Changes in insect population dynamics due to climate change

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Abstract:

Climate change can modify the population dynamics of insects. In this instance, "climate" encompasses temperature and precipitation patterns, including dry season or snow cover duration and timing. Also included are changes in both climate means and variances. Insect declines in response to climate change are real, but population dynamics are heterogenous across space and taxa. Both rates of climate change and the location of a population within its climate envelop affect the outcome. Our understanding is currently limited by five factors. First, insect monitoring studies cover a narrow geographic range. Second, other anthropogenic changes, such as land use change, jointly affect the results of climate change on insect dynamics. Third, species interactions may be affected by climate change, with resulting indirect effects on insect dynamics. Fourth, our understanding of the underlying physiological and fitness response to weather extremes is still limited for insects. Fifth, we have an insufficient understanding of the dynamics of changes in vital rates, which control population dynamics, in response to climate change. I examine these factors, with an emphasis on temperate and arctic

23 species.

1. Introduction

Climate change at local to global scales alters the environment that organisms inhabit. Effects of climate change propagate back and forth across levels of biological organization, from metabolic, physiological and behavioral levels, to phenology, life history traits and fitness, to community and ecosystem structure and function. A full integration of climate change effects across these levels would of necessity also include all interacting organisms. An integrated understanding of the effects of climate change on any set of organisms is therefore a daunting enterprise. Nonetheless, we can obtain some general insight from a focus on one set of taxa and one organizational level, including other actors as needed. Here I focus on the effects of climate change on insect population dynamics and underlying life history traits, emphasizing examples from temperate and arctic taxa. Insects occupy nearly all trophic levels and most terrestrial and fresh-water habitats. Due to the abundance and diversity of insects, they are fundamental to life as we know it (Wilson, 1987). Insects are thus a critical group that is inclusive of many lifestyles. I begin this section with a short review of climate parameters that are relevant to insect life history and population dynamics, next briefly examine how these are changing on different scales, and then outline the scope of this chapter.

1.1. Relevant climate & weather parameters

Individual insects experience weather, or the specific expression of a particular climate regime at a particular point in space and time. As discussed further below, which climate and weather parameters are critical depends on whether the insect's habitat is terrestrial or aquatic; arctic/antarctic, temperate or tropical; and sheltered or not from weather extremes. Not only are weather values for a given climate parameter important, but we must also be

cognizant of the moderating effects of insect behavior, physiology, morphology, and access to microhabitats.

1.1.1. Climate & weather parameters important to terrestrial insects

The temporal scale studied determines in part which climate variables have important effects on individuals and populations. Air and substrate temperature, solar flux, and windspeed are important modulators of body temperature and hence activity of terrestrial insects on minute-to-minute time scales, taking into account mechanisms used to buffer weather events (e.g., Kingsolver and Watt, 1983). At the scale of parts of a lifetime, growing degree days, or the sum of time above a minimum temperature, is also critical for various life history traits, including development rate, fecundity, and survival, and resulting phenology. Precipitation (either as rain or snow) comes into play as a modulator of air temperature and solar flux, especially for diapausing insects.

These climate parameters also have indirect effects on insect life history and population dynamics through effects on the plants on which the insects depend, as well as on their competitors, predators and parasites. For example, drought and heat can alter plant traits ranging from nectar quantity and quality (Descamps et al., 2021) to secondary defense compounds (Kuczyk et al., 2021), which will affect the quantity and quality of both preferred and less-preferred resources available to insects. In an extension of this idea, Foote et al. (2017) documented asymmetrical competition between two aphid species (*Metopolophium festucae cerealium* and *Rhopalosiphum padi* both Hemiptera: Aphidae) on wheat (*Triticum aestivum* Poaceae). Competitive effects suppressing population growth of *M. festucae cerealium* vanished under drought conditions.

1.1.2. Climate & weather parameters important to aquatic life stages

Insect orders with aquatic life stages include Collembola, Ephemeroptera, Odonata, Plecoptera, Megaloptera, Neuroptera, Coleoptera, Hemiptera, Hymenoptera, Diptera, Mecoptera, Lepidoptera, and Trichoptera – in short, the major insect orders. As for terrestrial insects discussed above, successful survival and development of aquatic life stages of insects depend on ambient temperature and precipitation patterns. However, oxygenation, turbidity and solute concentrations are uniquely critical to the niche structure of aquatic life forms. In turn, water level and flow rates are critical determinants of water temperature, oxygenation, turbidity and solute concentrations (Showalter, 2011; Knouft and Ficklin, 2017). Water level and flow rates are determined by precipitation patterns, air temperature, solar flux, and groundwater and soil water flow. Precipitation patterns include rainfall amount, intensity and duration; snow cover depth and duration; and seasonal timing of both rain and snow. Similarly to terrestrial systems, aquatic systems can be affected by human land and water use patterns, as well as pollution.

1.1.3. Buffering of climate phenology, means and variances in the absence of climate change

The statistical description of a given climate parameter includes its mean and variance, which may change across seasons. However, individual insects generally experience climate as shorter-term weather phenomena, drawn from the distribution that makes up climate. Where an individual's performance optimum falls within the range of weather values that comprise a given climate parameter will determine how sensitive that individual is to changes in that climate parameter. Performance optima have been described by measuring fitness

components such as survival or fecundity across a range of, e.g., temperatures. The shape of the thermal performance curve and the lower and upper critical temperatures at which the organism loses the ability to move defines the organism's response to temperature. The performance curve is often skewed, with the optimal performance closer to the upper critical point. The superimposition of the performance curve on weather distributions underlying a given climate parameter will determine the performance of the individual in a given climate scenario (Figure 1). However, Kingsolver and Woods (2016) showed that the details of shape of the performance the curve depend on duration of temperature exposure, which complicates interpretation in the context of climate change.

Some insects can acclimatize to set of weather conditions that change on a short time scale relative to the individual's lifespan. Such plasticity results in shifts in the performance curve with respect to the specific weather condition. For example, populations of the emerald ash borer, *Agrilus planipennis* (Coleoptera: Buprestidae), in Winnipeg, Canada exhibit freeze tolerance plasticity that allows them to survive extreme cold temperature events (Duell et al., 2022). In contrast, *Nysius groenlandicus* (Hemiptera: Lygaeidae) exhibits a rapid heat hardening response in the arctic (Sørensen, 2019). Hence, temporal and spatial autocorrelation in weather parameters or in extreme events also affect performance. Correlations resulting in seasonal weather shifts are predictable and may be accommodated via selection for plasticity. However, not all weather patterns are so straightforward. For example, sea surface temperature and air pressure anomalies such as the El Niño-Southern Oscillation (ENSO) or the Arctic Oscillation (AO) create patterns of drought or excess rainfall regionally for several months at a time. Such patterns differ from seasonality in their lack of predictability. As a result, individual life history

traits and resulting population dynamics may not be able to be buffered against such weather patterns by selection for plasticity, since selection fluctuates through time.

