent, thermal evolution can be a way to buffer EHTs, but its mechanisms are still poorly understood.

5. KNOWLEDGE GAPS AND FUTURE PERSPECTIVES

5.1. Ecological Relevance of Experimental Designs

The biological impacts of complex EHTs are difficult to investigate experimentally because of their stochastic nature. Open-top chambers, infrared irradiation, and electronic heating systems are widely used to simulate climate warming, including EHTs, in the field (51). However, results from these studies are difficult to apply broadly because the mechanisms are not fully understood. The different statistical moments of EHTs (intensity, duration, and frequency) may have biological impacts that differ in their direction and amplitude, and their interactive effects could generate counterintuitive responses in insects. Simulated regimes of EHTs are highly diverse in the literature, including constant temperature for given periods or fluctuations with fixed cycles. Currently, these regimes do not include alternative patterns of EHTs and mild periods, which allow stress recovery (89, 155). In this section, we suggest that experimental designs be given enhanced ecological relevance in future studies by incorporating the complete statistics of EHTs, despite the inherent logistic complexity of factoring several variables. In addition, the simulated temperature regimes should be based on microclimatic rather than macroclimatic patterns to improve the ecological relevance. Such levels of complexity are mandatory to help us fully understand insect performance under EHTs in natural thermal conditions.

5.2. Expanding Our Vision of Extremes

EHTs are, by climatological definition, relatively infrequent but intense (e.g., heat waves). The biological perspective is the converse in the sense that the thermal events challenging the physiology of insects are likely frequent. Environmental conditions may become suddenly challenging for organisms when several normal events co-occur, leading to environmental extremes (32). This shift in perspective has only rarely been applied to insects, but the methodology and the concepts exist (34). Insects are constrained by several factors in their microhabitats. Dryness aggravates the physiological stress during hot periods. Wind decreases body temperature in the short term, but it incurs higher water loss. The same set of environmental conditions may be extreme for individuals deprived of appropriate endosymbionts but near optimal for those that host these microorganisms. Entomological sciences need to embrace more original and innovative characterizations of extreme events, to be combined with the standard climatological view.

5.3. Rise of Integrative Approaches

The ultimate goal of global change biologists is to anticipate the future trend of biodiversity. This goal can only be achieved through comprehensive understanding of the mechanisms for organism–environment interactions and predictions of population dynamics and community structure across time and generations. It seems crucial to link physiological mechanisms of thermal stress and demographic variables. Physiological and genomic approaches have been successfully integrated in studies to link physiological impacts of environmental changes and field patterns of thermal stress. Intertidal ecologists led the investigation of this vision for decades (54), but entomologists have now become more involved (48). The next challenge is to integrate the field ecophysiology of thermal stress, especially during EHTs, with the population dynamics. Given the importance of individual processes (e.g., carry-over effects; hardening of thermal tolerance; and, more generally, phenotypic plasticity), approaches including individual-based models (28) are promising candidates to interconnect these processes and link individual and population scales. In addition, microclimate models are needed (65, 114, 115) to simulate the heterogeneous environmental arena within which individuals and species interact. All of these processes need to be fine-scaled to incorporate cross-seasonal impacts of EHTs at given moments in the life cycle of insects. Intense collaborations between physiologists, ecologists, climatologists, and modelers are key for successful developments.

6. CONCLUDING REMARKS

Thermal extremes are complex events that combine different statistical moments. This complexity increases the difficulty of developing a comprehensive understanding of their impacts on biological processes. While thermal extremes are defined as rare events by climatologists, ecologists have realized that thermal extremes are much more frequent once they are defined relative to the thermal biology of organisms. Nevertheless, the impacts of ongoing climate change on these biologically relevant thermal extremes remain to be identified. In this context, the most studied biological models are *Drosophila* species (40, 52, 67) and other species with conservation importance (62, 84). The thermal ecology of most species with economic importance for agriculture, horticulture, and forestry remains largely unknown. Our lack of knowledge is an important frontier limiting our ability to anticipate the ecological consequences of extreme heat events.

SUMMARY POINTS

1. Thermal extremes are complex, multicomposite events. Despite the lack of a unified definition of thermal extremes due to this complexity, we can describe natural temperature extremes with several variables related to both the environment and the species thermal biology, defining together the intensity, frequency, and temporal variance of EHT events.
2. Classic TPCs derived from constant temperature experiments cannot be used to estimate the biological impacts of thermal extremes. More sophisticated TPCs are needed to include the influence of all statistical moments of thermal extremes.
3. EHTs often, but not always, affect insects at various levels, ranging from molecular and physiological responses at individual to population scales to community structure and functioning.
4. Thermal extremes can instantaneously affect survival. They can also produce long-lasting impacts on life history traits and demographics of insects. The magnitude of these effects depends mainly on thermal history, traits, and life cycle stage. Collectively, all of these effects translate into population dynamics.
5. Insects may partly or completely buffer thermal extremes via behavioral thermoregulation, phenotypic plasticity, ontogenetic variations, tradeoffs among different traits, and evolutionary adaptation. However, most of these buffering strategies probably have limited quantitative potential, and they may incur costs for other fitness-related traits.

