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Direct and indirect effects of altered temperature regimes and phenological mismatches on insect populations

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Climate change is transforming ecosystems by altering species ranges, the composition of communities, and trophic interactions. Here, we synthesize recent reviews and subsequent developments to provide an overview of insect ecological and evolutionary responses to altered temperature regimes. We discuss both direct responses to thermal stress and indirect responses arising from phenological mismatches, altered host quality, and changes in natural enemy activity. Altered temperature regimes can increase exposure to both cold and heat stress and result in phenological and morphological mismatches with adjacent trophic levels. Host plant quality varies in a heterogenous way in response to altered temperatures with both increases and decreases observed. Density-dependent effects, spatial heterogeneity, and rapid evolutionary change provide some resilience to these threats.

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Introduction

The profound environmental transformation resulting from global climate change is a major threat to biodiversity. Altered weather and precipitation patterns as well as increased frequencies of extreme events are important drivers of insect population declines [1,2,3•,4•,5•]. Altered temperature regimes can affect insects both directly (e.g. by exceeding their physiological thermal limits) and indirectly, through phenological alterations [6,7•,8] and via adjacent trophic level effects [9•,10]. These effects are not always negative, however. Warmer temperatures can benefit some insect populations by allowing them to grow faster and complete more generations in a growing season, depending on local initial conditions and population-specific thermal sensitivities [11]. Insects possess characteristics that can allow them to survive and adapt to rapid environmental change, including high mobility, remarkable phenotypic plasticity, and short generation times [12,13•]. However, extreme temperatures can push insects beyond their adaptive limits, disrupting interactions and food webs, and ultimately leading to outbreak-breakdown cycles that affect ecosystem functioning and resilience [4•,14].

Over the last several decades, empirical studies documenting the physiological, ecological, and evolutionary effects of altered temperature regimes on insects have proliferated, but major gaps remain. Assessing the magnitude and pervasiveness of the threat that climate change poses for insects is complicated by a paucity of long-term monitoring data and by the cyclic dynamics of insect populations that often include recurrent outbreaks and declines caused by a variety of well-known intrinsic and extrinsic factors [15]. Additionally, attributing population responses to causative pathways of direct and indirect effects is challenging to do in practice. Nonetheless, we attempt to separate them conceptually in this review to highlight emerging patterns and to encourage future studies that explicitly address these important questions. Here, we synthesize 29 recent reviews and subsequent developments to provide an overview of insect ecological and evolutionary responses to direct and indirect effects of altered temperature regimes. More specifically, we discuss 1) direct responses to thermal stress, and 2) indirect responses arising from phenological mismatches, decreased resource quality, and changes in arthropod natural enemy activity.

Direct effects of thermal stress

Warmer temperatures can result in increased exposure of insects to both heat and cold stress (Table 1). Heat stress impairs insect neural performance, muscular control, immune function, and can result in coma and eventually death [16,17••]. In addition, exposure to heat stress can result in morphological changes that may compromise dispersal capabilities [18]. As a result, weather events that expose insects to higher temperatures and lower humidity (e.g. summer droughts) often result in increased mortality [19] and may trigger population declines [20,21]. Multiple

Table 1

Recent studies documenting direct effects of altered temperature regimes on insects, bold numbers correspond to review articles and italics to studies in which the focal species is not a model organism or agricultural pest.

Direct effects

Exposure to:	*Alterations in:*
Cold stress [4•**4•**,30,31]	Development time [19,78]
Heat stress [4•**4•**,17•**17••**]	Growth [78,79]
Depletion of energy reserves [25]	Mortality [4•**4•**,17•**17••**,26,27]
Population declines [14,20]	Diapause timing [19**19**,25**25**,55•**55•**]
Population outbreaks [20]	Voltinism [13•]
Loss of endosymbiont protection against parasitoids [19]	Caterpillar capacity to induce plant defenses [78]
	Immune [16,19**19**]
	Phenology [3•**3•**,18,45,50**50**,55•**55•**,62]
	Wing length [18,79]
	Body size [18,80]
	Metabolic rate [66]
	Expression of polyphenisms [81]

factors affect heat tolerance, including sex, life stage, color, body size, presence of other environmental stressors, resource deprivation, parent's thermal environment [17••], caste [22••], and the presence of endosymbionts. Bacteria such as *Serratia symbiotica* and *Rickettsia* can protect their hosts against heat stress [19]. In addition, insects use a diverse array of behavioral and physiological mechanisms to mitigate the harmful effects of heat stress. Many of these mechanisms are energetically costly and these costs can restrict the evolution of thermal tolerance [17••]. Consistently, upper thermal limits are more conserved among species and life stages than lower thermal limits [17••,23,24•], suggesting greater negative impacts on populations when upper limits are exceeded.