In addition, insects experience weather on a micro-scale, or below 10cm in horizontal distance (Storlie et al., 2014; Pincebourde &Woods, 2020; Gols et al., 2021; reviewed in Harvey et al., 2022). Climate heterogeneity goes up as the scale on which climate is measured goes down, due to increasing architectural heterogeneity of the habitat. As a result, insects may buffer exposure to climate variance by habitat choice (e.g., Pincebourde & Woods, 2020, Gols et al., 2021).

1.2. Current and projected patterns of climate change across space and time

In order to understand how climate change has and will affect insects, we must also understand both current and projected changes in climate. With respect to temperature, the global temperature was 1°C warmer in 2010-19 relative to 1850-1900 (IPCC, 2021). The incidence of hot extremes increased on every land mass except for central and eastern North America (southern South America and central Africa had insufficient data) (IPCC, 2021). Over the next century, Arctic and Antarctic regions, the South American monsoon region, and some mid-latitude and semi-arid regions are projected to experience warming at a rate that is much higher than the global rate (IPCC, 2021). In general, land masses are projected to warm more rapidly than the oceans (IPCC, 2021), such that "average" global warming will be greater over land areas.

With respect to precipitation, average global precipitation has increased relative to 1950, and storm tracks at mid-latitudes have shifted towards the poles (IPCC, 2021). Changes in precipitation are somewhat consistent across the globe, where long-term data exist. The IPPC

Working Group 1 divided global land areas minus Antarctica into 45 regions of equal land mass (IPCC, 2021). The incidence of heavy precipitation has increased since 1950, with low to high certainty, in 9 of those 45 regions across the globe, with no decreases in any of the 45 regions (IPCC, 2021). There is low agreement in the type of change in 8 regions, and insufficient data from the remaining 18 regions, mostly in the Global South, to determine precipitation changes. Drought has decreased in northern Australia, but has increased in 12 of 45 global regions since 2010 (IPCC, 2021). Taken together, this reflects an intensification of the global water cycle (IPCC, 2021). Projections call for a continuation of this pattern. They include an increase in precipitation in the Arctic and Antarctic, the equatorial Pacific and some other regions, and a decrease in some areas of the subtropics and tropics (IPCC, 2021). The intensity of precipitation is expected to increase in general, leading to more variable surface water flows in most areas within and between years (IPCC, 2021). This variation in water flow will be exacerbated in temperate and montane areas, as snow melt is expected to occur earlier, leading to less water storage as snow and higher earlier run-off (IPCC, 2021).

1.3. Chapter overview

I synthesize the recent literature concerning documented insect responses to climate change. I focus on local and regional changes in population dynamics, including population state changes, or stable shifts in mean abundances. The recent focus on whether or not insects are declining globally has led to a number of reviews that summarize the available literature for changes in species richness, abundance or total biomass (Sánchez-Bayo and Wyckhuys, 2019; Høye, 2020; van Klink et al., 2020a; van Klink et al., 2020b; Wagner, 2020; Halsch et al., 2021; Hill et al., 2021; Wagner et al., 2021a; Wagner et al., 2021b), as well as the mechanisms by

157 which insect respond to climate change (Harvey, et al., 2022). I rely on these reviews and
158 integrate additional studies appearing in the last two years, using key words based on each
159 section below. Note that this was not meant to be an exhaustive literature search as would be
160 done for a meta-analysis. I then examine climate-driven shifts in population vital rates at the
161 local scale. These changes in vital rates are the mechanism underlying changes in population
162 size. I end with an agenda for further understanding the impact of climate change on insects.

163 **2. Is climate change driving an 'Insect Apocolypse'?**

164 Early reports of declines in insect abundance and biomass at specific locations led to a *New*
165 *York Times* article in 2018, titled 'The Insect Apocolypse is Here' (Jarvis, 2018). That title
166 notwithstanding, most questions remained unresolved. These questions are critical for
167 understanding first, whether insect abundance and biomass is declining globally and
168 catastrophically, and second, whether the primary driver of such declines is climate change. The
169 first set of questions includes the geographical extent of declines; whether species' declines
170 globally outweigh expansions; whether biomass, species richness and population numbers are
171 all declining; what taxonomic groups are declining; and what species' traits are associated with
172 declines. The second set of questions includes determination of the factors are driving observed
173 changes in insect mass and numbers. To grasp the limits of our current understanding, I next
174 examine basic extinction dynamics, the types of evidence available, indirect effects of climate
175 change and interactions with other types of global change, including land use change.

176 **2.1 Scales and trajectories of population declines and species extinctions**

177 Extinction events can happen on several organizational, spatial and temporal scales.
178 Populations may go extinct. Populations may go extinct on a regional scale, associated with

changes in species' ranges. And populations may go extinct globally, such that the species is extinct. Population extinction may also be permanent. Alternatively, extinction may be an element of metapopulation dynamics, with repeated local extinction and colonization. Depending on the turnover rate for demes within metapopulations, and the spatial and temporal scale of monitoring, data from a metapopulation may look like a simple population extinction. This confounds efforts to document extinctions due to climate or other environmental changes.

Population extinction also may follow different temporal trajectories. These include a gradual decline in population size, extinctions due to large population fluctuations around a given mean, extinction vortices in which feedback loops hasten extinction (e.g., Fagan and Holmes, 2006), and extinction debts in which extinctions are delayed beyond that expected (e.g., Hylander and Ehrlén, 2013; Figueiredo et al., 2019). We have mathematical theories supporting these trajectories (e.g., Lande, 1993; Fagan and Holmes, 2006; Nieddu et al., 2014; Williams et al, 2021). However, there is almost no experimental or observational data in wild insect populations connecting climate change to these specific dynamics. An example un-connected with climate change is the work of Estay et al (2012), who examined changes in the variance in population size in eight populations of each of two species of aphids in Britain. They showed that most changes in population size variance in *Elatobium abietinum* (Hemiptera: Aphididae) were associated with changes in the carrying capacity, but most observed changes in variance in *Drepanosiphum platanoidis* (Hemiptera: Aphididae) were associated with changes in the growth rate, hence reproductive and/or mortality rates. While none of these shifts resulted in population extinctions, they did alter the structure of the population dynamics. As

we accumulate extinctions of populations that have long-term monitoring data, the opportunity exists to develop a better understanding of the trajectory leading to extinction itself, rather than just population dynamic state changes. This is important, because which trajectory a given population follows has implications for rates of decline and extinction.

