

REVIEW

Scientists' warning on climate change and insects

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Abstract

Climate warming is considered to be among the most serious of anthropogenic stresses to the environment, because it not only has direct effects on biodiversity, but it also exacerbates the harmful effects of other human-mediated

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threats. The associated consequences are potentially severe, particularly in terms of threats to species preservation, as well as in the preservation of an array of ecosystem services provided by biodiversity. Among the most affected groups of animals are insects—central components of many ecosystems—for which climate change has pervasive effects from individuals to communities. In this contribution to the scientists' warning series, we summarize the effect of the gradual global surface temperature increase on insects, in terms of physiology, behavior, phenology, distribution, and species interactions, as well as the effect of increased frequency and duration of extreme events such as hot and cold spells, fires, droughts, and floods on these parameters. We warn that, if no action is taken to better understand and reduce the action of climate change on insects, we will drastically reduce our ability to build a sustainable future based on healthy, functional ecosystems. We discuss perspectives on relevant ways to conserve insects in the face of climate change, and we offer several key recommendations on management approaches that can be adopted, on policies that should be pursued, and on the involvement of the general public in the protection effort.

KEYWORDS

arthropods, conservation, ecology, evolution, extreme events, global warming, temperature

INTRODUCTION

Of the many trends that are worrying scientists across the planet, the loss of biodiversity is among the most serious, because it may lead to the breakdown of ecological communities with concomitant, detrimental effects on critical ecosystem services and functions (Steffen et al., 2015). Across the biosphere, the most prominent drivers of biodiversity change and decline are habitat alteration, overexploitation, (agrochemical) pollution, biological invasions, and anthropogenic climate change (IPBES, 2019; Millennium Ecosystem Assessment, 2005; Venter et al., 2016). The biosphere has already warmed by $\sim 1.1^{\circ}\text{C}$ since industrialization and is projected to warm a further two to five degrees by 2100 (Figure 1) unless greenhouse gas emissions are significantly reduced (IPCC, 2021). Climate change can lead not only to the extinction of species, but also to profound changes in their abundances, distributions, and species' assemblages, compositions, and interactions with other species (Pecl et al., 2017; Schleuning et al., 2020; Sinervo et al., 2010; Steinbauer et al., 2018). Moreover, it is expected to act in either additive or synergistic ways with other drivers to exacerbate impacts on biodiversity (e.g., Boggs, 2016; Halsch et al., 2021; Hulme, 2017; Raven & Wagner, 2021; Verberk, Durance, et al., 2016; Verheyen & Stoks, 2019). A growing body of empirical literature is showing that many populations of insects are

declining rapidly across many parts of the biosphere, although patterns vary geographically and among different taxa or functional groups (Biesmeijer et al., 2006; Crossley et al., 2020; Didham, Barbero, et al., 2020; Didham, Basset, et al., 2020; Hallmann et al., 2017; Janzen & Hallwachs, 2021; Sánchez-Bayo & Wyckhuys, 2019; van Klink et al., 2020; Wagner, 2020; Wagner, Fox, et al., 2021; Warren et al., 2021). These declines are considered to be of profound concern, with terms like an emerging "insect apocalypse" being increasingly used by the media and even some scientists to describe this phenomenon (Goulson, 2019; Jarvis, 2018). Observed trends in the demographics of many taxa—including important functional groups like pollinators, nutrient cyclers, and natural enemies, as well as in the abundance of crop, forest, and urban pests—is currently considered serious enough to merit profound concern (Wagner, Fox, et al., 2021). Insects are important components of biodiversity (García-Robledo, Kuprewicz, et al., 2020; Stork, 2018; Wilson, 1987) contributing in diverse and well-documented ways to aboveground and belowground diversity, ecosystem functioning, and to various ecosystem services (Dangles & Casas, 2019). Important ecosystem services provided by insects are pollination, pest control, and nutrient recycling (Schowalter, 2013; Schowalter et al., 2018). Insects and their products also provide resources for higher trophic level organisms, including humans (Ramos-Elorduy, 2009;

Forecast change: current (annual means 1986–2005) ► end of century (annual means 2081–2100)

[Access 1.0 RCP8.5 CMIP5 model]