Warmer temperatures during autumn and winter can have stressful effects despite falling within insects' physiological thermal limits. Warmer winters can result in depletion of energy reserves of overwintering insects [25], as well as increased mortality of both overwintering larvae [26] and diapausing pupae [27]. Counterintuitively, milder winters can result in increased exposure to cold stress. Snow often provides insulation from extreme cold, so milder winters in which this protective layer melts can increase exposure to inclement temperatures [25]. Additionally, warmer temperatures during winter and spring can trigger premature diapause termination and advance phenology [25,28]. Phenological advances in spring can expose vulnerable life stages to frosts [20].

Cold stress affects multiple metabolic pathways, and can cause mechanical damage and cellular dehydration, loss of neuromuscular function, and imbalance in ion and water homeostasis [29,30]. These metabolic changes can result in increased incidence of deformities, premature pupation, decreased mobility, longevity, and fecundity, and male biased sex ratios of parasitoids [9•]. Thus, events such as late spring frosts can trigger dramatic population declines for a multitude of reasons [20].

Insects possess a diversity of adaptations to cope with cold stress [12,25,29], and traits associated with cold hardiness exhibit variable genetic architecture, heritability, and a strong genetic basis for plasticity [25]. In addition, cold hardiness [25] and lower thermal limits vary within and among species and life stages [31,32]. Notably, there is some evidence suggesting that cold hardiness can evolve independently among life stages in *Drosophila melanogaster* [33] and the butterfly *Bicyclus aninana* [34]. Biotic interactions can also affect cold hardiness, as when hymenopteran parasitoids physiologically manipulate their hosts to avoid freezing by lowering their supercooling points [9•]. Taken together, these variable patterns indicate high potential for cold hardiness to evolve [25]. Despite this potential, studies documenting cold hardiness evolution in response to recent climate change are lacking [25]. By contrast, there are multiple studies showing recent local adaptation in diapause induction and termination [25].

Terrestrial insects can thermoregulate behaviorally and implement microenvironmental modifications to buffer stressful temperatures. Some of the most striking examples come from social insects, as they can build complex insulating structures (e.g. termite nests) and engage in collaborative thermoregulation. Bees can regurgitate gut fluids that cool the nest as they evaporate, and they also use the bodies of workers as insulation to protect the young from heat stress [22••]. While sociality allows for sophisticated thermoregulation strategies, it also entails trade-offs, for example, cuticular hydrocarbons play a role in thermoregulation, but selection to enhance this role can be restricted due to their key function in colony communication [22••]. Other thermoregulation strategies simply consist in moving across microhabitats. Vulnerability to climate change can be buffered or magnified by the small microhabitats terrestrial insects can exploit, as surface temperatures can differ greatly (>30°C) from air temperatures, and among features of the same tree trunk, rock or set of leaves (~10°C) [35]. By contrast, microhabitat variation is more restricted in aquatic environments, increasing insect vulnerability to climate change [36]. While still water bodies exhibit thermal stratification, water's high-specific heat capacity buffers temperature changes, particularly in rapidly moving streams, resulting in a more homogeneous thermal environment [36]. In high-elevation streams, the effect of warmer temperatures on insects is further complicated by changes in oxygen concentration, water flow, ultraviolet radiation and salinity [37]. Warming of streams stimulates metabolic demand for oxygen [37] and can lead to declines in insect abundance and altered community composition [38].

At the macro scale, vulnerability to warming can be estimated by calculating thermal safety margins, which are the difference between mean habitat temperature and the insect's maximum thermal limits [39]. Tropical species were believed to be particularly vulnerable to warming due to their smaller safety margins, as they historically experienced ambient temperatures close to their physiological thermal limits [39]. However, a new analysis suggests that temperate species might face levels of threat from climate change similar to those of their tropical counterparts [40]. This re-analysis accounted for latitudinal differences in activity periods by calculating thermal limits using mean temperature during the months insects are active, instead of annual mean temperature [40]. There are, however, geographic areas of particular interest because of the accelerated rates of change they are experiencing. High elevation streams, where aquatic insects are the dominant fauna [37], and the arctic, where snow cover is the main regulator of phenology [41] are relatively understudied areas that are experiencing rapid changes. In the Arctic, warming has resulted in an increase of populations of herbivores and a decrease of detritivores [41].

