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The fingerprints of global climate change on insect populations

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Synthesizing papers from the last two years, I examined generalizations about the fingerprints of climate change on insects' population dynamics and phenology. Recent work shows that populations can differ in response to changes in climate means and variances. The part of the thermal niche occupied by an insect population, voltinism, plasticity and adaptation to weather perturbations, and interactions with other species can all exacerbate or mitigate responses to climate change. Likewise, land use change or agricultural practices can affect responses to climate change. Nonetheless, our knowledge of effects of climate change is still biased by organism and geographic region, and to some extent by scale of climate parameter.

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Introduction

Insects are ectothermic creatures with relatively short generation times. Their physiologies, and resultant fitness, are strongly influenced by the microclimate that they experience. Insects could therefore be sensitive to climate change at the population level over short time periods, such that we might see the fingerprints even of early stages of climate change on insect population traits. One of the earliest documentations of changes in population dynamics reflecting changes in climate comes from the butterfly *Euphydryas editha*, whose southern and low elevation populations in California were more likely to have gone extinct than northern and high elevation populations [1].

Climate change itself, and the metrics that we use to measure it, vary with spatial scale. Global metrics of climate change include sea surface temperature changes and their associated teleconnections, such as the El Nino Southern Oscillation (ENSO) or the Arctic Oscillation (AO). Regional and local climate may be affected by these global metrics, but regional and local topography, land use, latitude and other factors are also relevant. The particular microclimate experienced by an insect results from a mix of factors operating on diverse spatial scales, with variation in the relative importance of each of these scales.

Likewise, climate parameters vary with time in any one location. Parameter means and variances can change, and changes in means and variances may be correlated [e.g., 2,3]. The frequency and amplitude of disturbances or extreme events may also change, and these too may be correlated with changes in overall means and variances of climate parameters [e.g., 4]. To make matters more complicated, all of these metrics can change at varying rates through time.

I synthesize the recent literature (from 2014 to early 2016) asking: On which aspects of population processes — demography, population dynamics, phenology — do we see fingerprints, or effects, of climate change in insects? Which climate parameters and metrics are important in driving population changes? Can we yet identify emerging generalizations concerning such effects? Is our knowledge biased with respect to agricultural versus non-agricultural, native versus non-native insect species, with respect to spatial or temporal scale of climate change, or with respect to population or climate metrics? I purposely do not address explicitly observed effects on physiology, ranges and distributions, evolution, or adaptation, although these interact with observed population changes. I then summarize missing pieces of the research puzzle.

Tracing fingerprints of climate change on population dynamics

At the simplest level, insects have long been known to exhibit plastic physiological responses to changes in temperature, which translate to alterations in vital rates [reviewed in 5], thence population dynamics. More recent work expands this view, to address the effects of temporal variation in climate parameters, including extreme events, fluctuating climate and interactions of climate variance and means on population dynamics [e.g., 6,7]. Other recent work extends our understanding to include the mediation of climate effects on population dynamics via phenological changes, species interactions or changes in land use. Empirical observations of effects of climate change are continuing to accumulate [e.g., 8–12], but equally importantly, researchers are developing models that allow empirical tests of underlying assumptions about the drivers of responses to climate change and/or make predictions about future effects of climate change [e.g., 13•,14–17].

Temporal changes in climate parameters

For changes in temperature means and variances, changes in both the observed and predicted population dynamics depend on where the population resides initially with respect to the insect's thermal niche, defined as the range of temperatures within which the insect has positive fitness and calculated via thermal performance curves in the laboratory [5]. The degree of plasticity and/or genetic variance present in the population for thermal tolerance is also crucial [e.g., 13•,18,19]. For example, a modeling effort indicates that, under increasing temperature means, variances or combinations of the two, changes in a population's growth rate should depend on whether the population is initially residing in a microhabitat at the cool end of its thermal niche, the middle or the warm end [13•]. For populations at the middle of their thermal niche, the effect varies depending on whether the temperature variance, the mean or a combination of the two are changing. This work forms an excellent predictive framework for tests using long-term data sets in the field, for species for which the weather drivers of population growth are understood. The addition to the model of genetic variance and plasticity for thermal response to temperature within a population would be a significant extension.

Beyond changes captured by the variance of climate parameters, the frequency, duration and amplitude of climate extremes may change. The response of vital rates and population dynamics to fluctuations that encompass stressful temperatures may be positive or negative, depending on the frequency and duration of exposure to stressful temperatures, hence the opportunity for physiological repair mechanisms to operate [reviewed in 20]. To make matters more interesting, vital rates may have different responses to fluctuating temperature extremes, resulting in population outbreaks. For example, *Aedes aegypti* larval survival in Thailand decreased under extreme high temperatures while female fecundity increased [21•]. When temperatures drop below the extreme, the survival of larvae resulting from excess eggs increased back to normal, resulting in a population outbreak. Such changes in population growth rates can be reflected even at the level of community composition [22].

The influence of phenology

Changes in developmental rates driven by climate change result in changes in phenology, which may then interact with the rest of the organism's ecology. For a univoltine grasshopper, Buckley *et al.* [23] showed that high elevation populations prolonged development in response to climate change, increasing adult body size, whereas populations of the same species from low elevations advanced development. Hence, plasticity of developmental response to climate change may vary across populations, depending on previous seasonal constraints and on the position of current climate relative to the thermal performance curve.

Such shifts in phenology may lead to dramatic population declines for species that are multi-voltine with an over-wintering or over-summering generation, but whose generations always remain discrete through the growing season. That is, if the phenological window for development is extended, an additional discrete generation can be added before diapause. However, the degree of increase of the phenological window is important: If a population is not able to complete a full generation before diapause, the diapausing generation is smaller, and the population declines. This phenomenon has been termed a ''developmental trap'' [24•], and was demonstrated for the butterflies *Lasiommata megera* in north-western Europe [24•] and *Agrotis segetum* in Denmark [25]. Developmental traps may be limited to species with discrete generations immediately before diapause, and hence to species with long generation times relative to the length of the growing season. Earlier eclosion of the first generation of *Helicoverpa armigera* due to warming generated larger over-wintering population sizes and increasing growth rates [26].

Alternatively, changes in developmental rates and phenology can result in changes in the dynamics of species interactions, again leading to population outbreaks or declines [27]. For example, increasing temperatures in western Greenland were observed to increase the growth rates of mosquito larvae, but also increased the daily predation rates of their primary predator, a dytiscid beetle [28]. The balance between growth and death favored growth rates, resulting in a predicted increase in mosquito population numbers. Likewise, the butterfly *Melanargia galathea*'s flight period in Britain has advanced in response to climate change, while the onset of flowering of its primary nectar source remains unchanged [29]. In this case, however, topographic variation results in considerable variation in the duration of flowering, which appears to buffer the butterfly population.

In this context, Bewick *et al.* [16] developed a more general model addressing the effects on insect population dynamics of uneven phenological changes between univoltine insect consumers and their plant resources. Depending on fecundity, duration of the emergence period of both insect and host, and rapidity of resource deterioration, uneven phenological changes are predicted