Complex responses of insect phenology to climate change
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Insect phenologies are changing in response to climate warming. Shifts toward earlier seasonal activity are widespread; however, responses of insect phenology to warming are often more complex. Many species have prolonged their activity periods; others have shown delays. Furthermore, because of interspecific differences in temperature sensitivity, warming can increase or decrease synchronization between insects and their food plants and natural enemies. Here, I review recent findings in three areas — shifts in phenology, changes in voltinism, and altered species interactions — and highlight counterintuitive responses to warming caused by the particularities of insect life cycles. Throughout, I emphasize how an appreciation of the evolutionary processes shaping insect life histories is necessary to forecast changes in insect phenology and their demographic consequences.

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Introduction
Changes in phenology — the seasonal timing of biological events — have been among the most conspicuous signs of global warming. Rising temperatures have been accompanied by earlier first appearances of spring flowers, migratory birds, and breeding frogs, to list just a few examples [1–3]. By the early 2000s, long-term records showed that first flights of butterflies had advanced by as much as a month over the preceding three decades [4,5]. New and longer-term datasets continue to add evidence of a general shift of springtime phenologies toward earlier dates in temperate-region and polar-region insects, in association with rising temperatures ([6–8], but see [9]).

Although advances in springtime phenology are widespread, they are not universally observed, nor are they the only way in which insect phenology can be altered by climate change. As ectotherms, insects are strongly affected by environmental temperatures, but insect phenologies are also shaped by other features of their biology. Diapause, a physiologically controlled state of dormancy, is often a major component of insect life histories [10]. Photoperiod (daylength) cues are important in dictating developmental decisions, including diapause termination, in many insects; as such, they can interact with temperature in complex ways to influence phenology. Furthermore, in the many insects that complete variable numbers of generations in a year, warming can affect generation time. Finally, evolutionary responses to warmer and longer seasons may lead to phenological changes that differ from those one would expect based on phenotypic plasticity alone.

In this article, I start by considering some reasons for variation in how insect phenology responds to warming — in other words, why climate change is not always accompanied by springtime advances. In the next section, I discuss how warming can change the number of generations per year (voltinism), with consequences for population growth and range expansion. However, predicting changes in voltinism is complex, because of the frequent involvement of photoperiod cues and diapause [11]. Lastly, I review the likelihood of — and the likely consequences of — mismatched shifts in phenologies of interacting species. My focus will be predominantly (though not exclusively) on temperate and high-latitude regions, in which seasonality is conspicuous, well-studied, and defined primarily by temperature (rather than precipitation). Throughout, I emphasize how an understanding of insect life histories — both the mechanisms underlying them and the evolutionary processes that shape them — is necessary to make sense of these responses and to predict their long-term consequences for insect populations.

Explaining variation in phenological shifts
Insects commonly respond plastically to warm temperatures by speeding up their rates of development. As a result, warm springs in temperate regions are typically associated with early insect emergence and activity [12–16]. However, the temperature–phenology relationship is more complex than this generalization suggests, and it tends to be strongest for species that are active early in the season — frequently those that overwinter as adults [6,9,14,15,17]. Late-season species sometimes fail to respond to warming, or respond in the opposite way (i.e., with delays) [17,18]. Furthermore, many species that first
appear early in the season (and whose dates of first appearance have been getting earlier) are also extending their activity periods later in the season [4,8,16,19]. These patterns are not easily explained as effects of heat on rates of development, although in some species, they may be the result of an added late-summer generation (see ‘Changes in voltinism’, below). In some cases, lengthening of the active season, or delays in first appearances of adults, may reflect an evolutionary response to longer growing seasons. For example, Buckley et al. [20**] suggest that longer growing seasons have relaxed selection for rapid development in some high-elevation grasshoppers, such that these insects now reach maturity later — but at a larger size — than in the past. Delayed activity or emergence might also reflect dependence of phenology on cues such as rainfall (e.g., [21]), the seasonality of which may also be changing. Alternatively, failure of late-season species to respond to winter or springtime warming may simply indicate that these species overwinter in a diapause state in which they are refractory to warmth [22]. Finally, extended activity periods could be the result of reduced population synchrony at the time of emergence. Many insects require an extended period of cool temperatures in winter for diapause development [10,23,24*], and the loss or reduction of this chilling period can increase among-individual variation in timing of emergence [24*,25].