FUTURE ISSUES

1. Innovative, ecologically relevant experimental designs are crucially needed to better understand the effects of realistic natural thermal extremes on insect populations, communities, and ecosystems.
2. Beyond the instantaneous impacts of thermal extremes, the carry-over effects of heat stress and the stage-specific responses of insects deserve more comprehensive studies to better detail the consequences of thermal extremes.
3. We lack studies on the relative effects of the various strategies to buffer against thermal extremes, including physiological and behavioral thermoregulation, ontogenetic variation, phenotypic plasticity, and adaptive evolution in insects. These buffering strategies may incur tradeoffs with fitness-related traits, generating complex interactive effects that need to be identified to contribute to prediction models.
4. The mechanisms underlying heat injury and thermal recovery of insects at the molecular, physiological, and ecological levels should be investigated to better comprehend the combined effects of alternating thermal extremes and mild periods.
5. The impacts of EHTs occurring in fall, winter, and spring, as well as at night, on insect diapause, phenology, interspecific interactions, and communities remain relatively understudied.

6. Microclimate models should be used more extensively to generate realistic thermal environments within which insects experience thermal extremes under field conditions in their microhabitats.
7. The thermal biology in the context of thermal extremes of insect species of economic importance, such as agricultural, horticultural, and forestry pests and their potential biological control agents, should be given priority to improve pest management and beneficial conservation worldwide.

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LITERATURE CITED

1. Alexander LV, Zhang X, Peterson TC, Caesar J, Gleason BE, et al. 2006. Global observed changes in daily climate extremes of temperature and precipitation. *J. Geophys. Res.* 111:D05109
2. Altermatt F. 2010. Climatic warming increases voltinism in European butterflies and moths. *Proc. R. Soc. B* 277:1281–87
3. Angilletta MJ. 2009. *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford, UK: Oxford Univ. Press
4. Atkinson D. 1994. Temperature and organism size: a biological law for ectotherms? *Adv. Ecol. Res.* 25:1–58
5. Bai CM, Ma G, Cai WZ, Ma CS. 2019. Independent and combined effects of daytime heat stress and nighttime recovery determine thermal performance. *Biol. Open* 8:bio038141
6. Bailey LD, van de Pol M. 2016. Tackling extremes: challenges for ecological and evolutionary research on extreme climatic events. *J. Anim. Ecol.* 85:85–96
7. Barton BT, Schmitz OJ. 2009. Experimental warming transforms multiple predator effects in a grassland food web. *Ecol. Lett.* 12:1317–25
8. Barton BT, Schmitz OJ. 2018. Opposite effects of daytime and nighttime warming on top-down control of plant diversity. *Ecology* 99:13–20
9. Battisti A, Stastny M, Buffo E, Larsson S. 2006. A rapid altitudinal range expansion in the pine processionary moth produced by the 2003 climatic anomaly. *Glob. Change Biol.* 12:662–71
10. Battisti A, Stastny M, Netherer S, Robinet C, Schopf A, et al. 2005. Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecol. Appl.* 15:2084–96
11. Bokhorst S, Phoenix GK, Bjerke JW, Callaghan TV, Huyerbrugman F, Berg MP. 2012. Extreme winter warming events more negatively impact small rather than large soil fauna: shift in community composition explained by traits not taxa. *Glob. Change Biol.* 18:1152–62
12. Bonebrake TC, Boggs CL, Stamberger JA, Deutsch C, Ehrlich PR. 2014. From global change to a butterfly flapping: biophysics and behaviour affect tropical climate change impacts. *Proc. R. Soc. B* 281:20141264
13. Bowler K. 2018. Heat death in poikilotherms: Is there a common cause? *J. Therm. Biol.* 76:77–79
14. Bowler K, Terblanche JS. 2008. Insect thermal tolerance: What is the role of ontogeny, ageing and senescence? *Biol. Rev.* 83:339–55