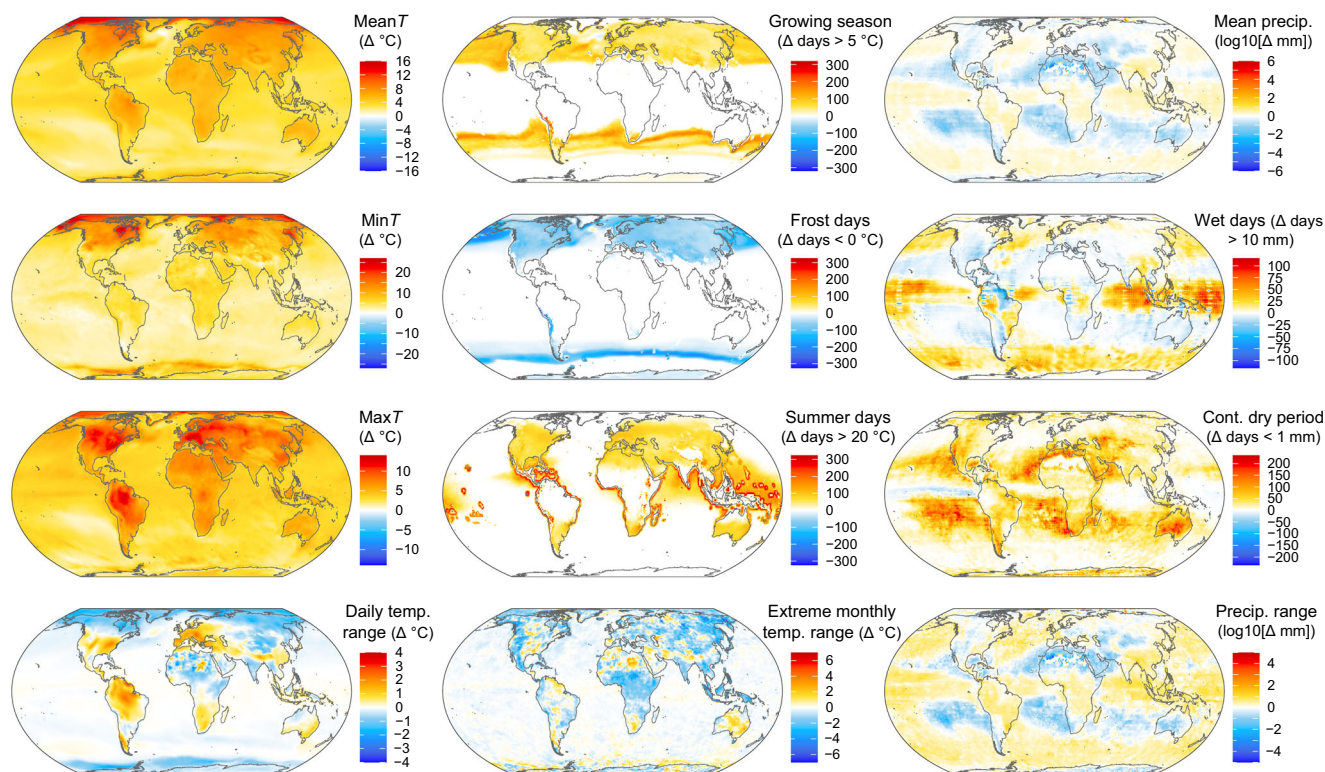


FIGURE 1 Changes to the abiotic environment relevant to insect life history. Each panel is the difference between current and 2100 conditions (T = temperature). Extreme indices are based on those suggested by the COE for climate extremes (<https://www.climdex.org>).

Schowalter, 2013). However, some insect species negatively affect human health and welfare by vectoring pathogens or by eating our crops (Schowalter et al., 2018). In natural (unmanaged) ecosystems, abundances of pathogen and vector species are controlled through various food web interactions and habitat conditions, whereas anthropogenic land use changes such as deforestation, habitat fragmentation, and agricultural development can modify these interactions with consequences for disease transmission (Burkett-Cadena & Vittor, 2018; Gottdenker et al., 2014). In addition, it is predicted that global warming will affect the length of the transmission season and facilitate the expansion of the geographical range of the disease (Woodward et al., 2014). How this will affect spread and severity of vector-borne diseases is difficult to predict as it depends on the complex interplay between many factors, including socio-economic ones, which themselves can be affected by global warming (Caminade et al., 2019; Rogers & Randolph, 2006). Pest incidence and severity is predicted to increase under conditions of global warming by, e.g., direct effects of higher temperature on insect survival, development, and reproduction, and by expansion of their geographical ranges, which is often exacerbated by global trade and the introduction of exotic pests (Lamichhane et al., 2015; Skendžić et al., 2021).

Given their generally small body size, and the fact that the vast majority of species are ectothermic (Harrison et al., 2012), insects are considered to be especially susceptible to the direct effects of changing temperature and moisture regimes (Halsch et al., 2021; Harvey, Heinen, Gols, & Thakur, 2020; Wagner, 2020). Climate change can, therefore, shape the physiology and behavior of insects, with concomitant effects on life-cycles, life-history traits, reproduction, and population persistence (García-Robledo et al., 2016; Wagner, 2020). For example, the temperature-size rule predicts that insect size is to some degree plastic, and under warmer conditions, ectothermic species develop faster but become smaller in body size (Atkinson, 1994; Verberk et al., 2021). However, there are many exceptions to the temperature-size rule among insect groups or populations (Horne et al., 2015). In a phylogenetically controlled analysis of temperature-size relationships in tropical insects, the main conclusion is that size differences among populations are heritable rather than the result of body size plasticity, and global warming will not inevitably lead to body size decreases (Duffy et al., 2015; García-Robledo, Baer, et al., 2020). Nevertheless, significant direct impacts of climate change on insect populations are to be expected for many species and

taxonomic groups. However, given the great diversity of insect life histories, behavioral and ecophysiological adaptations, habitats and environments globally, there will inevitably be some exceptions to the generally negative impacts of excessively high temperatures (e.g., García-Robledo, Baer, et al., 2020) or increases in growing season length in typically cold environments (Sinclair, 2014). For instance, warming is enabling, at least transiently, some species of thermophilic forest and agricultural pests and disease vectors such as mosquitoes to expand their ranges to higher latitudes (Battisti & Larsson, 2015; Hill et al., 2011; Jactel et al., 2019; Kovats et al., 2001; Skendžić et al., 2021). The economic costs of these climate-mediated range expansions on food production and human health could be enormous. Responses of insects and different functional groups to climate change are thus taking a wide variety of forms in different parts of the globe, including in both natural and human-dominated environments such as forests, wetlands, agricultural landscapes, and urban environments.