Reductions in winter chilling also tend to increase the amount of heat required subsequently for emergence [24*,25,26]. Consequently, winter warming may partially negate the phenological effects of spring and summer warming. Reduced winter chilling could therefore explain why some insects have not shown the expected advance in springtime phenology; however, to my knowledge, this has not yet been demonstrated. In the processionary moth Thaumetopoea processionea, for example, Wagenhoff et al. [27] showed that cold days (<0 °C) in winter reduce the subsequent heat requirement for egg-hatching. Nevertheless, springtime warming has been more than adequate to compensate for a long-term reduction in the number of cold days: the authors’ phenology model for this species, applied to long-term weather records, suggests that moth egg hatch has shifted earlier since the 1940s.

These findings illustrate several reasons to expect varied phenological responses to warming. ‘Failure’ of a population to advance its activity period need not indicate a lack of plasticity or the attainment of a limit to phenological change (cf. [8,28]); rather, it may reflect an appropriate plastic response to an environment that is changing along multiple axes simultaneously (e.g., warming in winter as well as in spring). Alternatively, a lack of phenological advance could reflect the fact that organisms are under selection to maximize lifetime reproductive output, which is not necessarily achieved by speeding up the life-cycle. Evolutionary forces may therefore drive phenologies in a different direction than what is expected as a plastic response to warming (see [29]). Researchers must consider these possibilities when interpreting unexpected shifts in phenology.

Changes in voltinism
Longer and warmer growing seasons are enabling many insect populations to complete more generations per year than was typically possible in the past. Since 1980, several European Lepidoptera species have added a second or third generation to what were previously univoltine or bivoltine life cycles [30]; in Finland, an increasing number of moth species have become multivoltine [31]. Warmer and longer summers will likely allow several species, including North American spruce beetles (Dendroctonus rufipennis), to complete a generation in a single year in areas where previously a generation took at least two [32,33]. Some observations suggest that mountain pine beetles (Dendroctonus ponderosae) have switched from a univoltine to a bivoltine life cycle in Colorado [34], although this finding has been contested [35,36]. Other economically important insects, such as the bark beetle Ips typographus in northern Europe [37], maize borers (Chilo partellus) in Africa [38], and mealybugs (Pseudococcus solenopsis) in tropical areas worldwide [39], are expected to achieve more generations per year as temperatures rise. Such changes could increase population growth, with potentially devastating consequences for the plants attacked by these insects. On the other hand, rapid development at higher temperatures is often accompanied by smaller size at maturity and, hence, lower fecundity [40], which might counteract the demographic impacts of shorter generations. Regardless, since the ability to complete a generation within a growing season can dictate species’ range limits [41], reductions in generation times owing to climate change may allow range expansion toward the poles [42] and toward higher elevations.

However, some insects are not expected to increase the number of generations per year, despite rising temperatures. Many insects have an obligate seasonal diapause and are not multivoltine even in warm parts of their range [43]. Others may be capable of multiple generations, but fail to experience the necessary photoperiodic cues to prevent diapause and stimulate continued development. Grevstad and Coop [44**] have pointed out that because the seasonal pace of heat accumulation is shifting relative to photoperiod — which is unaffected by climate change — some insects could even experience a reduction in voltinism as the climate warms. This could occur, for example, in a normally multivoltine population that enters diapause when a certain life stage coincides with short, post-solstice daylengths (a signal of the imminent end of the growing season). As warmer springs allow more rapid development, these insects might reach the photoperiod-sensitive stage during the short days before the
summer solstice and be induced to enter an early diapause. However, this phenomenon has not yet been demonstrated empirically as a response to climate change.

Finally, some insects may suffer demographically from attempting a second generation in areas where summer temperatures have warmed but seasons are not yet long enough to allow completion of the second generation. Chinnellato et al. [45] have presented data consistent with such an effect in a southern European population of the normally univoltine pine bark beetle, Ips acuminatus. Population growth rate is reduced following warm years, in which many individuals attempt a second summer generation, possibly because most second-generation beetles do not reach the cold-tolerant adult stage before winter [45]. Similarly, Van Dyck and Bonte [46] have argued that observed declines in the butterfly Lasionnata megera could be the result of a newly attempted (incomplete) third generation — a ‘developmental trap’ caused by new climate patterns.