15. Bozinovic F, Bastías DA, Boher F, Clavijobaquet S, Estay SA, Angilletta MJ. 2011. The mean and variance of environmental temperature interact to determine physiological tolerance and fitness. *Physiol. Biochem. Zool.* 84:543–52
16. Buckley LB, Huey RB. 2016. How extreme temperatures impact organisms and the evolution of their thermal tolerance. *Integr. Comp. Biol.* 56:98–109
17. Buckley LB, Huey RB. 2016. Temperature extremes: geographic patterns, recent changes, and implications for organismal vulnerabilities. *Glob. Change Biol.* 22:3829–42
18. Cahon T, Caillon R, Pincebourde S. 2018. Do aphids alter leaf surface temperature patterns during early infestation? *Insects* 9:34
19. Caillon R, Suppo C, Casas J, Woods AH, Pincebourde S. 2014. Warming decreases thermal heterogeneity of leaf surfaces: implications for behavioural thermoregulation by arthropods. *Funct. Ecol.* 28:1449–58
20. CaraDonna PJ, Cunningham JL, Iler AM. 2018. Experimental warming in the field delays phenology and reduces body mass, fat content and survival: implications for the persistence of a pollinator under climate change. *Funct. Ecol.* 32:2345–56
21. Cerda X, Retana J, Manzaneda A. 1998. The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. *Oecologia* 117:404–12
22. Chen B, Feder ME, Kang L. 2018. Evolution of heat-shock protein expression underlying adaptive responses to environmental stress. *Mol. Ecol.* 27:3040–54
23. Chen C, Gols R, Biere A, Harvey JA. 2019. Differential effects of climate warming on reproduction and functional responses on insects in the fourth trophic level. *Funct. Ecol.* 33:693–702
24. Chen YY, Zhang W, Ma G, Ma CS. 2019. More stressful event does not always depress subsequent life performance. *J. Integr. Agric.* 18:2321–29
25. Chown SL, Nicolson SW. 2004. *Insect Physiological Ecology: Mechanisms and Patterns*. Oxford, UK: Oxford Univ. Press
26. Chown SL, Sorensen JG, Terblanche JS. 2011. Water loss in insects: an environmental change perspective. *J. Insect Physiol.* 57:1070–84
27. Colinet H, Sinclair BJ, Vernon P, Renault D. 2015. Insects in fluctuating thermal environments. *Annu. Rev. Entomol.* 60:123–40
28. Crespo-Pérez V, Regniere J, Chuine I, Rebaudo F, Dangles O. 2015. Changes in the distribution of multispecies pest assemblages affect levels of crop damage in warming tropical Andes. *Glob. Change Biol.* 21:82–96
29. De Frenne P, Rodriguez-Sanchez F, Coomes DA, Baeten L, Verstraeten G, et al. 2013. Microclimate moderates plant responses to macroclimate warming. *PNAS* 110:18561–65
30. De Frenne P, Zellweger F, Rodríguez-Sánchez F, Scheffers BR, Hylander K, et al. 2019. Global buffering of temperatures under forest canopies. *Nat. Ecol. Evol.* 3:744–49
31. Denny M. 2017. The fallacy of the average: on the ubiquity, utility and continuing novelty of Jensen's inequality. *J. Exp. Biol.* 220:139–46
32. Denny M, Hunt L, Miller L, Harley C. 2009. On the prediction of extreme ecological events. *Ecol. Monogr.* 79:397–421
33. Diamond SE. 2017. Evolutionary potential of upper thermal tolerance: biogeographic patterns and expectations under climate change. *Ann. N. Y. Acad. Sci.* 1389:5–19
34. Dowd WW, Denny MW. 2020. A series of unfortunate events: characterizing the contingent nature of physiological extremes using long-term environmental records. *Proc. R. Soc. B* 287:20192333
35. Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO. 2000. Climate extremes: observations, modeling, and impacts. *Science* 289:2068–74
36. Ern R. 2019. A mechanistic oxygen- and temperature-limited metabolic niche framework. *Philos. Trans. R. Soc. B* 374:20180540
37. Esperk T, Kjaersgaard A, Walters RJ, Berger D, Blanckenhorn WU. 2016. Plastic and evolutionary responses to heat stress in a temperate dung fly: negative correlation between basal and induced heat tolerance? *J. Evol. Biol.* 29:900–15
38. Evans EW, Carlile NR, Innes MB, Pitigala N. 2013. Warm springs reduce parasitism of the cereal leaf beetle through phenological mismatch. *J. Appl. Entomol.* 137:383–91