In addition to a geographic bias, taxonomic and methodological biases also affect our understanding of insect responses to thermal stress. These responses have been studied mostly in laboratory settings [24•] and with a strong focus on agricultural pests [11,42,43], model organisms [17••,29], and, in the case of social insects, bees and ants [22••]. Most of the work on genetic variation in heat resistance, selection experiments, and evolutionary change have been performed in *Drosophila* [17••,24•]. This bias is problematic because insects are a heterogeneous group and vary in key traits that mediate their ability to detect and respond to warming. Recent studies focusing on species outside these popular study groups are highlighted in Tables 1 and 2.

Indirect effects — phenological mismatches

Temperature, rainfall, and photoperiod are the main drivers of phenology [12,44,45]. Thus, shifts in temperature regimes that alter the historical correlation of thermal and photoperiodic conditions can disrupt insect seasonal activities (e.g. breeding) [46]. Warmer temperatures during the growing season typically accelerate ectotherm development; however, not all species respond at the same rate, which can result in consumers missing resource availability [47]. In temperate areas, warming during winter can result in delayed phenology, because some species require exposure to a certain period of low temperatures before they can resume development in the spring [12,48,49••]. More commonly, however, warmer springs result in phenological advances and accelerated development [25]. Differences in sensitivity and responsiveness to these environmental changes can result in phenological mismatches and disrupt historical patterns of trophic interactions [47,50].

Phenological mismatches arise when consumers and resources occur asynchronously. Assessing synchrony at the community level involves evaluating the overlap of the occurrence distribution of the relevant phenophase of consumers and producers [7•]. For herbivores, synchrony involves fitting their larval stage within the period of foliage availability [51]; for pollinators, synchronizing foraging with flower occurrence; for parasitoids, co-existence between ovipositing adults and susceptible life stages of the hosts. The shapes of these occurrence distributions vary according to both heat accumulation and life history traits. The degree of overlap in the distributions of interactants, as well as the abundance of resources can define the severity and outcomes of mismatches [7•]. For example, when resources are abundant, mild mismatches, in which occurrence curves partially overlap, are not likely to have negative effects on consumers [7•]. Evaluating the role of recent climate change in triggering or exacerbating phenological mismatches requires establishing a pre-climate change baseline, which is the degree of synchrony a given interaction had before recent climate change (∼1980) [52]. This baseline is important because cases of adaptive asynchrony are commonly due to factors other than climate change, including trade-offs such as fertility vs offspring survival, or bet-hedging strategies [53,54]. For example, larval starvation due to asynchrony with host plants is common in the bay Checkerspot (*Euphydryas editha*), because of a trade-off between fertility and offspring survival. Females that feed for longer periods are more fecund, but their offspring are less likely to occur within the period of host plant availability [53].

The likelihood of a phenological mismatch, as well as its outcome for producers and consumers, varies according to interaction type, consumer diet breadth, and the environmental cues triggering phenology of each trophic level. Mutualisms, where both interactants experience selection for synchrony, are expected to be more robust to mismatches than antagonisms, where interactants experience opposite pressures, as synchrony is favorable for consumers and unfavorable for producers. Parasitoids constitute a special case of antagonism because they often follow phenological cues similar to those of their hosts and even directly from their host, by engaging in endogenous physiological synchronization [6,55•]. Despite this intimacy, a long-term field study showed that different weather components explain variation in the phenology of aphids and their parasitoids [49••].

Table 2

Recent studies documenting indirect effects of altered temperature regimes on insects, bold numbers correspond to review articles and italics to studies in which the focal species is not a model organism or agricultural pest

Indirect effects	
Phenological mismatches	
[6**6**,7•**7•**,8**8**,9•**9•**,45*45*,51,52**52**,53*53*,56*57*,59*59*,60*60*,61*61*,82*82*,83*83*]	
Altered performance of parasitoids:	*Altered resource quality:*
Survival [4•**4•**,9•**9•**,19,68]	Foliage quality [10**10**,13•**13•**,66]
Development [4•**4•**,9•**9•**,68]	Concentration of plant defenses [4•**4•**,78]
Flight [4•**4•**,9•**9•**]	Emission of volatile compounds [4•**4•**,9•**9•**,71*71*]
Host-finding efficiency [4•**4•**,9•**9•**]	Plant/floral morphology [4•**4•**,8**8**]
Oviposition behavior [4•**4•**]	Plant physiology [4•**4•**]
Parasitism rate [19**19**,82*82*]	Plant biomass [78]
Host preference [9•**9•**,19**19**]	Trichome density [78]
Sex allocation [9•**9•**,19**19**]	
Mating [9•**9•**]	Host quality for parasitoids [19**19**]
Fecundity [9•**9•**]	
Altered performance of predators:	Altered relationships with endosymbionts [19**19**,75*75*,76,77]
Consumption rate [4•**4•**]	
Growth [4•**4•**]	
Behavior [4•**4•**,72*72*,23*23*]	