2.2 Sources of evidence of population decline and species extinction

The first step in linking population declines and species extinctions to climate change is to demonstrate that in fact populations are declining and species are going extinct. Several approaches have been used to examine possible declines or extinctions of insect populations or species. First, long-term trapping sites have used malaise traps, pitfall traps, pan traps, light traps, emergence traps, fruit traps, etc. Standardized transect sighting surveys (summarized in Halsch et al., 2021) have also been done, usually for Lepidoptera with some version of a Pollard walk (Pollard and Yates, 1993). These all generate data on species richness and often abundance and/or biomass (summarized in Halsch et al., 2021; see also Burner et al., 2021). Increasingly, DNA metabarcoding has been used to document trapped samples (e.g., Villalta et al., 2021). A twist on the trapping approach is Janzen and Wallach's (2021) surveys of tri-trophic interactions among plants, Lepidoptera and their parasitoids in Costa Rica. With colleagues, they have collected and reared lepidopteran larvae, and simultaneously passively sampled their parasitoids. These data yield information on changes in abundance of the parasitoid species through time. Perhaps the most exciting developing approach to trapping integrates technology with deep learning to fully automate monitoring (Besson et al., 2022).

A second approach relies on databases accumulated by citizen scientists. The most famous of these are the UK Butterfly Monitoring Scheme (UKMBS, 2022), along with the North

American Butterfly Association's (NABA) 4th of July butterfly counts (North American Butterfly Association, 2017), PollardBase (PollardBase, 2022) and Monarch Watch (MonarchWatch, 2022). Some of these surveys occur sporadically at any given locale. This can make it difficult to detect trends, since the timing of the survey may occur at different phenological points across years. Correcting for accumulated degree days can help solve this problem (Clarridge, 2016). The more robust of these datasets have yielded valuable insights (e.g., Wepprich et al., 2019). iNaturalist (2022) also provides a growing repository of community-vetted information on more diverse species occurrences, which may prove productive in the future.

Third, either museum records or earlier surveys combined with modern-day re-sampling can generate insights into population declines (e.g., Grixti et al., 2009; Theng et al., 2020; Sheard et al. 2021). Museum records may be biased by either geography or preference for rare species or phenotypes. For example, readily accessible locales, such as near campgrounds, may be more heavily sampled than areas far from roads. This can be an advantage, as more time depth is often available for these sites. Preference for rare species means that museum records provide a better approximation to species richness than to abundance.

All these methods have limitations for use in determining whether insect populations are declining. The first limitation derives from geographic coverage. Many long-term trap sites are in Europe, and to a lesser extent in North America and Costa Rica. Only 6 of 73 sites recorded by Sánchez-Bayo and Wyckhuys (2019) are located in the Global South. Citizen science efforts have historically been likewise biased, but a search on iNaturalist indicates that this is changing (iNaturalist.org). The second limitation derives from temporal depth of the data. Insect populations include classic examples of time-lagged population dynamics, population cycling,

chaos, and outbreak dynamics (e.g., Turchin and Taylor, 1992; Kozlov et al., 2009). Avoiding confounding such dynamics with population declines is best done using data sets with multi-generational time depth.

Once we understand which populations and species are declining, determining whether climate change is a driver is the next step. Are the dynamics altered, compared to dynamics prior to an identifiable change in a relevant climate variable? This requires first separating effects of climate from land use changes. This is not always easy for European long-term trapping sites, which are generally located at the interface between agricultural and non-agricultural land (e.g., Halsch et al., 2021). Long-Term Ecological Research sites (LTER) in the United States are generally located in areas where land use change is not as prevalent, allowing a focus on effects of climate change (e.g., Crossley et al., 2020). Second, trap, transect and citizen science data generally date from no earlier than the 1960s (e.g. Hellmann et al., 2003; Halsch et al., 2021), whereas climate variables have been changing since the the beginning of the industrial revolution in the 1800s (Abram et al., 2016). Finally, assigning temporal variation to climate change drivers is particularly problematic for community samples, for which some species may be increasing while others are declining due to differently lagged responses.

2.3 Spatial distribution and time-lines of declines and extinctions due to climate change

Determining the extent of insect declines and extinctions that are due to climate change has proven to be a difficult undertaking. Early synthetic studies were critiqued as over-reach for global extrapolation from geographically limited data sets (e.g., by Wagner, 2020); for an inability to partition land use change from other factors driving declines (e.g., by Wagner, 2020); or in some cases on grounds of faulty statistical methodology (by Daskalova et al., 2021).

Wepprich et al. (2019) and Høye et al. (2021) also note that inclusion of even a few outlier data points, capturing sample variability, can affect the statistical analysis. Nonetheless, here I make some predictions and compare those to available data to draw some conclusions. I also discuss factors that will confound measurement of species' declines and extinctions.

2.3.1 Where a given species resides within its climate envelop determines its fate

As noted earlier (section 1.1.3; figure 1), insects experience weather on spatial scales approximating the insect's size (e.g., Kingsolver and Watt, 1983), and insect performance is dependent in part on where a given weather value falls within the performance-weather envelop. This leads to two predictions. First, declines should be greater for insects in architecturally or topographically simpler environments, where they are less likely to be able to buffer weather through behavior. Second, declines should be greater for populations at the edge of their climate envelop, in the context of their microclimate (e.g., Storlie et al., 2014).