A recent study argues that the combined effects of climate change and agricultural intensification are

negatively affecting insect biodiversity (Outhwaite et al., 2022). In this synthesis “warning paper,” we explore insect responses to climate change and climatic extremes, what is known about them, what knowledge is still needed to reduce uncertainty, and what key recommendations scientists can formulate for policy makers and the general public to reduce the harmful impacts. We address the effects of gradual changes in climate and increased climatic variability i.e., frequency of extreme, abrupt, and punctuated events (Figure 2), and how they are possibly modulated by other global change drivers. These changes cannot be ignored, as they are already having major consequences on insects and will have implications for insect conservation and management in the coming decades (Cardoso et al., 2020). Although much information is available on the ecophysiology of individuals and the survival of different insect species, it is necessary to keep in mind that our warning is about the impact this will have on humankind. This impact will be mediated by the wider effects of climate change for the disruption of interaction networks within ecosystems (Tylianakis & Morris, 2017), and the ecosystem services

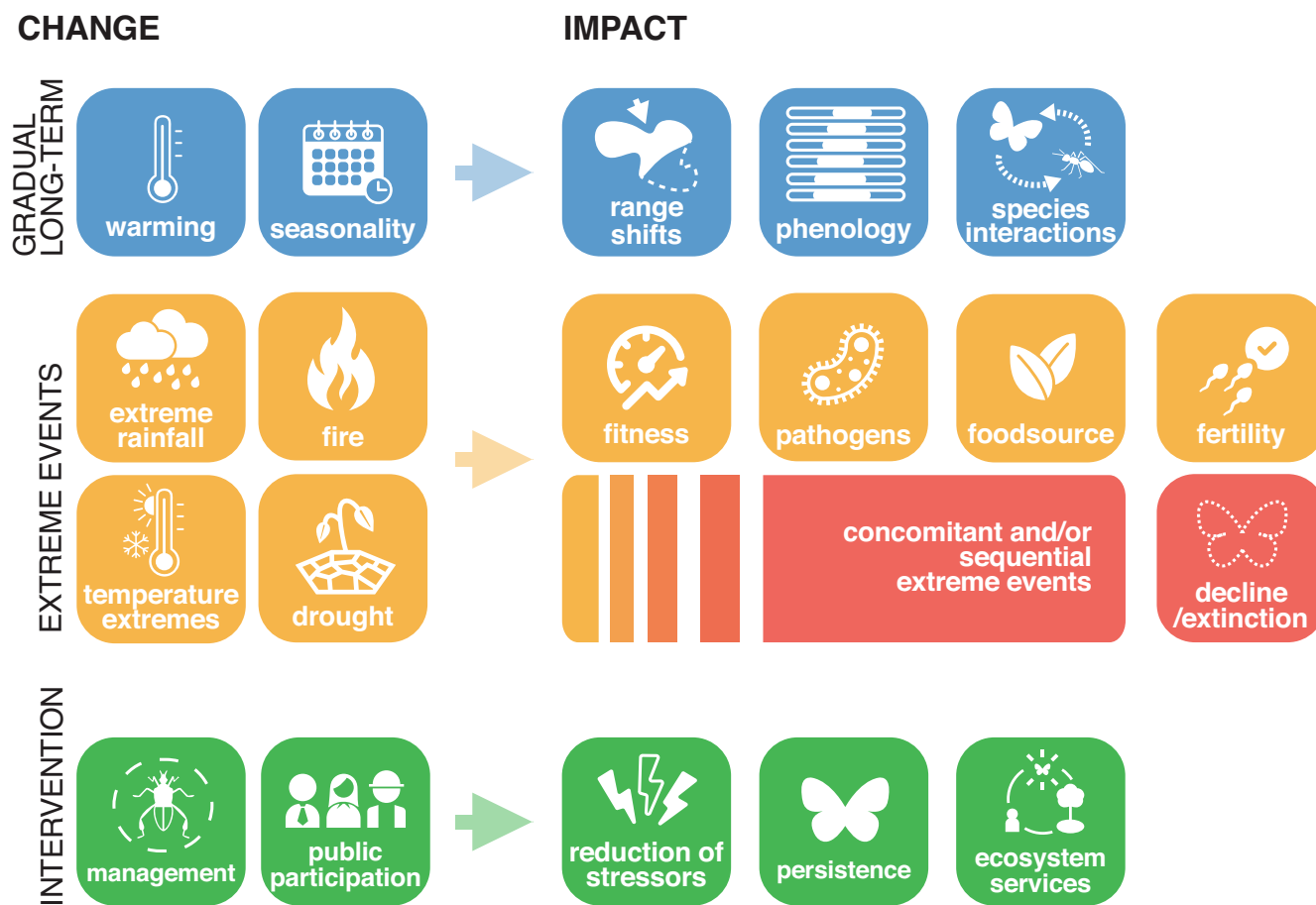


FIGURE 2 Climate change impacts on insects can be categorized into two major categories: Gradual long-term change and extreme events that will increase in frequency and severity, while interventions include formal mitigation of change through policy and public approaches which in turn help to reduce impacts in various ways.