39. Fan YL, Wernegreen JJ. 2013. Can't take the heat: High temperature depletes bacterial endosymbionts of ants. *Microb. Ecol.* 66:727–33
40. Feder ME, Blair NT, Figueras H. 1997. Natural thermal stress and heat-shock protein expression in *Drosophila* larvae and pupae. *Funct. Ecol.* 11:90–100
41. Folk DG, Zwollo P, Rand DM, Gilchrist GW. 2006. Selection on knockdown performance in *Drosophila melanogaster* impacts thermotolerance and heat-shock response differently in females and males. *J. Exp. Biol.* 209:3964–73
42. Forster J, Hirst AG, Atkinson D. 2012. Warming-induced reductions in body size are greater in aquatic than terrestrial species. *PNAS* 109:19310–14
43. Franken O, Huizinga M, Ellers J, Berg MP. 2018. Heated communities: large inter- and intraspecific variation in heat tolerance across trophic levels of a soil arthropod community. *Oecologia* 186:311–22
44. García-Robledo C, Kuprewicz EK, Staines CL, Erwin TL, Kress WJ. 2016. Limited tolerance by insects to high temperatures across tropical elevational gradients and the implications of global warming for extinction. *PNAS* 113:680–85
45. Gardner JL, Peters A, Kearney MR, Joseph L, Heinsohn R. 2011. Declining body size: a third universal response to warming? *Trends Ecol. Evol.* 26:285–91
46. Gibbs AG, Louie AK, Ayala JA. 1998. Effects of temperature on cuticular lipids and water balance in a desert *Drosophila*: Is thermal acclimation beneficial? *J. Exp. Biol.* 201:71–80
47. Gillespie DR, Nasreen A, Moffat CE, Clarke P, Roitberg BD. 2012. Effects of simulated heat waves on an experimental community of pepper plants, green peach aphids and two parasitoid species. *Oikos* 121:149–59
48. Giron D, Dubreuil G, Bennett A, Dedeine F, Dicke M, et al. 2018. Promises and challenges in insect-plant interactions. *Entomol. Exp. Appl.* 166:319–43
49. Goodsman DW, Grosklos G, Aukema BH, Whitehouse C, Bleiker KP, et al. 2018. The effect of warmer winters on the demography of an outbreak insect is hidden by intraspecific competition. *Glob. Change Biol.* 24:3620–28
50. Gunderson AR, Stillman JH. 2015. Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. *Proc. R. Soc. B* 282:20150401
51. Halbritter AH, De Boeck HJ, Eycott AE, Reinsch S, Robinson DA, et al. 2020. The handbook for standardized field and laboratory measurements in terrestrial climate change experiments and observational studies (ClimEx). *Methods Ecol. Evol.* 11:22–37
52. Hangartner S, Hoffmann AA. 2016. Evolutionary potential of multiple measures of upper thermal tolerance in *Drosophila melanogaster*. *Funct. Ecol.* 30:442–52
53. Harmon JP, Moran NA, Ives AR. 2009. Species response to environmental change: impacts of food web interactions and evolution. *Science* 323:1347–50
54. Helmuth B, Kingsolver JG, Carrington E. 2005. Biophysics, physiological ecology, and climate change: Does mechanism matter? *Annu. Rev. Physiol.* 67:177–201
55. Hendrix DL, Salvucci ME. 1998. Polyol metabolism in homopterans at high temperatures: accumulation of mannitol in aphids (Aphididae: Homoptera) and sorbitol in whiteflies (Aleyrodidae: Homoptera). *Comp. Biochem. Physiol. A* 120:487–94
56. Higgins JK, MacLean HJ, Buckley LB, Kingsolver JG. 2014. Geographic differences and microevolutionary changes in thermal sensitivity of butterfly larvae in response to climate. *Funct. Ecol.* 28:982–89
57. Hill MP, Chown SL, Hoffmann AA. 2013. A predicted niche shift corresponds with increased thermal resistance in an invasive mite, *Halotydeus destructor*. *Glob. Ecol. Biogeogr.* 22:942–51
58. Hoffmann AA, Chown SL, Clusella-Trullas S. 2013. Upper thermal limits in terrestrial ectotherms: How constrained are they? *Funct. Ecol.* 27:934–49
59. Huey RB, Hertz PE, Sinervo B. 2003. Behavioral drive versus behavioral inertia in evolution: a null model approach. *Am. Nat.* 161:357–66
60. Huey RB, Kingsolver JG. 1989. Evolution of thermal sensitivity of ectotherm performance. *Trends Ecol. Evol.* 4:131–35
61. IPCC. 2013. Technical summary. In *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, ed. TF Stocker,

D Qin, G-K Plattner, M Tignor, SK Allen, J Boschung, A Nauels, Y Xia, V Bex, PM Midgley, pp. 1–127. Cambridge, UK: Cambridge Univ. Press