Available studies support both predictions. However, data are scarce in support of the first prediction that lack of microclimate diversity derived from spatial or topographic heterogeneity should be associated with population declines (Pincebourde and Woods, 2020). In one example, populations of *Euphydryas editha bayensis* (Lepidoptera: Nymphalidae) in topographically flatter habitats went extinct more rapidly than those in topographically heterogeneous habitats (Hellmann et al., 2003). More extensive support is accruing for the influence of a species' location within its climate envelop on population expansions versus extinctions. For example, Antão et al., (2022) documented a shift in location within the climate envelop for moths and butterflies across a latitudinal gradient in Finland. Such shifts led to both increases and decreases in species' presence, depending on the extent of climate change and the initial

location of the species in its climate envelop. Likewise, ant communities at 33 sites across the United States showed a significant non-linear relationship between average upper critical temperature for species within a genus and the proportion of sites with higher incidence for that genus over a 20-year period (Roeder et al., 2021). That is, the incidence of genera increased under climate change with increasing average upper critical temperature to a maximum, and then fell slightly. This would be expected if the sampling sites span species with a range of locations within the thermal range, and suggests that the upper value of the insects' climate envelop affected their fate. No such relationship was found for the average lower critical temperature, again as expected under climate change.

2.3.2 Rates of climate change are correlated with rates of decline and extinction

Geographic areas with a greater change in climate means, variances or extremes should exhibit a faster rate of decline and more extinctions. However, we still expect to considerable variation in responses due to the relationship between the baseline weather relative to the species' climate envelop (see figure 1).

Areas with greater rates of temperature increase include northern latitudes, while extremes in hot temperature were less pronounced in central and eastern North America (IPCC, 2021). The work of Antão et al. (2022) across a latitudinal gradient in Finland (discussed above) yielded differences in population response rates as a function of rates of climate change. The authors noted that initial position within the species' climate envelop was critical to the type of response detected. This further highlights the need for more fine-grained studies.

However, not all high latitude studies provide support for the hypothesis. In the Arctic, using 24 years of data from Zackenberg, Greenland, Høye et al. (2021) found, first, that

311 temperature and winter duration did not change linearly with time, and summer precipitation
312 showed no trend with time. Thus, local change did not follow regional patterns. Second, as
313 expected based on local change, they found either non-linear changes in abundance and
314 diversity, or no detectable trend, depending on habitat. Third, trends differed among families,
315 as well as by position in the food web. Amalgamating across species with diverse positions in
316 their climate envelop, diverse microhabitats, and diverse relations to other species muddies the
317 analysis.

318 **2.3.3 Extreme weather events have significant effects on insects**

319 A shift in mean climate and/or in climate variance results in an increase in the frequency
320 and/or severity in extreme weather events (Figure 2). Even if the new mean climate is included
321 within a species' climate envelop, there may be more extreme events that fall outside the
322 climate envelop. The effects on population dynamics of these extreme weather events will of
323 course depend in part on the duration of the event relative to the tolerance of the insect. Ma
324 et al. (2021) and Filazzola et al. (2021) review the effects of more extreme events on insects.
325 Such effects range from shifts in ion balance in response to heat extremes, which lead to
326 reduced mobility in *Locusta migratoria* (Orthoptera: Acrididae) (O'Sullivan et al., 2017); to
327 changes in thermoregulatory morphology as a plastic response to heat stress in the dragonfly
328 *Erythemis collocata* (Odonata: Libellulidae), which leads to reduced flight ability (McCauley et al.,
329 2018); to dessication in response to drought stress in collembolans (Elnitsky et al. 2008).

330 **2.3.4 Confounding factors: Metapopulation structure**

331 Detection of declines and extinctions will be particularly fraught for species with a
332 metapopulation structure. Local demes normally go extinct and are re-colonized, independent

of climate change. Detecting extinctions due to metapopulation dynamics versus true extinctions, or changes in rates of extinctions will necessitate regional sampling. This dynamic is so far not addressed in analyses of general insect trap data.

Rates of colonization-extinction in a metapopulation may also affect the response to climate change. Johansson et al. (2021) showed that *Euphydryas aurinia*'s (Lepidoptera: Nymphalidae) survival of an extreme drought in Gotland was due in part to high connectivity among metapopulation patches resulting in favorable colonization-extinction dynamics. This metapopulation also has relatively large patches, which may insulate it from climate extremes due to both increased colonization associated with large patches and increased availability of diverse microclimatic refuges. The increase in overall butterfly population size and patch occupancy occurred in spite of a lack of full recovery of the larval host plant. The authors acknowledge that factors such as drought-induced changes in host plant quality could have played a role in the rapid recovery of the butterfly, but point to documented effects of patch connectivity and size as critical factors. Acevedo et al. (2015) found that asymmetric differences in effective distances between patches affected colonization-extinction dynamics in a wind dispersed orchid. That is, prevailing winds make distances effectively shorter for downwind patches, and longer for upwind patches. Since climate change could affect wind intensity and direction, this needs greater attention in insects.

Climate change may also alter the spatial synchrony of weather drivers of metapopulation dynamics. The classic metapopulation system, *Melitaea cinxia* (Lepidoptera: Nymphalidae) in the Åland Islands provides an example. Increasing frequency of drought (a spatially synchronized weather driver) has increased the synchrony of regional metapopulation

355 dynamics. This has resulted in an increased risk of extinction of the system (Tack et al., 2015).

356 **2.3.5 Confounding factors: Direct effects of phenology and voltinism**

357 Climate change can lead to changes in insect phenology, and in particular to changes in
358 voltinism. As the climate warms in temperate and arctic areas, a longer growing season can
359 lead to opportunities for an increase in the number of generations per year (reviewed in
360 Forrest, 2016). Three patterns may result from the longer growing season, depending on the
361 relative importance of temperature and photoperiod in controlling diapause. First, if
362 photoperiod plays no role, an increase in growing season length may lead to population growth
363 and outbreaks (see section 3). Second, a longer growing season for these same species can lead
364 to a final partial generation, which results in a decline in the first generation the following year.
365 If this pattern repeats over several years, it may manifest as a population decline, as in
366 *Lasiommata megera* (Lepidoptera: Nymphalidae) (Van Dyck et al., 2015) in Europe. The decline
367 may be temporary in the face of continued climate change. As the growing season continues to
368 expand, the last generation becomes a complete generation, and the population may resume
369 increasing in size. This will be true as long as the insects' thermal climate envelop is not
370 exceeded. Third, heat accumulation may result in a cue for diapause induction before the
371 solstice, such that the insect interprets the short daylength as fall and goes into diapause early
372 (Grevstad and Coop, 2015). This reduces voltinism, and may result in a decline in abundance,
373 since sequential generations cannot build population numbers through the growing season.

374 These diverse responses to changes in temperature and growing season highlight
375 underlying causes of diverse changes in species richness, abundance or mass over time at
376 sampling stations. This draws attention again to the need to analyze such data at finer

taxonomic scales.