and functions provided by insects. Unfortunately, along with climate change denial, other incipient forms of scientific denial are becoming more prevalent in recent years, including extinction denial (Lees et al., 2020). However, if we fail to recognize the importance of insects and their vitally important role in the functioning of natural and managed terrestrial and freshwater ecosystems (Losey & Vaughan, 2006), or the impacts that climate change and other anthropogenic stressors are having on them, then we are essentially limiting our ability to act. Recognizing and acting upon the clear and striking evidence of climate change effects on insects is critical to support our collective efforts to build an ecologically sustainable future.

EFFECTS OF LONG-TERM, ANTHROPOGENIC CLIMATE CHANGE ON INSECTS

The effect of long term, gradual warming on insect declines is not always immediately apparent. Discernible changes in insect population dynamics, their distributions, phenology, or abundance are usually detected after critical performance thresholds affecting fecundity, survival, and other vital rates are surpassed (Harvey, Heinen, Gols, & Thakur, 2020). Furthermore, warming is occurring unequally across the biosphere and across time-scales, with temperate, boreal, and polar ecosystems at higher latitudes warming at much faster rates than subtropical and tropical ecosystems at lower latitudes (Parmesan, 2007; Post et al., 2018). Temperatures along tropical mountains are increasing 0.017°C per year, and ecosystems are already shifting upslope (Feeley et al., 2013). Winter is warming faster than any other season (IPCC, 2014), and nights are becoming warmer worldwide (Karl et al., 1991).

In ectothermic organisms, warmer temperatures are generally associated with increased metabolic rates that may lead to increased physiological costs (Irwin & Lee, 2003; Williams et al., 2012). While warming stimulates growth, development, and reproduction up to some optimal temperature, beyond this temperature, metabolic costs increase disproportionately and thermal injuries accumulate, eventually leading to developmental failure, reduced fecundity, impaired dispersal capacity, and, ultimately, decreased fitness and increased mortality (Gilbert & Raworth, 1996). Exposure to elevated temperatures affects insect growth and development, often resulting in body size reductions, with negative effects on fecundity, longevity and dispersal, all of which can reduce their resilience in the face of climate change and in the worst-case scenarios lead to population crashes (Abram et al., 2017; Gardner et al., 2011; Hof et al., 2011;

Sweeney et al., 2018). As a result, climate change may reduce genetic diversity through processes including population bottlenecks, loss of genetic diversity that is not related to selection, and outbreeding or inbreeding depression (Halsch et al., 2021; Pauls et al., 2013), which threatens the persistence of populations. Insect populations may display very limited genetic variation in traits associated with thermal tolerance and it is concerning that in such populations, local adaptation is already lagging behind current temperatures (García-Robledo & Baer, 2021a, 2021b). Studies with ants show that thermal tolerance (or intolerance) varies across different species and under different thermal niche conditions, with tolerance or even benefits of marginally higher temperatures on colony fitness offset beyond critical thermal thresholds (Diamond et al., 2013). This paper primarily focuses on ecological responses to climate change, with less attention paid to physiological responses at the individual (=organism) level. One of the most notable phenotypic responses to warming seen in some insects are changes in body color and, in particular, a reduction in melanization (Brakefield & de Jong, 2011; Clusella-Trulas & Nielsen, 2020; Kingsolver et al., 2011; Roulin, 2014). Reduced melanization is potentially adaptive, as lighter individuals may be able to more effectively thermoregulate when exposed to extreme heat than darker individuals (Roulin, 2014). Consequently, phenotypic plasticity can to some extent counter other physiological stresses induced by climate change.

We argue that the most important outcome of climate warming is that insect communities become destabilized (Diamond et al., 2016; Pelini et al., 2014; Pureswaran et al., 2021), and that populations and even entire species may go extinct unless they alter their geographical distributions and/or adjust their spatial and temporal behavioral activity patterns and seasonal phenologies to the new climatic conditions (García-Robledo et al., 2016; Halsch et al., 2021; Harvey, Heinen, Gols, & Thakur, 2020). This leads to changes in the structure of ecological communities at given locations in ways that affect species interactions, with potentially severe repercussions on ecosystem stability and functioning, and subsequently the provisioning of ecosystem services.

Effect on species distributions

Species' distributions are strongly determined by climatic factors and are labile, expanding or contracting during long-term climatic fluctuations (Hewitt, 2000). Similarly, the rapid rate of current climate warming strongly determines how successfully insects are able to track climatic shifts, since they may or may not keep pace with these changes. Projections of how global warming will affect species geographic ranges are based on bioclimatic

envelope models (Vieilledent et al., 2016), the response of insects to extreme temperatures (Sunday et al., 2014), or simple graphical models of species elevational ranges (Colwell et al., 2008), which calculate the potential loss of suitable habitats. The general consensus among these different approaches is that species at lowest latitudes or elevations must migrate to cooler environments to avoid extinction (Colwell et al., 2008; Sunday et al., 2011, 2014) (Figure 3a,b). Moreover, the ability of insects to track shifting thermoclines will be affected by various aspects of their eco-evolutionary dynamics (Miller et al., 2020;

Wellenreuther et al., 2022). Predicting this to inform management strategies will increasingly require the use of modeling and genomic sequencing (Wellenreuther et al., 2022).