62. Isbell F, Craven D, Connolly J, Loreau M, Schmid B, et al. 2015. Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* 526:574–77
63. Jensen A, Alemu T, Alemneh T, Pertoldi C, Bahrndorff S, et al. 2019. Thermal acclimation and adaptation across populations in a broadly distributed soil arthropod. *Funct. Ecol.* 33:833–45
64. Karl I, Stoks R, De Block M, Janowitz SA, Fischer K. 2011. Temperature extremes and butterfly fitness: conflicting evidence from life history and immune function. *Glob. Change Biol.* 17:676–87
65. Kearney M, Porter WP. 2016. NicheMapR—an R package for biophysical modelling: the microclimate model. *Ecography* 40:664–74
66. Kearney M, Shine R, Porter WP. 2009. The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. *PNAS* 106:3835–40
67. Kellermann V, Overgaard J, Hoffmann AA, Flojgaard C, Svenning JC, Loeschcke V. 2012. Upper thermal limits of *Drosophila* are linked to species distributions and strongly constrained phylogenetically. *PNAS* 109:16228–33
68. Kellermann V, Sgro CM. 2018. Evidence for lower plasticity in $\mathrm{CT}_{\mathrm{MAX}}$ at warmer developmental temperatures. *J. Evol. Biol.* 31:1300–12
69. Kellermann V, van Heerwaarden B. 2019. Terrestrial insects and climate change: adaptive responses in key traits. *Physiol. Entomol.* 44:99–115
70. Kellermann V, van Heerwaarden B, Sgro CM. 2017. How important is thermal history? Evidence for lasting effects of developmental temperature on upper thermal limits in *Drosophila melanogaster*. *Proc. R. Soc. B* 284:20170447
71. Kikuchi Y, Tada A, Musolin DL, Hari N, Hosokawa T, et al. 2016. Collapse of insect gut symbiosis under simulated climate change. *mBio* 7:e01578-16
72. King AM, MacRae TH. 2015. Insect heat shock proteins during stress and diapause. *Annu. Rev. Entomol.* 60:59–75
73. Kingsolver JG, Buckley LB. 2017. Quantifying thermal extremes and biological variation to predict evolutionary responses to changing climate. *Philos. Trans. R. Soc. B* 372:20160147
74. Kingsolver JG, Diamond SE, Buckley LB. 2013. Heat stress and the fitness consequences of climate change for terrestrial ectotherms. *Funct. Ecol.* 27:1415–23
75. Kingsolver JG, MacLean HJ, Goddin SB, Augustine KE. 2016. Plasticity of upper thermal limits to acute and chronic temperature variation in *Manduca sexta* larvae. *J. Exp. Biol.* 219:1290–94
76. Kingsolver JG, Woods A, Buckley LB, Potter KA, MacLean HJ, Higgins JK. 2011. Complex life cycles and the responses of insects to climate change. *Integr. Comp. Biol.* 51:719–32
77. Klockmann M, Günter F, Fischer K. 2017. Heat resistance throughout ontogeny: Body size constrains thermal tolerance. *Glob. Change Biol.* 23:686–96
78. Koussoroplis AM, Pincebourde S, Wacker A. 2017. Understanding and predicting physiological performance of organisms in fluctuating and multifactorial environments. *Ecol. Monogr.* 87:178–97
79. Kudo G, Ida TY. 2013. Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology* 94:2311–20
80. Lawton JH. 1983. Plant architecture and the diversity of phytophagous insects. *Annu. Rev. Entomol.* 28:23–29
81. Lehmann P, Javal M, Terblanche JS. 2019. Oxygen limitation is not the cause of death during lethal heat exposure in an insect. *Biol. Lett.* 15:20180701
82. Liang LN, Zhang W, Ma G, Hoffmann A, Ma CS. 2014. A single hot event stimulates adult performance but reduces egg survival in the oriental fruit moth, *Grapholitha molesta*. *PLOS ONE* 9:e116339
83. Lindo Z. 2015. Warming favours small-bodied organisms through enhanced reproduction and compositional shifts in belowground systems. *Soil Biol. Biochem.* 91:271–78
84. Lister BC, Garcia A. 2018. Climate-driven declines in arthropod abundance restructure a rainforest food web. *PNAS* 115:E10397–406
85. Loeschcke V, Hoffmann AA. 2007. Consequences of heat hardening on a field fitness component in *Drosophila* depend on environmental temperature. *Am. Nat.* 169:175–83