Studies documenting the consequences of phenological mismatches between plants and pollinators have focused primarily on the effects on plant fitness. Thus, there are multiple field empirical studies documenting detrimental effects of phenological mismatches on plant reproduction [28,56], but a dearth of studies documenting the effects on pollinator populations or individual fitness [8]. A simulation using empirical interaction network data found that pollinators are expected to experience severe population declines due to mismatches [57]. Consistently, an analysis of the same historical data set identified phenological mismatches between pollinators and flower resources as a factor contributing to the extirpation of pollinators and degradation of plant-pollinator interaction networks [58], with higher vulnerability of specialists than generalists [8,58]. An analysis of over 2000 species of European pollinators documented not only phenological advances, but also flight period reductions in the last 60 years; as a result, flight period overlap of pollinators decreased, limiting redundancy and complementarity of pollinator assemblages, which could result in decreases in pollinator function [59]. An experimental study on two species of solitary bees (*Osmia*) showed that males advanced their spring phenology in response to warmer temperatures, but females did not, and that male bees emerged on or before the onset of host flowering and females after flowering [60]. A recent study reported a pollinator behavior that, if widespread, could serve to mitigate asynchrony with floral resources. Pashalidou *et al.* [61] found that when facing pollen scarcity, workers of the bumblebee *Bombus terrestris* damaged plants, and this damage accelerated flower production. To our knowledge this is the only study documenting such a response, so it remains unclear how ubiquitous this behavior is for pollinators.

There are more studies directly documenting adverse effects of phenological mismatches on consumers in plant-herbivore than in plant-pollinator interactions. Mismatches among herbivores and their host plants can have adverse effects on the consumers and trigger evolutionary responses. The best documented example of recent evolutionary change in an insect due to the pressures of phenological mismatches is the case of the winter moth (*Operophtera brumata*), whose larvae hatch in spring and feed on expanding oak foliage. Warmer temperatures have led to earlier hatching and have precipitated caterpillar population declines; after a decade of this selective pressure, the *O. brumata* population responded by delaying its hatching time, decreasing asynchrony with foliage availability [7•,62]. However, not all phenological mismatches have negative consequences on insect populations, as mechanisms such as density-dependent compensation can offset negative effects on population size [49••]. In this context, density-dependent compensation occurs when asynchrony-triggered mortality is compensated by a subsequent increase in fecundity of the survivors due to reduced competition, resulting in a stable population size.

Environmental heterogeneity is another factor that may buffer consumers from phenological mismatches [28]. Caterpillar peak abundance has been found to vary across habitat types within a region [63] and across altitudinal gradients [64]. In addition, intraspecific and interspecific sensitivity to phenological cues can vary across both space and time [45]. A study of butterfly communities in a Mediterranean ecosystem where seasonality is driven by temperature and rainfall, showed that early spring species were more sensitive to temperature than late species, and that butterfly phenology responded more strongly to variation in temperature than to rainfall [45]. In tropical ecosystems, rainfall mediates plant-herbivore relationships [65], so altered precipitation patterns could trigger asynchrony between consumers and producers; however, this possibility remains understudied as research on phenological mismatches has been strongly biased towards temperate systems [48].

Indirect effects — host quality and natural enemies

Altered temperature regimes can also affect insects indirectly by altering the quality of the resources they utilize and/or the performance of their natural enemies (Table 2). These alterations are important because resource quality influences numerous life history traits including lifespan, fecundity, immune response, metabolic and growth rates, and tolerance to thermal stress [10,26,43,66]. Warming can affect plant traits relevant for pollinators such as plant height, floral diameter, volatile emissions, and the nutritional quality of pollen and nectar [8]. In addition, changes in floral morphology, in conjunction with decreasing body size of insects (a common response to temperature increases), can create morphological mismatches between plants and pollinators, particularly for specialist pollinators [8]. Miller-Struttman *et al.* [67] found that two alpine bumblebee species have evolved shorter tongue lengths over the past 40 years, but the flowers they pollinate have not become shallower, suggesting that generalist pollinators will be more successful as this environment continues to change. Similarly, higher temperatures can affect foliage quality for herbivores, as temperature affects plant growth, primary production, and inducibility of plant defenses (Table 2); however, the effects of warming on foliage quality are not uniform, as both increases and decreases in nutrient concentration have been reported [4•,10,13•]. Moreover, many aspects of plant quality are more heavily influenced by atmospheric CO_2 concentration as well as drought, which are simultaneously increasing due to climate change [10,13•,21]. Altered foliage quality in combination with the direct effects of thermal stress on herbivores often results in increased feeding rates, particularly in agricultural systems [13•].