Warren et al. (2018) generated bioclimatic models predicting the effects of slight, moderate and extreme warming on geographic range losses incurred by 34,000 insect species across the biosphere. They found an exponential effect of temperature on range losses by the year 2100. With an increase of 3.2°C, the ranges of almost half of the insect species will contract by 50% or more, whereas

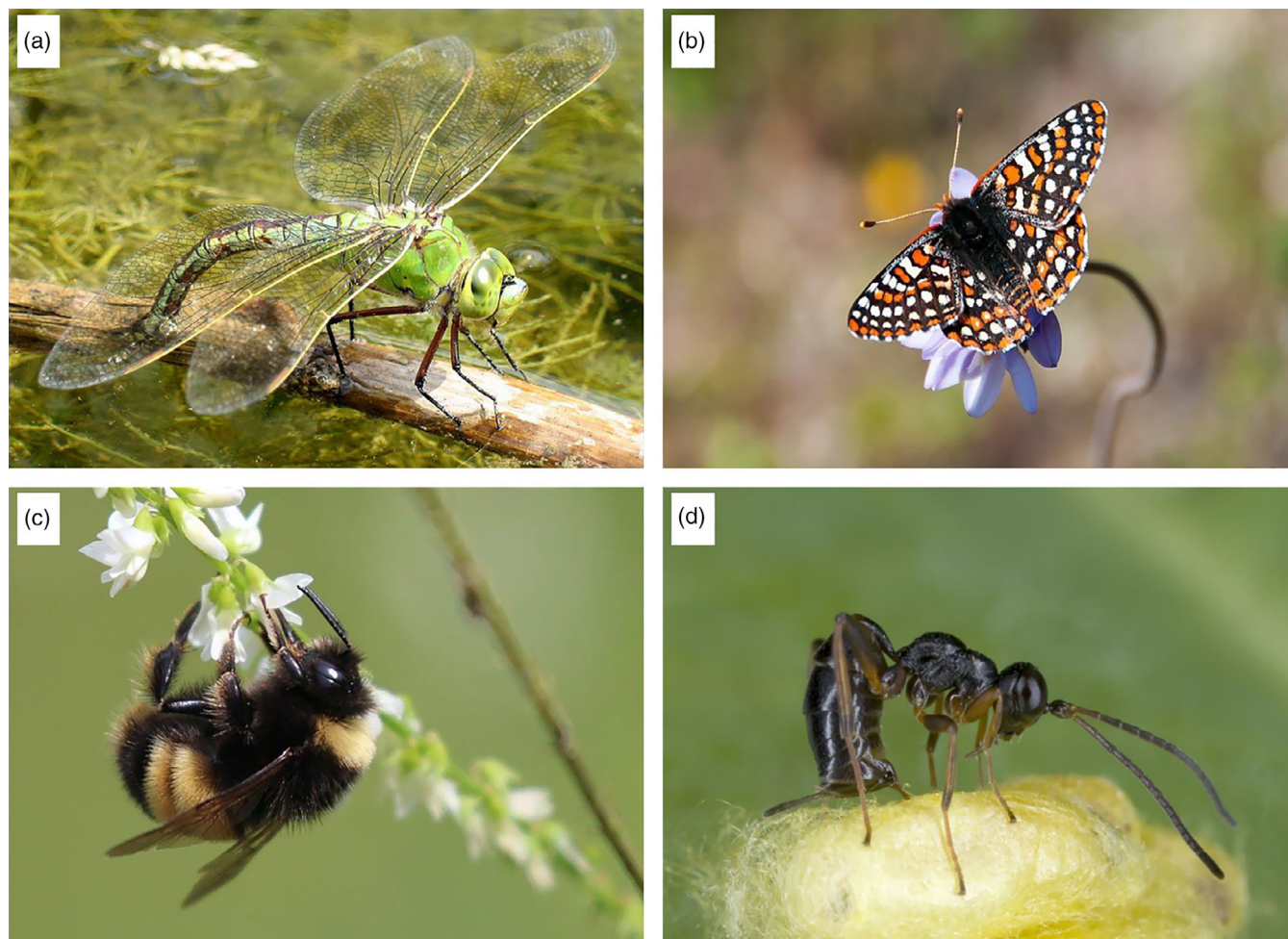


FIGURE 3 (a) Many insects are showing a range of ecophysiological responses to longer-term climatic changes. For example, the emperor dragonfly (*Anax imperator*) has shifted its distribution northward and to higher elevations in Europe since 2000 in response to warming (Platts et al., 2019). (b) In California and Mexico, the Quino Checkerspot butterfly (*Euphydryas editha quino*) has responded to recent warming by moving to higher elevations, and by shifting from its preferred lowland food plant (a *Plantago* species) to *Collinsia concolor*, which is more abundant at higher elevations. Increased warming, however, still threatens this endangered subspecies (Parmesan et al., 2015). (c) Many recent insect declines, such as the now vulnerable yellow-banded bumblebee (*Bombus terricola*), have been attributed to climate extremes, and especially hotter maximum temperatures during the summer (Martinet et al., 2015). (d) Exposure to heat waves can have significant effects on insect reproduction. Functional responses in the facultative hyperparasitoid, *Gelis agilis*, are strongly correlated with ambient temperature, and at high temperatures their ability to exploit hosts is greatly impaired (Chen, Gols, et al., 2019). Photograph of emperor dragonfly by Tim Bekaert; photograph of Quino Checkerspot butterfly by Andrew Fisher (USFWS volunteer biologist); photograph of yellow-banded bumblebee by rob Foster (<https://www.inaturalist.org/users/264273>); photograph of *Gelis agilis* by Tibor Bukovinszky (NVWA Wageningen University & Research. Wageningen).