2.3.6 Confounding factors: Declines in abundance vs. biomass vs. species richness

Depending on the monitoring scheme, researchers record some combination of species richness, biomass, and abundance. These can show different patterns of change (Vereecken et al., 2021). For example, species may be going extinct over time at a particular location but new species may be recorded as species' ranges change, such that species richness remains constant. Likewise, the relationship between biomass and abundance will depend on the relative numbers of small- and large-bodied insects. For example, Homburg et al. (2019) found no change in carabid beetle biomass in a 24-year trapping study in a nature reserve in northern Germany, but significant declines in species richness and phylogenetic diversity. In northwestern China, a carabid beetle assemblage showed different rates of decline in species abundance and richness (Liu et al., 2022). In Greenland, Høye et al. (2021) documented opposing trends in abundance and diversity for total arthropod trap data across three habitat types, but with large variation at the family level.

Declines in species richness, biomass, and abundance, along with functional and phylogenetic diversity, have different implications for ecosystem health, including food web structure. Discussion of insect declines needs to be broadened to include and separate all of these metrics, at various taxonomic and functional groups resolutions if we are to be able to assess the full impact of climate change. This discussion also necessitates data collection across an increased geographic range, with varying land uses, at a finer-grained scale than currently occurs.

2.4. Indirect effects of climate on insect declines and extinctions

399 Climate change directly affects species with which insects interact, leading to indirect
400 effects on the focal insect's population dynamics. Affected species can be food resources,
401 predators, parasites and pathogens, or competitors. Mechanisms include phenological
402 mismatches (reviewed in Renner and Zohner, 2018); changes in host plant quality (e.g. , Kuczyk
403 et al., 2021) or floral resources (e.g., Descamps et al., 2021); and changes in abundance of one
404 or both interacting species.
405 Evidence for phenological mismatches between insects and flowers or between insects and
406 their herbaceous larval hosts in temperate areas is scant (reviewed in Renner and Zohner,
407 2018; Kharouba and Wolkovich, 2020). Kudo and Ida (2013) present one of the most thorough
408 studies, showing that in early springs, onset of flowering of *Corydalis ambigua* (Papaveraceae)
409 was earlier than first emergence of its queen bee pollinators. They demonstrate negative
410 effects on seed set under such circumstances, but do not address effects on abundances of the
411 insects.
412 Selection or plasticity that allows populations to buffer their phenology will be critical to
413 whether a mismatch occurs. Examining a set of Mediterranean butterflies, Colom et al. (2022)
414 found that the sensitivity of phenology to climate change, and the ability to match changes in
415 climate variability across years, is critical to avoiding a phenological mismatch.
416 The question also arises as to at what point the phenologies of two interacting species no
417 longer overlap, even under extreme selection to do so. Simmonds et al. (2020) used structural
418 equation modeling to explore the point at which the great tit-caterpillar system becomes
419 phenologically mismatched. Even under directional selection, if the bird phenology lagged the
420 caterpillar phenology by more than 24 days, the birds went extinct. Potentially, the result for

421 the insects is new predator-free space, and a population outbreak.

422 Currently available studies of phenological mismatch have several limitations. First, they
423 have generally neglected consideration of the distribution of phenological events (Inouye et al.
424 2019). Using data from a long-term monitoring project in Colorado, USA, Stemkovski et al.
425 (2022) show that bees and flowers differ in the extent of skew in their phenology curves for
426 emergence. Such differences, if common, would have significant implications for resilience of
427 interactions to climate change. Second, studies have ignored community context – that is, the
428 broader set of competitors, predators and mutualists within which the two focal species are
429 embedded. Pardikes et al. (2022) demonstrated in a laboratory experimental setting using
430 *Drosophila* and its parasitoids that community context could alter the effects of phenological
431 mismatch.

432 Changes in host plant quality in temperate regions as a function of heat and drought are
433 relatively well-studied. For example, Kuczyk et al. (2021) showed that *Sinapis alba*
434 (Brassicaceae), the host plant for larval *Pieris napi* (Lepidoptera: Pieridae) in Europe, had
435 greater C:N ratios and glucosinolate concentrations in response to high temperatures, but
436 lower glucosinolate concentrations in response to drought stress. Female butterflies preferred
437 to lay eggs on plants with high glucosinolate concentrations, but larvae performed better on
438 plants with low glucosinolate concentrations. These results reflect species interaction
439 responses that will alter the population dynamics of both participants in the interaction, under
440 scenarios of changes in the means and extremes of temperature and precipitation.

441 Finally, changes in the abundance of one or more competitors, predators or mutualists may
442 affect the probability of a given insect species' decline. For example, the population dynamics

443 of *Speyeria mormonia* (Lepidoptera: Nymphalidae) in Colorado, USA, are partially determined
444 by floral nectar availability, which in turn is affected by early season frosts in years with early
445 snow melt (Boggs and Inouye, 2012). Top-down changes in insect population size can also
446 occur via indirect effects of climate change on predator behavior. Barton (2014) showed that
447 reduced wind results in more efficient foraging by lady bugs (*Harmonia axyridis* (Coleoptera:
448 Coccinellidae)) on aphids (*Aphis glycines* (Hemiptera: Aphididae)), reducing aphid population
449 sizes. One observed change in climate is reduced average wind speeds (e.g., Vautard et al.,
450 2010). While not yet the case for the butterfly or the aphid, such indirect effects of climate
451 change may result in extinction cascades, as reviewed for insects by Kehoe et al. (2021).
452 McPeek (2022) provides a template for using food web dynamics to understand the effects of
453 changes in abundance on other members of a community. Such an approach will be necessary
454 to tease apart the complex effects of climate change via species interactions.

455 **2.5. Interaction between climate and other types of global change**

456 One of the difficulties in detecting effects of climate change on insect dynamics is that
457 ongoing global change includes not just climate, but also land use, pollution, etc. Interactions
458 among climate and other global change parameters may be non-additive and/or indirect,
459 complicating analyses at the species level, let alone the community level (see Yang et al., 2021;
460 Outhwaite et al. 2022 for recent reviews). For example, Forister et al. (2010) documented
461 greater declines through time in butterfly species richness at lower elevations in California's
462 Sierra Nevada as compared to higher elevations. They attribute this difference to more
463 extensive habitat loss at lower elevations. Likewise, Assandri (2021) argued that changes in land
464 use (including drainage and reclamation, intensification, or abandonment), and change in

pollutant levels have interacted with climate change to result in significant extinctions of dragonfly communities in low elevations of the European Alps. For freshwater systems, van Klink et al. (2020a; 2020b) suggested that increases in species abundance in freshwater systems was due to cleaning up pollution, which outweighed effects of climate change. At the most basic level, understanding whether and how the effects of climate change on insect populations are amplified or lessened by other aspects of global change is critical in order to mitigate insect declines.