These findings suggest that while warming may often allow more rapid insect population growth, thanks to shorter generation times, the opposite effect could be observed if diapause-induction cues become mismatched with growing-season temperatures. If such mismatches occur, insects should be under strong selection to adjust their responses to diapause triggers: genotypes that take full advantage of suitable environmental conditions for growth and reproduction, rather than entering dormancy, will have greater fitness. Indeed, evolutionary shifts in the critical (diapause-inducing) photoperiod, in response to climate change, have occurred in the mosquito Wyeomyia smithii [47]. Understanding the environmental triggers of diapause induction, and the potential for evolutionary change in those triggers, will be essential for predicting the long-term demographic consequences of climate change.

**Community consequences of shifting phenologies**

By causing species-specific shifts in phenology, climate change can alter interspecific interactions. An early study of winter moth (Operophthera brumata) suggested that herbivorous insects might be at growing risk of emerging before the leaves of their food plants were available [48]. However, recent work has illustrated a broader range of possible shifts between insect herbivores and plants. A study of another oak folivore, Thaumatopoea processionea, concluded that synchrony between caterpillar eclosion and budburst had probably not changed since the 1960s [27]. Warming experiments with forest tent caterpillars (Malacosoma disstria) found that the host trees were more responsive than moth eggs to warming, such that warming caused budburst of trees to precede egg hatch [49]. Although late egg hatch relative to budburst could impose fitness costs on caterpillars because of declining leaf quality, no negative effect on pupal mass (a fitness proxy) was observed [50]. Conversely, an experiment that induced western tent caterpillars (Malacosoma californi- cum) to emerge before budburst found no fitness costs to caterpillars of being without food for up to three weeks [51]. Furthermore, while heating decreased synchrony between *M. disstria* egg hatch and budburst of one tree host, it increased synchrony with an alternate host [49*], emphasizing the resilience of this generalist species to phenological changes. Other systems, too, have shown an increase in synchrony between insect herbivores and their host plants: growing synchronization between larval feeding and budburst is the likely cause of a northward range expansion of the geometrid pest Agriopus aurantiaria [52]; and there are concerns that phenological shifts will facilitate range expansion by spruce budworm, Choristoneura fumiferana, into the black-spruce-dominated Canadian boreal forest [53*]. In agricultural settings, both increases [19] and decreases [54] in synchrony between insect pests and crop plants have been predicted, depending in part on how planting seasons are altered in the future.

Synchrony between pollinating insects and plants could also be disrupted by species-specific responses to warming. Differential responses to the timing of snowmelt on the part of a spring-flowering plant and its bumble bee (Bombus spp.) pollinators seem to reduce reproductive output by the plant in early springs [55]. Population declines in arctic flower-visiting Diptera may be due to reduced overlap between the flowering period (which is shorter in warm years) and the flight season of the flies [56]. In contrast to the situation for folivores, experimental investigations of the consequences of phenological mismatch for pollinator populations are lacking [57].

Antagonistic interactions among insects will also be affected by shifts in phenology. Bewick et al. [58] have illustrated, through simulations, how anct community composition could be changed by an extension of the growing season, even if all species experience parallel shifts in phenology, because of changes in competitive outcomes. A few recent studies show that warmer temperatures may provide some insects a temporal escape from natural enemies, though in each case the specific mechanism differs. Cereal leaf beetles (Oulema melanopus) experience fewer attacks by their parasitoid (Tetrastichus julis) in warm years, when the two species are less well synchronized because of a delay in host phenology relative to that of the parasite [59]. Similarly, parasitoids fail to reduce egg production by the scale insect *Pulvinicoccus querocifex* in warmer sites, in this case apparently because host phenology is advanced in these sites relative to the parasites [60]. Culler et al. [61*] have shown, using field observations of arctic ponds and controlled-temperature laboratory experiments, that warmer conditions allow mosquito larvae to partially escape dytiscid beetle predation, thanks to faster development.

We do not yet know how evolutionary change will compensate for the plastic shifts in phenology that alter
species interactions. In specialist herbivores and parasitoids, temporal mismatch with food sources should drive strong selection for adjustments in phenology — perhaps via change in the photoperiod response [47,62] or the thermal response [63] — or, alternatively, for a shift in diet. Future evolutionary trajectories are difficult to predict, but a better understanding of the fitness costs and benefits of alternative strategies would certainly help (e.g., see [64]).