86. Loeschcke V, Krebs RA. 1996. Selection for heat-shock resistance in larval and in adult *Drosophila buzzatii*: comparing direct and indirect responses. *Evolution* 50:2354–59
87. Lopez-Martinez G, Denlinger DL. 2008. Regulation of heat shock proteins in the apple maggot *Rhagoletis pomonella* during hot summer days and overwintering diapause. *Physiol. Entomol.* 33:346–52
88. Ma CS, Hau B, Poehling HM. 2004. The effect of heat stress on the survival of the rose grain aphid, *Metopolophium dirhodum* (Hemiptera: Aphididae). *Eur. J. Entomol.* 101:327–31
89. Ma CS, Wang L, Zhang W, Rudolf V. 2018. Resolving biological impacts of multiple heat waves: interaction of hot and recovery days. *Oikos* 127:622–33
90. Ma G, Bai CM, Wang XJ, Majeed MZ, Ma CS. 2018. Behavioural thermoregulation alters microhabitat utilization and demographic rates in ectothermic invertebrates. *Anim. Behav.* 142:49–57
91. Ma G, Hoffmann AA, Ma CS. 2015. Daily temperature extremes play an important role in predicting thermal effects. *J. Exp. Biol.* 218:2289–96
92. Ma G, Ma CS. 2012. Climate warming may increase aphids' dropping probabilities in response to high temperatures. *J. Insect Physiol.* 58:1456–62
93. Ma G, Ma CS. 2012. Effect of acclimation on heat-escape temperatures of two aphid species: implications for estimating behavioral response of insect to climate warming. *J. Insect Physiol.* 58:303–9
94. Ma G, Rudolf V, Ma CS. 2015. Extreme temperature events alter demographic rates, relative fitness, and community structure. *Glob. Change Biol.* 21:1794–808
95. Macagno ALM, Zattara EE, Ezeakudo O, Moczek AP, Ledonrettig C. 2018. Adaptive maternal behavioral plasticity and developmental programming mitigate the transgenerational effects of temperature in dung beetles. *Oikos* 127:1319–29
96. Martinet B, Lecocq T, Smet J, Rasmont P. 2015. A protocol to assess insect resistance to heat waves, applied to bumblebees (*Bombus latreille*, 1802). *PLOS ONE* 10:e0118591
97. May ML. 1979. Insect thermoregulation. *Annu. Rev. Entomol.* 24:313–49
98. McKechnie AE, Wolf BO. 2019. The physiology of heat tolerance in small endotherms. *Physiology* 34:302–13
99. Meehl GA, Tebaldi C. 2004. More intense, more frequent, and longer lasting heat waves in the 21st century. *Science* 305:994–97
100. Merrill RM, Gutierrez D, Lewis OT, Gutierrez J, Diez SB, Wilson RJ. 2008. Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. *J. Anim. Ecol.* 77:145–55
101. Mitchell KA, Hoffmann AA. 2010. Thermal ramping rate influences evolutionary potential and species differences for upper thermal limits in *Drosophila*. *Funct. Ecol.* 24:694–700
102. Mitton JB, Ferrenberg SM. 2012. Mountain pine beetle develops an unprecedented summer generation in response to climate warming. *Am. Nat.* 179:163–71
103. Montllor CB, Maxmen A, Purcell AH. 2002. Facultative bacterial endosymbionts benefit pea aphids *Acyrthosiphon pisum* under heat stress. *Ecol. Entomol.* 27:189–95
104. Montserrat M, Guzman C, Sahun RM, Belda JE, Hormaza JI. 2013. Pollen supply promotes, but high temperatures demote, predatory mite abundance in avocado orchards. *Agric. Ecosyst. Environ.* 164:155–61
105. Nguyen TT, Michaud D, Cloutier C. 2009. A proteomic analysis of the aphid *Macrosiphum euphorbiae* under heat and radiation stress. *Insect Biochem. Mol. Biol.* 39:20–30
106. O'Sullivan J, MacMillan HA, Overgaard J. 2017. Heat stress is associated with disruption of ion balance in the migratory locust, *Locusta migratoria*. *J. Therm. Biol.* 68:177–85
107. Overgaard J, Kearney MR, Hoffmann AA. 2014. Sensitivity to thermal extremes in Australian *Drosophila* implies similar impacts of climate change on the distribution of widespread and tropical species. *Glob. Change Biol.* 20:1738–50
108. Paaijmans KP, Heinig RL, Seliga RA, Blanford JI, Blanford S, et al. 2013. Temperature variation makes ectotherms more sensitive to climate change. *Glob. Change Biol.* 19:2373–80
109. Piessens K, Adriaens D, Jacquemyn H, Honnay O. 2009. Synergistic effects of an extreme weather event and habitat fragmentation on a specialised insect herbivore. *Oecologia* 159:117–26
110. Pike DA, Webb JK, Shine R. 2012. Hot mothers, cool eggs: Nest-site selection by egg-guarding spiders accommodates conflicting thermal optima. *Funct. Ecol.* 26:469–75

111. Pincebourde S, Casas J. 2015. Warming tolerance across insect ontogeny: influence of joint shifts in microclimates and thermal limits. *Ecology* 96:986–97

112. Pincebourde S, Casas J. 2016. Hypoxia and hypercarbia in endophagous insects: Larval position in the plant gas exchange network is key. *J. Insect Physiol.* 84:137–53

113. Pincebourde S, Casas J. 2019. Narrow safety margin in the phyllosphere during thermal extremes. *PNAS* 116:5588–96

114. Pincebourde S, Murdock CC, Vickers M, Sears MW. 2016. Fine-scale microclimatic variation can shape the responses of organisms to global change in both natural and urban environments. *Integr. Comp. Biol.* 56:45–61