2.6. So – is there an insect apocalypse?

Despite concerns mentioned above about geographic, habitat and taxonomic coverage, effects of land use change and pollution, and statistical analysis, overall current mean rates of local extinction for insect species as a result of climate change are estimated in the vicinity of 1%/year (summarized in Pinedo-Escatel et al., 2020; Theng et al., 2020; van Klink et al. 2020b; Wagner, 2020; Warren et al., 2021; Wagner et al., 2021). Rates vary across habitats, location, and taxa (reviewed in Wagner et al., 2021), and depend on the time depth of the study (Bell et al., 2020). Not all groups in all locations are declining; there is much heterogeneity in the record. Intriguingly, insect cyclic outbreak dynamics are also damped in some species (Esper et al., 2007). In contrast, Harvey et al. (2020) argued that the interplay between climate-driven change and trophic disruption may lead to increased incidence of outbreaks. We do not yet have the data or the insights to understand the mechanistic drivers underlying this heterogeneity.

The data thus suggest that insects are participating in the global Sixth Extinction. But are they? Schachat and Labandeira (2021) argue that the insect fossil record shows faunal turnover,

rather than mass extinction during previous global mass extinction events. If extinctions progress to the loss of families or orders, they argue that insects will actually be entering their first mass extinction. That would indeed be an insect apocalypse.

3 Is climate change driving insect population increases and explosions?

Not all insect populations are declining. We see a mix of "winner and loser species" (*sensu* Filgueiras et al., 2021). Especially in terrestrial temperate and arctic areas, species at the cooler edge of their thermal climate envelop are increasing (e.g., Antão et al., 2022). In areas where winter temperatures are warming, species that used to suffer high mortality from winter cold stress are generally increasing in abundance, although species subjected to changes in snow cover leading to intermittent freeze-thaw cycles or that lose their required chilling period during diapause may not show this pattern (reviewed in Bale and Hayward, 2010; Simler-Williamson et al., 2019). Species that can now add an entire additional generation during the growing season are also increasing in abundance, as exemplified by European Lepidoptera (Altermatt, 2009). However, as for population declines, responses to climate change are dependent on species, community, and habitat characteristics. This mix of winners and losers has implications beyond the idea of an insect apocalypse, encompassing changes in community structure that will propagate through the ecosystem.

4 Underlying vital rates

Vital rates, or age-specific survival and fecundity, are the mechanism that underly changes in population abundances, hence species richness, abundance, and biomass. Development rates control generation time, which also influences population dynamics. Dispersal is also important at a regional scale. To build a predictive understanding of insect declines and

outbreaks, we must understand (1) how vital rates respond to climate change, (2) which vital rates control rates of population growth, and (3) whether the identity of vital rates controlling population growth change with changes in climate. Changes in climate means and variances, including extreme events, are important considerations.

4.1 Effects of climate change on vital rates

4.1.1 Survival, fecundity, and virility: responses to change

In general, survival and fecundity in insects follow a hump-shaped curve in response to temperature. There is a peak at some intermediate temperature, with declines around that peak (reviewed in Kingsolver and Buckley, 2020). The response can be plastic. For example, heat-hardening improves survival under temperature extremes in *Drosophila virilis* (Diptera: Drosophilidae) (Walsh et al., 2021).

Virility, including sperm production and viability, is reduced under temperature extremes in those insects that have been studied (e.g., in *D. virilis*: Walsh et al., 2021; in *Tribolium castaneum* (Coleoptera: Tenebrionidae): Sales et al., 2018). Heat extremes can sterilize males. Sales et al. (2018) further describe a transgenerational effect of heat extremes on male sperm viability. Offspring fathered by males subjected to heat stress, or by sperm stored in females subjected to heat stress, had reduced survival and fecundity. In *T. castaneum*, the same heat extreme had no effect on female fecundity, indicating that the effects of heat waves on each sex's reproductive vital rates are independent (Sales et al. 2018).

Complicating matters, survival and reproduction may have different thermal optima. Survival was better at low temperatures in the field for two damselfly species (*Calopteryx splendens* and *C. virgo* (Odonata: Calopterygidae)), while male mating success and hence

female fecundity was better at higher temperatures (Svensson et al. 2020). Integrating these different optima and responses to extreme events into a population dynamics model would allow us to explore the population dynamic response to changing temperatures (see Amarasekare and Savage, 2012 for a review and interesting approach). Exploring population dynamic outcomes for an array of temperature responses would give insight into both the characteristics of species that are likely to decline in response to temperature change, and to the breadth of declines across types of species in response to give climate scenarios.

Understanding the interaction between precipitation (including snow) and temperature on vital rates in the field has proven elusive. Diverse studies have documented effects or lack thereof on both on population growth patterns or on over-winter survival (e.g., Convey, 2015; Mitrus, 2016; Roland et al., 2021), but studies across the life cycle are missing. One exception is work by Radchuk et al. (2013), who document differences in the effects of warming on different life stages of *Boloria eunomia* (Lepidoptera: Nymphalidae). Warming had a positive impact on nearly all life stages, except for over-winter larval survival, for which the effect was negative. The net result of warming for population dynamics was also negative.

4.1.2 Development rate and generation time: responses to change

Thermal sensitivity in insects varies through ontogeny (reviewed in Kingsolver and Buckley, 2020). Eggs, larvae, and pupae differ in their minimum temperature threshold for development, and in the total number of degree-days above that minimum required to move to the next life stage. The minimum temperature threshold was on average greater for pupae than for eggs and larvae (Kingsolver and Buckley, 2020). Insect order also was a significant effect. Although the differences among life stages were small, they have a significant impact on time spent in

each life stage, and on overall generation time. Such differences in thermal sensitivity will also influence the effect on development rate of differences among seasons in thermal climate change. For example, if the minimum temperature for development is high for larvae compared to current temperatures during the spring, increasing spring temperatures should result in faster larval development, shorter generation times, alterations in phenology, and possibly, population growth. This area cries out for more work to enhance our understanding.