Conclusions
Climate change is altering insect phenology in ways that go beyond simple shifts toward earlier seasonal activity. While documenting such shifts is still worthwhile, it is not scientifically exciting — at least in temperate regions, where the pattern is well established. On the other hand, we still lack information on how insect phenology is being altered by climate change in the seasonal tropics. In regions where seasonal temperature fluctuations are weak, phenology is unlikely to be tied to temperature [65]; consequently, expectations for phenological responses to warming are less clear. Nevertheless, as climate change alters seasonal precipitation patterns, we can expect changes in insect phenology. In this light, even straightforward observational studies of tropical insect phenology, conducted in standardized fashion over multiple years or sites such that correlations between seasonal activity and environmental variables could be investigated (e.g., [66]), would be valuable.

Studies of insect phenology in relation to climate change also need to better integrate an understanding of insect life histories. As the Buckley et al. [20]** study illustrates, insect phenology can respond to warming in ways that seem counterintuitive but that make sense in the context of life-history trade-offs between age and size at reproduction. Several of the other studies reviewed here (e.g., [24,*44**]) highlight how insect diapause affects predictions of phenological responses to climate change. Given the wealth of long-term datasets on temperate insect phenology that are now available, there is an opportunity to test whether information on life-histories (e.g., diapausing stage; strength of selection on size at reproduction) can help explain some of the observed variation in phenological changes.

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References

Using collection data from the 1950s along with recent re-surveys, the authors show that some early-season, high-elevation grasshopper populations now progress through development more slowly than in the past. This contrasts with the findings for lower-elevation and later-season populations, which now develop more quickly. This study is conceptually important in proposing that phenological delays occur in response to
warming because natural selection can favour slower development and larger adult body size when seasonal constraints are relaxed.  


Butterflies from sites along a latitudinal gradient were reared in the laboratory under different (simulated) durations of winter. Despite possible local adaptation in chilling requirements, all populations exhibited longer and more variable time to emergence when winter duration was shorter. The authors suggest that future warmer winters, particularly in southern localities, might be insufficient to trigger diapause termination in these butterflies.


42. Régnière J, St-Amant R, Duval P: Predicting insect distributions under climate change from physiological responses; spruce budworm as an example. Biol Invasions 2012, 14:1571-1586.


44. Grevstad FS, Coop LB: The consequences of photoperiodism for organisms in new climates. Ecol Appl 2015, 25:1506-1517. The authors present a conceptual model of insect volitism that incorporates both temperature-dependent development and photoperiod-sensitiveness into diapause. By applying this model to the life cycle of a beetle biocontrol agent, superimposed on the photoperiod and thermal conditions of localities throughout the United States, they show how latitudinal gradients in volitism (and changes in volitism in response to climate warming) can differ dramatically from what would be predicted based on temperatures alone. The authors also resurrect the use of ‘photothermographs’, an effective tool for illustrating the intersection of an insect’s life cycle with local combinations of climate and photoperiod.


49. Uelmen JA, Lindroth RL, Tobin PC, Reich PB, Schwartzberg EG, Raj KF: Effects of winter temperatures, spring degree-day accumulation, and insect population source on phenological synchrony between forest tent caterpillar and host trees. Forest Ecol Manage 2016, 362:241-250. This paper presents results from ‘Bi4Warmed’, a replicated forest-warming experiment conducted in Minnesota, USA. The authors show that tree phenology is more responsive than caterpillar phenology to warming; however, because of differential responses among host tree species, warming is unlikely to disrupt overall synchrony between young caterpillars and young leaves. There is also considerable phenological variation within and among caterpillar populations, suggesting plenty of opportunity for response to changing selection pressures.


52. Jepsen JU, Kapari L, Hagen SB, Schott T, Vindstad OPL, Nilssen AC, Ims RA: Rapid northwards expansion of a forest


57. Forrest JRK: Plant-pollinator interactions and phenological change: what can we learn about climate impacts from experiments and observations? Oikos 2015, 124:4-13.


Using a combination of field collections, temperature measurements, and laboratory experiments in controlled-temperature conditions, the authors quantify the temperature-dependence of development and survival in an arctic mosquito. They find that although beetle predators can catch more mosquitoes at higher temperatures, mosquito survival to adulthood increases with warming, thanks to faster development — illustrating the demographic consequences of altered phenology in a predator-prey context.