this drops to 18% of insects at $+2^{\circ}\text{C}$, and 6% of insects at $+1.5^{\circ}\text{C}$ (Warren et al., 2018). Insects, like other organisms, are responding to warming by shifting their distributions poleward and to higher elevations (Grewe et al., 2013; Heiser & Schmitt, 2013; Parmesan & Yohe, 2003). However, range retractions at lower latitudes or altitudes have received less attention (but see Kerr et al., 2015; Merrill et al., 2008), as the disappearance of a population is a more gradual process. Moreover, as climate suitability continues to decline in these so-called trailing edge populations, more and more insect species, such as butterflies, will accumulate an extinction debt (Devictor et al., 2012; Thomas et al., 2004).

Despite the fact that insect extinction is a demographic process, only two studies have determined the effect of global warming on insect population dynamics, range shifts, and fitness (Deutsch et al., 2008; García-Robledo & Baer, 2021b). Deutsch et al. (2008) combined life table analysis with global temperature records to estimate changes in fitness at current and future temperatures. One limitation of this study is that it only includes fitness estimates for pantropical crop pests and tropical biocontrol agents reared in the laboratory, which are usually tolerant to high temperatures or adapted to laboratory conditions. Nevertheless, their results support the hypothesis that tropical insect species are at higher risk of extinction than temperate insects (Deutsch et al., 2008). For example, the leaf beetle *Cephaloleia belti* includes high- and low-elevation mitochondrial haplotypes locally adapted to cold and warm temperatures. Both haplotypes interbreed in a hybridization zone at mid elevation. Demographic models, combined with long-term temperature datasets, show that, with an increase of just 2°C , trailing-edge populations will decline, and middle elevations will become refuges to global warming (García-Robledo & Baer, 2021a, 2021b).

As long as population losses at lower latitudes or elevations are compensated by range expansions at other boundaries of the range, most species may be able to persist (Deutsch et al., 2008). Range shifts most likely will be accompanied by loss of genetic diversity; however, not all species are able to perform such range shifts, as their capability to do so depends on several factors, including active or passive dispersal abilities, population dynamics, genetic diversity, width of the thermal safety margins, habitat availability, intra- and interspecific interactions, and co-shifting of food sources (Amundrud & Srivastava, 2020; Berg et al., 2010; Bybee et al., 2016; Deutsch et al., 2008; Hof et al., 2011; Menzel & Feldmeyer, 2021). Thus, different times of response to climate change in insects are evident, and the existence of a time-lag in species response implies caution in predicting species' occurrence shifts following climate change. For

instance, Román-Palacios and Wiens (2020) found that “hot” years coincided with increased rates of local extinction, and suggested that more than half of insect species may not be able to adjust their distributions rapidly enough to avoid extinction. However, Sunday et al. (2012) reported that terrestrial ectotherms at the warmest (or “trailing”) edge of their ranges, including insects, do not appear to be delimited by insufficient heat tolerance, suggesting that factors other than temperature (e.g., drought, competition, light) may shape their range boundaries and thus, warming may not result in consistent shifts in these trailing edges (Spence & Tingley, 2020). Studies with damselflies show plasticity to warming at range margins and that gene switching for thermal tolerance appears to be under strong selection (Dudaniec et al., 2018; Lancaster et al., 2015), suggesting that some species can thus adapt rapidly to shifting thermoclines. However, historical and ongoing habitat loss and fragmentation and isolation as a consequence of human land use changes is a major current threat to insects that exacerbates climate change impacts by hampering range expansions, especially across uneven landscapes with elevational gradients (Samways et al., 2020; Yadav et al., 2018, 2021). It is also important to acknowledge that range shifts in response to warming may lead to the elimination of native competitors in the new range where there is strong niche overlap (or vice-versa). This area is in urgent need of further investigation.