4.2 Buffering, lability, and changes in which vital rate(s) drives the population size… and implications for unexpected state changes in population dynamics

The relationship between age-specific vital rates and population dynamics in the context of climate change will be affected by two factors. First, what is the elasticity of population growth in response to changes in means and variance in each vital rate (e.g., Boyce at al., 2006)? This reflects the extent to which the vital rate drives the population dynamics, with greater elasticity reflecting a greater importance of the vital rate. Second, how buffered or labile is each vital rate to changes in the mean and variance of climate parameters (e.g., McDonald et al., 2017)? I know of no case studies in insects exploring this question. It is particularly important because of the possibility that the degree of buffering or lability of vital rates to changing climates might alter the relative importance of each vital rate as drivers of population dynamics. It is not inconceivable that such an event could result in a permanent state change (extinction or explosion) in population size. Exploration of this possibility is needed, through some combination of modeling, experimentation, or observation.

5 Conclusions

The available evidence indicates that insects are generally declining, although the decline is

far from uniform across space and taxa, or with respect to abundance, species richness, and biomass. Separating the effects of climate change from other global changes is challenging. Much of the available evidence is correlative, rather than either experimental or based on a solid understanding of the mechanisms driving insect population and community dynamics. Gaining that insight, and moving beyond correlations, will be crucial for advancing our understanding of the effects of climate change.

In addition, much of our present understanding focuses on the effects of temperature. Precipitation, be it as rain or snow, is also changing and projected to change further. More attention is needed to the effects of this climate variable, including its interaction with temperature, humidity, and soil moisture.

I have focused here primarily on terrestrial insects. But insects with aquatic life stages are a significant component of insect biomass. Some of the conclusions drawn here apply to aquatic insects as well. Nonetheless, a deeper understanding of the trends in abundance, richness and biomass separated from changes in land use and pollution is warranted.

Of necessity, ecologists tend to focus on one or a few levels of organization when understanding challenges posed by climate change. How is species richness changing? How is the food web changing? How is abundance changing? But nature doesn't have such a restricted focus. To fully understand the effects that we are having on the insect world via climate change, we need to integrate across levels of organization, from cellular to community, and then return to our key questions about insect decline (Harvey et al., 2020). One way to accomplish this is through integrative studies at "model" locations, using information from basic and applied studies, to generate and test models, using techniques such as piece-wise

structural equation modeling. An alternative is a similar focus on “model” communities or habitats. Either or both will help provide the answers that we need to understand the effects of climate change on insects, as important parts of terrestrial and freshwater ecosystems.

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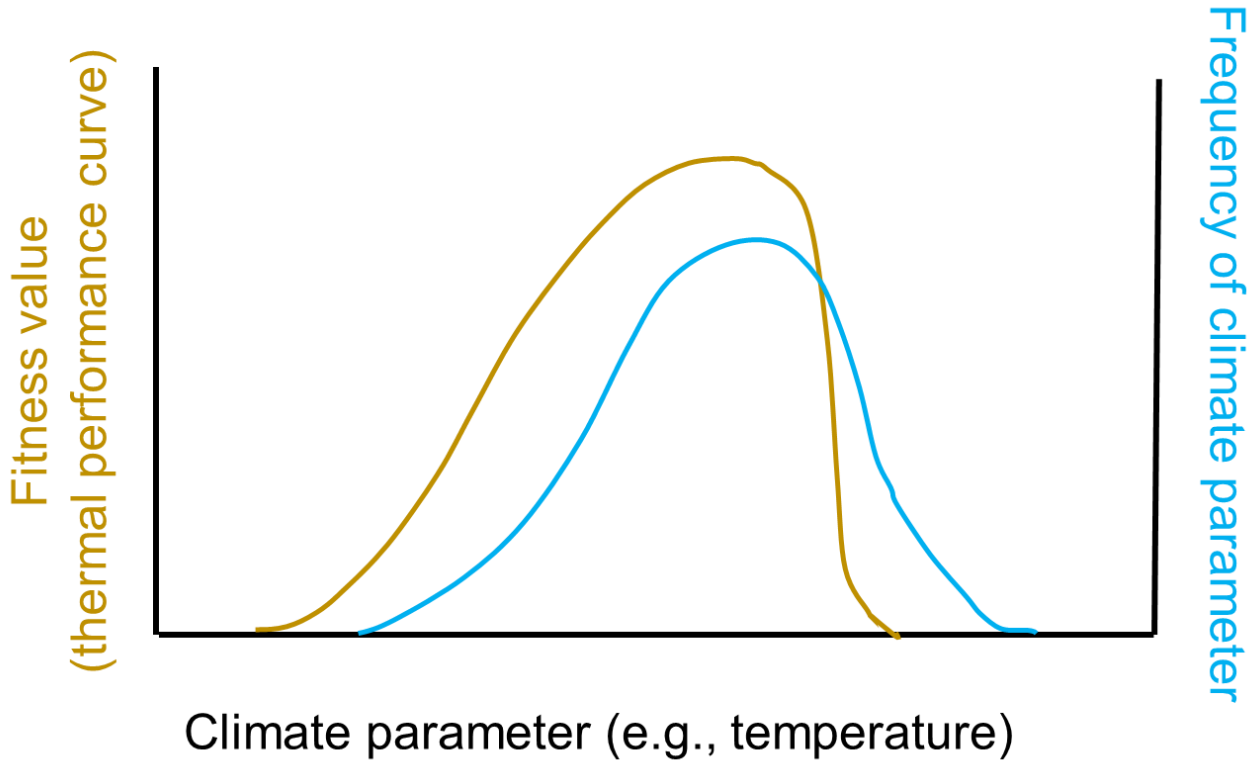
874 Figure Legends

875 Figure 1. Examplar of a hypothetical relationship between the performance curve of a species
876 (blue line) and the distribution of values (e.g., temperature) of a climate parameter (brown).
877 Fitness is 0 outside the performance curve envelop, which will result in a population decline.

878 Figure 2. Change in the (a) mean or (b) variance of a climate parameter result in a change in the
879 frequency or severity of extreme events. The blue curve represents the original distribution of
880 values for the climate parameter. The brown curve represents the new distribution.