115. Pincebourde S, Sinoquet H, Combes D, Casas J. 2007. Regional climate modulates the canopy mosaic of favourable and risky microclimates for insects. *J. Anim. Ecol.* 76:424–38

116. Pincebourde S, Suppo C. 2016. The vulnerability of tropical ectotherms to warming is modulated by the microclimatic heterogeneity. *Integr. Comp. Biol.* 56:85–97

117. Porras MF, Navas CA, Marden JH, Mescher MC, De Moraes CM, et al. 2020. Enhanced heat tolerance of viral-infected aphids leads to niche expansion and reduced interspecific competition. *Nat. Commun.* 11:1184

118. Portner H. 2001. Climate change and temperature-dependent biogeography: oxygen limitation of thermal tolerance in animals. *Naturwissenschaften* 88:137–46

119. Posledovich D, Toftegaard T, Wiklund C, Ehrlen J, Gotthard K. 2018. Phenological synchrony between a butterfly and its host plants: experimental test of effects of spring temperature. *J. Anim. Ecol.* 87:150–61

120. Potter KA, Davidowitz G, Woods HA. 2011. Cross-stage consequences of egg temperature in the insect *Manduca sexta*. *Funct. Ecol*. 25:548–56

121. Potter KA, Woods A, Pincebourde S. 2013. Microclimatic challenges in global change biology. *Glob. Change Biol.* 19:2932–39

122. Prange HD. 1990. Temperature regulation by respiratory evaporation in grasshoppers. *J. Exp. Biol.* 154:463–74

123. Radchuk V, Turlure C, Schtickzelle N. 2013. Each life stage matters: the importance of assessing the response to climate change over the complete life cycle in butterflies. *J. Anim. Ecol.* 82:275–85

124. Robinet C, Roques A. 2010. Direct impacts of recent climate warming on insect populations. *Integr. Zool.* 5:132–42

125. Ruel JJ, Ayres MP. 1999. Jensen's inequality predicts effects of environmental variation. *Trends Ecol. Evol.* 14:361–66

126. Saudreau M, Ezanic A, Adam B, Caillon R, Walser P, Pincebourde S. 2017. Temperature heterogeneity over leaf surfaces: the contribution of the lamina microtopography. *Plant Cell Environ*. 40:2174–88

127. Sentis A, Hemptinne JL, Brodeur J. 2013. Effects of simulated heat waves on an experimental plant-herbivore-predator food chain. *Glob. Change Biol.* 19:833–42

128. Sentis A, Hemptinne JL, Brodeur J. 2017. Non-additive effects of simulated heat waves and predators on prey phenotype and transgenerational phenotypic plasticity. *Glob. Change Biol.* 23:4598–608

129. Sinclair BJ, Marshall KE, Sewell MA, Levesque DL, Willett CS, et al. 2016. Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? *Ecol. Lett.* 19:1372–85

130. Sinclair BJ, Vernon P, Klok CJ, Chown SL. 2003. Insects at low temperatures: an ecological perspective. *Trends Ecol. Evol.* 18:257–62

131. Slimen B, Najar T, Ghram A, Abdrrabba M. 2016. Heat stress effects on livestock: molecular, cellular and metabolic aspects, a review. *J. Anim. Physiol. Anim. Nutr.* 100:401–12

132. Smith MD. 2011. An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. *J. Ecol.* 99:656–63

133. Stevenson RD. 1985. The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. *Am. Nat.* 126:362–86

134. Stillman JH. 2019. Heat waves, the new normal: Summertime temperature extremes will impact animals, ecosystems, and human communities. *Physiology* 34:86–100