The cryosphere (e.g., glaciers, permafrost) covers $\sim 10\%$ of the Earth's surface but is declining as a result of long-term warming trends (Pörtner et al., 2019; Zemp et al., 2019). Glacial retreat is indeed an iconic symbol of climate warming, and leaves habitats that are rapidly colonized by different biotic communities. Receding ice threatens many insects that are restricted to narrow habitat zones in front of glaciers (Gobbi et al., 2021). Studies report that cold-adapted and hygrophilous insects are moving to higher elevations in response to warming but with a reduction in their broader spatial distributions (Moret et al., 2016; Valle et al., 2020). Altitudinal shifts are not only triggered by the thermal requirements of cold-adapted species, but also by the increasing competition of warm-tolerant species coming from lower elevations, and this covers a wide range of taxa in both terrestrial and aquatic systems (Brighenti et al., 2021; Cauvy-Fraunié & Dangles, 2019; Ficetola et al., 2021; Pizzolotto et al., 2014). Climate warming in glaciated alpine areas produces both “winners” and “losers” (Cauvy-Fraunié & Dangles, 2019). The likely reason is that the response of insects to increasing temperature varies among species, communities and geographic area (Ficetola et al., 2021). Winners tended to be generalist/invasive species, good dispersers, generally colonizing

from downstream or downslope, such as grasshoppers (Yadav et al., 2018); conversely, the losers are often specialist species, adapted to cold habitats, among which some were restricted to isolated glacier-influenced ecosystems (Cauvy-Fraunié & Dangles, 2019). The spatial and temporal dynamics of the insect species assemblages linked to ice-related landforms is revealing a rapid turnover of species with the substitution of cold-adapted species with more eurythermal species (Gobbi et al., 2021).

It is important to temper the primarily negative effects of warming on insects by also stressing that some species—at least transiently—may benefit in response to milder winters and warmer conditions that enhance survival or voltinism (Marshall et al., 2020; Musolin, 2007; Tougeron et al., 2017). Winter is considered a major control agent of forest and crop pests and trends toward warmer winters or reduced numbers of deep frosts are leading to increased numbers of pest outbreaks (Cannon, 1998; Pureswaran et al., 2019). Moreover, since 1970 more species of generalist moths in Great Britain have increased in abundance than decreased in abundance (38% vs. 31%), presumably in response to warming (Wagner, Fox, et al., 2021). Moreover, caterpillar abundances in cloud forests in Ecuador increased between 2001 and 2019, because of an increase in sunny days as a result of climate change (Wagner, Grames, et al., 2021). It needs to be stressed that positive responses to warming may be transient, especially as climatic extremes are increasing, which imposes immense short-term stresses on insect populations (Harvey, Heinen, Gols, & Thakur, 2020), or else if warming continues unabated, pushing many species beyond their thermal optima for reproduction and survival (Buckley & Kingsolver, 2021). Effects of warming may also be disproportionate up the food chain, with more deleterious physiological effects on predators or parasitoids than on their prey or hosts (Jeffs & Lewis, 2013; Tougeron et al., 2019). Under this scenario, herbivores may benefit from enemy release (Moore et al., 2021). The net effect will still likely have negative consequences for food webs and communities, as the loss of top-down control might lead to all kinds of unpredictable, potentially destabilizing, effects over time.

Effect on phenology

In addition to range shifts, another well-documented aspect of insect response to climate change is a change in phenology. Elevated temperatures increase the duration of the growing season, which together with faster developmental rates allows some insect species to increase the number of generations in a given year (i.e., voltinism) (Bradshaw & Holzapfel, 2001). Even apparently modest temperature

risks can result in increases in seasonal or annual generations (Parmesan & Yohe, 2003). For example, Altermatt (2010) showed that 44 butterfly and moth species increased the number of generations after 1980 in response to rising temperatures. While warmer temperatures generally allow for extra generations in the summer, a higher voltinism may result in smaller adults being produced (Horne et al., 2015; Verberk et al., 2021). Moreover, the addition of extra generations later in the season is also affected by the overwintering strategy and photoperiod (i.e., shortening day length and the initiation of diapause), which is a dominant seasonality cue for many temperate insects (Lindstad et al., 2019; Marshall et al., 2020; Tougeron, 2019). Both parameters are therefore important to consider when projecting effects of climate change, and extreme temperatures, on patterns in insect voltinism and body size (Bale & Hayward, 2010; Forrest, 2016; Verberk et al., 2021).

Ecological consequences of changes in overwintering strategies, and more generally in activity timing, are still far from being well-understood (Williams et al., 2015). In some cases, an extended period of warm temperatures that promotes development may delay winter diapause induction. This may create a developmental trap resulting in the production of a complete or partial additional generation in the autumn that cannot survive or enter diapause (“the lost generation hypothesis” (van Dyck et al., 2015; Kerr et al., 2020). In addition, diapause maintenance and termination are disrupted because of warm winters. For example, many insects, like other organisms, require a period of chilling during diapause before they can resume development (Lehmann et al., 2017; Stålhandske et al., 2017). If a chilling cue is not received, individuals may emerge later or even not at all (Bale & Hayward, 2010; Tougeron et al., 2019). In line with this, forest experiments conducted by Fitzgerald et al. (2021) in North Carolina support the “cool-season sensitivity” hypothesis, showing that arthropods adapted to cooler conditions endured stronger negative effects of warming during warm winters. Alternatively, MacLean et al. (2017) found that exposure to warmer conditions in winter actually benefitted acorn ants by “priming” them metabolically for early activity in spring. Therefore, the effects of warmer winters on insects is likely to vary considerably among different taxa.