Agricultural systems face the additional challenge that parasitoids, important biocontrol agents, are particularly susceptible to altered temperature regimes. Parasitoids and other natural enemies frequently exhibit lower thermal tolerances than their hosts [9•,68] and have to cope with the cumulative effects of warming on lower trophic levels (Table 2). For example, water-stressed plants hosted fewer and smaller aphids, which in turn exhibited reduced parasitism rates [69,70]. Many parasitoids rely on chemical cues produced by plants to locate hosts, but the integrity of these signals can be compromised by altered temperature regimes, resulting in failed parasitoid recruitment and decreased rates of parasitism [9•]. Similarly, temperature can influence volatile emissions of predators, which in turn can affect predator-prey interactions. Ladybeetle larvae emit chemicals which inform oviposition decisions of conspecific females, and Sentis *et al.* [71] found that increased temperature altered ladybeetle infochemical emission and perception. The alterations in infochemicals resulted in decreased oviposition at higher temperatures, which should reduce local predation pressure on aphids.

Altered temperature regimes can also influence the behavior of natural enemies. Heat waves and cold snaps can have negative consequences for parasitoid flying, feeding, and host finding, resulting in decreased performance [9•]. Likewise, exposure to thermal stress can alter predator growth and consumption rates [4•]. Some predators can mitigate the effects of suboptimal temperatures by changing their habitat domain or foraging behavior. Sit-and-wait ambush spiders have been shown to alter their position in the grass canopy and adjust the time of day during which they forage in response to increased temperature, subsequently influencing predation on grasshopper prey [72,73]. High temperatures can also decrease foraging success of insectivorous birds by drying out soil, which makes it more difficult for birds to probe for invertebrate prey [74].

Finally, endosymbionts are well-known for their ability to mediate interactions between hosts and parasitoids by conferring resistance to hosts through multiple pathways, including enhanced encapsulation response and improved thermal tolerance [19]. However, endosymbionts themselves are sensitive to changes in temperature so the benefits they provide to hosts are also subject to change [19]. For example, endosymbionts that typically protect their aphid hosts against parasitoids (e.g. *Hamiltonella defensa*) fail to do so under heat stress [75]. Moreover, high temperatures can result in loss of host endosymbionts altogether, as evidenced by reduced vertical transmission of *Wolbachia* [76] and *Spiroplasma* [77]. Additional field studies, particularly in natural systems, are necessary to further our understanding of temperature effects on tri-trophic dynamics.

Conclusions

Altered temperature regimes affect insects through multiple mechanisms, both directly impacting their metabolism and phenology, and indirectly through their effects on adjacent trophic levels. Direct and indirect pressures exerted by thermal stress occur simultaneously and their distinction in practice is complicated; however, a conceptual separation of these effects can aid in study design and interpretation. Understanding the responses of insect populations to altered temperature regimes requires the integration of results from laboratory and field experiments, as well as long-term monitoring programs. Thanks to a proliferation of studies on thermal tolerances and insect responses at a variety of organizational levels, this integration is increasingly possible. However, some challenges remain given the rich diversity of insect taxa and variation in their traits. More field studies, particularly in natural systems, are necessary to further our understanding of temperature effects on insects that manifest through indirect effects on adjacent trophic levels. Similarly, there is a remarkable imbalance in the predicted effects of phenological mismatches on pollinators and the dearth of field studies documenting their individual or population-level responses. The assessment of these mismatches has been biased, focusing mainly on the effects on plants, probably due to the challenges involved in measuring pollinator mortality due to starvation. Phenological mismatches may very well be an underappreciated mechanism of insect decline, overlooked due to the logistical constraints associated with their assessment.

Altered temperature regimes pose an important challenge for ectotherms and it is particularly worrisome that insects appear to exhibit stronger potential for evolutionary change in response to cold stress than to heat stress. However, spatial heterogeneity, density-dependent effects, and short-term evolutionary change in seasonal traits can provide some resilience to the negative effects of climate change.

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Conflict of interest statement

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