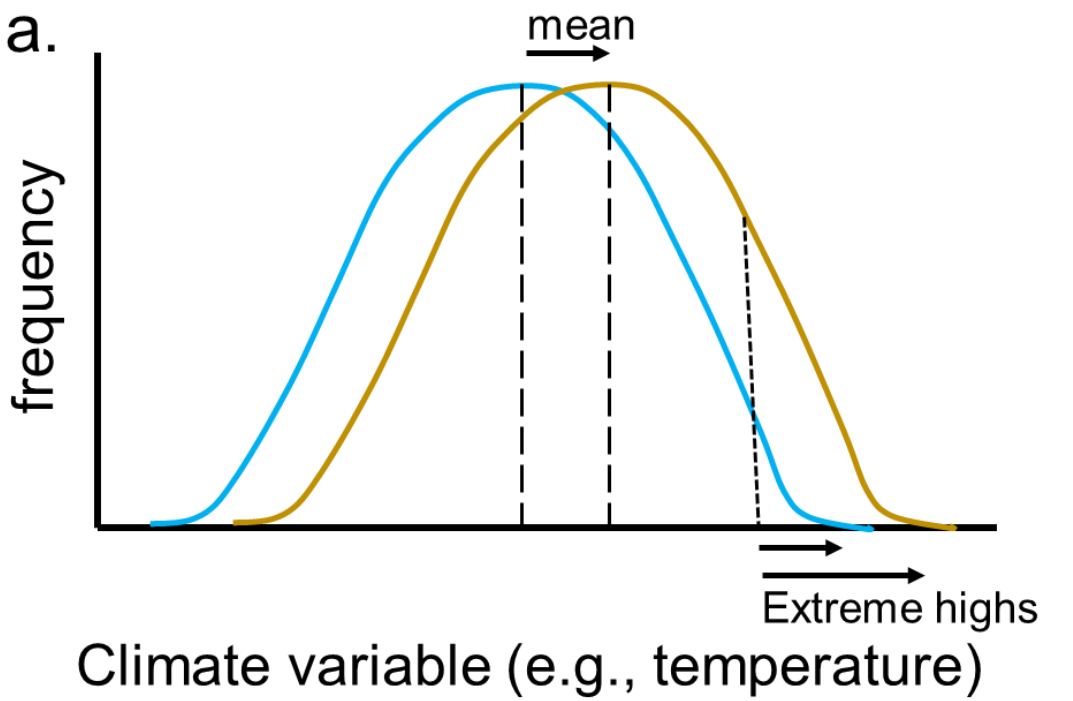
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882 Figure 1.
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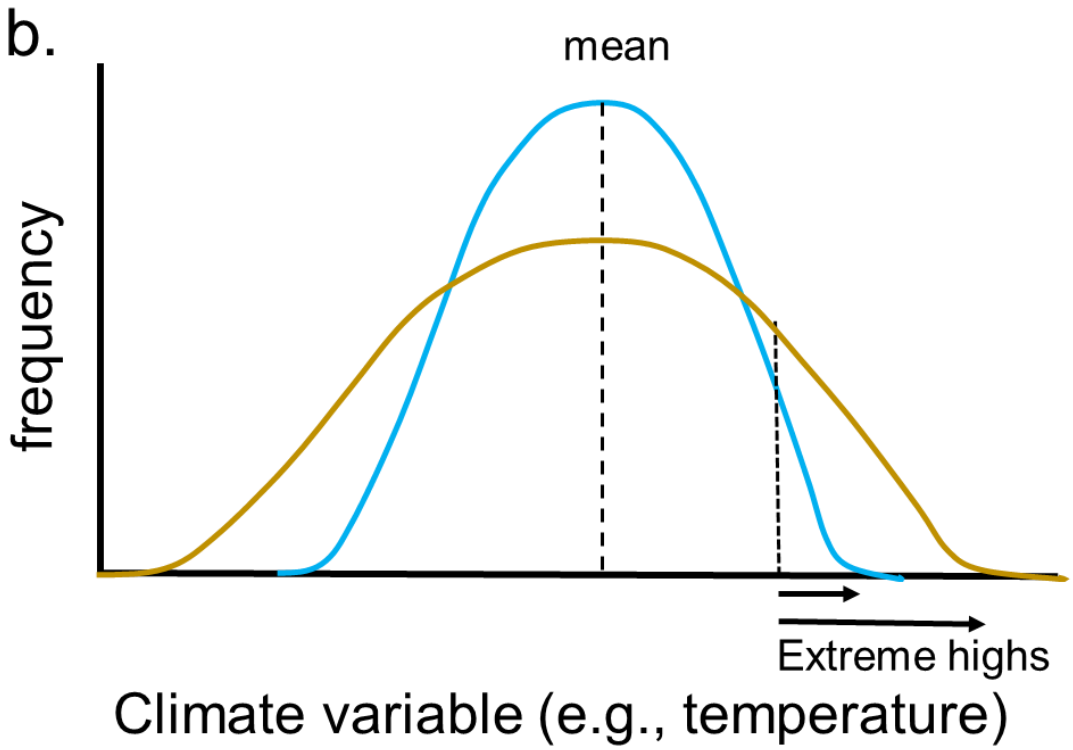


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886 Figure 2.



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Boxes:

Glossary

DNA barcoding: Identification of an insect (in this case) using sequencing of a short sequence of mitochondrial DNA, usually the cytochrome c oxidase I gene (COI or COX1), followed by comparison to a sequence reference library. Multiple species can be tested at once, in which case this is termed meta-barcoding.

Metapopulation: A set of demes (sub-populations) distributed across space, with migration among them but with independent population dynamics. Metapopulations are characterized by the rates of extinction and colonization of their demes.

Phenology: The timing of life events of a species or population.

Phenological mismatch: Shifts in the timing of life events among two or more species, such that life stages that previously overlapped no longer do to the same extent.

Vital rates: Measures of age-specific survival and reproduction. These elements are used in matrix models of population dynamics.

Voltinism: The number of generations per year.

Key reflections box:

- The response of insect diversity, abundance, and biomass to climate change is heterogeneous with respect to geography, habitat, and taxon. However, the data we have indicate that a number of groups are in significant decline in various locations.
- Our understanding of insects' population dynamics in response to climate change is hampered by confounding effects of other types of global change, insufficient baseline data across diverse geographies and habitats, and inadequate understanding of indirect effects due to changes in predator, competitor, and prey populations.
- We also lack an understanding of the responses of insect vital rates to climate change under field conditions. Are vital rates that control population dynamics buffered against climate change, or are they labile in situations where weather fluctuates on various time scales? Does climate change result in a shift in which vital rates control population dynamics? If so, what are the resulting effects on insect abundance?
- Answers to these questions will increase our ability to predict which species are most at risk of decline in response to climate change, and which are most likely to exhibit population outbreaks.

Key further reading

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