135. Stuhldreher G, Hermann G, Fartmann T. 2014. Cold-adapted species in a warming world—an explorative study on the impact of high winter temperatures on a continental butterfly. *Entomol. Exp. Appl.* 151:270–79
136. Suggitt AJ, Gillingham PK, Hill JK, Huntley B, Kunin WE, et al. 2011. Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos* 120:1–8
137. Sunday JM, Bates AE, Kearney MR, Colwell RK, Dulvy NK, et al. 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *PNAS* 111:5610–15
138. Tougeron K, Damien M, Le Lann C, Brodeur J, van Baaren J. 2018. Rapid responses of winter aphid-parasitoid communities to climate warming. *Front. Ecol. Evol.* 6:173
139. Tseng M, Kaur KM, Pari SS, Sarai K, Chan D, et al. 2018. Decreases in beetle body size linked to climate change and warming temperatures. *J. Anim. Ecol.* 87:647–59
140. Vallières R, Rochefort S, Berthiaume R, Hébert C, Bauce É. 2015. Effect of simulated fall heat waves on cold hardiness and winter survival of hemlock looper, *Lambdina fiscellaria* (Lepidoptera: Geometridae). *J. Insect Physiol.* 73:60–69
141. van Heerwaarden B, Kellermann V, Sgro CM. 2016. Limited scope for plasticity to increase upper thermal limits. *Funct. Ecol.* 30:1947–56
142. Vasseur DA, DeLong JP, Gilbert B, Greig HS, Harley CDG, et al. 2014. Increased temperature variation poses a greater risk to species than climate warming. *Proc. R. Soc. B* 281:20132016
143. Verberk WC, Bilton DT. 2013. Respiratory control in aquatic insects dictates their vulnerability to global warming. *Biol. Lett.* 9:20130473
144. Walsh BS, Parratt SR, Hoffmann AA, Atkinson D, Snook RR, et al. 2019. The impact of climate change on fertility. *Trends Ecol. Evol.* 34:249–59
145. Wehner R, Wehner S. 2011. Parallel evolution of thermophilia: daily and seasonal foraging patterns of heat-adapted desert ants: *Cataglyphis* and *Ocymyrmex* species. *Physiol. Entomol.* 36:271–81
146. Woods HA. 2013. Ontogenetic changes in the body temperature of an insect herbivore. *Funct. Ecol.* 27:1322–31
147. Woods HA, Dillon ME, Pincebourde S. 2015. The roles of microclimatic diversity and of behavior in mediating the responses of ectotherms to climate change. *J. Therm. Biol.* 54:86–97
148. Xing K, Hoffmann A, Ma CS. 2014. Does thermal variability experienced at the egg stage influence life history traits across life cycle stages in a small invertebrate? *PLOS ONE* 9:e99500
149. Zani PA, Cohnstaedt LW, Corbin D, Bradshaw WE, Holzapfel CM. 2005. Reproductive value in a complex life cycle: heat tolerance of the pitcher-plant mosquito, *Wyeomyia smithii*. *J. Evol. Biol.* 18:101–5
150. Zhang B, Leonard SP, Li Y, Moran NA. 2019. Obligate bacterial endosymbionts limit thermal tolerance of insect host species. *PNAS* 116:24712–18
151. Zhang W, Chang XQ, Hoffmann AA, Zhang S, Ma CS. 2015. Impact of hot events at different developmental stages of a moth: the closer to adult stage, the less reproductive output. *Sci. Rep.* 5:10436
152. Zhang W, Rudolf V, Ma CS. 2015. Stage-specific heat effects: Timing and duration of heat waves alter demographic rates of a global insect pest. *Oecologia* 179:947–57
153. Zhang W, Zhao F, Hoffmann AA, Ma CS. 2013. A single hot event that does not affect survival but decreases reproduction in the diamondback moth, *Plutella xylostella*. *PLOS ONE* 8:e75923
154. Zhao F, Hoffmann AA, Xing K, Ma CS. 2017. Life stages of an aphid living under similar thermal conditions differ in thermal performance. *J. Insect Physiol.* 99:1–7
155. Zhao F, Zhang W, Hoffmann AA, Ma CS. 2014. Night warming on hot days produces novel impacts on development, survival and reproduction in a small arthropod. *J. Anim. Ecol.* 83:769–78
156. Zhu L, Wang L, Ma CS. 2019. Sporadic short temperature events cannot be neglected in predicting impacts of climate change on small insects. *J. Insect Physiol.* 112:48–56

RELATED RESOURCES

1. Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, et al. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Glob. Change Biol.* 8:1–16

2. Grant PR, Grant BR, Huey RB, Johnson MTJ, Knoll AH, Schmitt J. 2017. Evolution caused by extreme events. *Philos. Trans. R. Soc. B* 372:20160146
3. Hance T, van Baaren J, Vernon P, Boivin G. 2007. Impact of extreme temperatures on parasitoids in a climate change perspective. *Annu. Rev. Entomol.* 52:107–26
4. Harris R, Beaumont LJ, Vance TR, Tozer CR, Remenyi TA, et al. 2018. Biological responses to the press and pulse of climate trends and extreme events. *Nat. Clim. Change* 8:579–87
5. Sgrò CM, Terblanche JS, Hoffmann AA. 2016. What can plasticity contribute to insect responses to climate change? *Annu. Rev. Entomol.* 61:433–51
6. Ummenhofer CC, Meehl GA. 2017. Extreme weather and climate events with ecological relevance: a review. *Philos. Trans. R. Soc. B* 372:20160135
7. van de Pol M, Jenouvrier S, Cornelissen JH, Visser ME. 2017. Behavioural, ecological and evolutionary responses to extreme climatic events: challenges and directions. *Philos. Trans. R. Soc. B* 372:20160134
8. Vázquez DP, Gianoli E, Morris WF, Bozinovic F. 2017. Ecological and evolutionary impacts of changing climatic variability. *Biol. Rev.* 92:22–42