Exposure to repeated heat waves in summer, or warmer spells during winter (or both), may also generate inappropriate cues that lead insects into developmental traps (e.g., resuming development in the middle of winter) (Boggs, 2016; Forrest, 2016). For example, unseasonably warm autumn conditions are causing the wall brown butterfly *Lasiommata megera*, to alter life-cycle decisions by breaking diapause at the end of the second generation. This makes the third generation highly susceptible to winter mortality, and as a result the butterfly is declining

rapidly across much of western Europe (van Dyck et al., 2015). In other cases, a partial or complete loss of winter diapause may result from successive years with permissive winter temperatures, which have been shown to result in the activity of some aphid parasitoids across the entire year (Tougeron et al., 2017). Therefore, individuals that remain active throughout the winter rely on physiological and behavioral thermotolerance to survive, including rapid cold hardening, or the induction of transient and easily reversible resting stages (Diniz et al., 2017). Warmer winter conditions have also been shown to affect colony phenology in honeybees, leading to mismatches with their floral resources (Nürnberg et al., 2019). Furthermore, warmer periods in winter also stimulate colony brood rearing activity and this benefits their main parasite, invasive *Varroa destructor* mites (Nürnberg et al., 2019; Vercelli et al., 2021). Seasonal changes in temperature therefore also need to be placed in the context of facilitating pathogens or parasites.

Winter conditions tend to be much more variable geographically and locally than summer conditions (Bonan, 2004) and this can affect latitudinal variation in biotic processes much more strongly than conditions during the growing season. Trends toward decreasing winter snow depth, increasing numbers of winter thaws, or later snowfalls and earlier winter melts are also being observed in many temperate parts of the world under climate warming (Fontrodona Bach et al., 2018; McCabe & Wolock, 2010). The “subnivium,” defined as the physical interface between the snowpack and ground, is an important refuge that protects overwintering insect species from extremely cold temperatures by providing insulation during diapause (Zhu et al., 2019). During periodic thaws, or when spring melt occurs early, insects are exposed to cold temperatures on bare soils that may be lethal (Bale & Hayward, 2010; Williams et al., 2015). The absence of snow cover also subjects diapausing stages to elevated rates of moisture loss and, as a consequence, desiccation. Loss of snow cover also alters insect metabolism leading to a potential phenological mismatches with key resources (Renner & Zohner, 2018). Moreover, diapausing insects are more exposed to winter-active predators when snow cover disappears for even short periods (Cooper, 2014). However, the longer-term effects of seasonal changes in temperature and precipitation on insect demographics are thus far little-studied.

Effect on species interactions

Insects, like most organisms, are embedded in complex communities, and their fate depends on interactions with other species. In general, predation and other multitrophic interactions often result from long co-evolutionary

processes that are specific to a particular environment under relatively stable climatic conditions. However, temperature changes may differentially affect the biology of each of the component species of a system. This has been demonstrated in multitrophic systems involving plants, their herbivores, natural enemies (parasitoids, predators and pathogens), and hyperparasitoids (Agosta et al., 2017; Bale et al., 2002; Bannerman et al., 2011; Moore et al., 2021; Pardikes et al., 2022; Romo & Tylianakis, 2013; Schreven et al., 2017; Tougeron et al., 2018). Studies show that the effects on survival, development, and reproduction are generally negative, e.g., plants growing under conditions of extreme temperatures, increased CO₂, and/or reduced rainfall could become suboptimal nutritional resources for herbivores, indirectly influencing natural enemy fitness and associated biocontrol services (Han et al., 2019, 2022). A double negative effect may occur when temperature increase promotes herbivorous pest populations while negatively impacting host plant defenses (Wang et al., 2021). Temperature increases may also induce slight shifts in feeding preference; e.g., with phytophagous insects feeding more on native plants versus invasive plants when temperature increases (Liu et al., 2021). Interactions between plants and insect pollinators are typically also known to be weakened by climate change (Tylianakis et al., 2008). The effects are likely to be even more important in higher trophic levels that depend on the host specificity and the capacity of the lower trophic levels to adapt to these changes and also because they are less numerous (Monticelli et al., 2022; Thackeray et al., 2016; van Baaren et al., 2010). These effects may be exacerbated in species-poor communities e.g., on islands or in increasingly homogeneous, chemically disrupted agro-landscapes (Raven & Wagner, 2021). Moreover, many vertebrates (e.g., small mammals, birds, reptiles, amphibians) depend on insects as food, and the loss of insects in a warming world is therefore likely to have enormous effects on broader ecological communities.

One major consequence of changes in the distribution and phenology of insects is the occurrence of potential spatial and temporal mismatches among interacting species. Differential responses between trophic levels may, for instance, decouple the timing of generations among interacting species (Damien & Tougeron, 2019; Gérard et al., 2020; Thackeray et al., 2016). This may be especially prevalent among specialized species that are constrained by the responses of their prey or hosts, or in species that already have narrow environmental niches (Damien & Tougeron, 2019; Tylianakis et al., 2008). The mismatch between insect food availability in spring and the breeding success of long-distance migratory birds is a well-studied example (Both et al., 2006). These mismatches may subsequently destabilize and reduce the efficacy of crucial interactions such as between plants

and pollinators (Peralta et al., 2020), or herbivores and natural enemies (Bale et al., 2002; Harvey, 2015; Singer & Parmesan, 2010). Mismatches may be countered by strong selective pressure leading to readjustments in the phenology, distribution, or physiology of interacting species (Klapwijk et al., 2010; Schleuning et al., 2020). Moreover, climate warming may lead to formation of new interactions among species that were previously disassociated in space or time (Shah et al., 2020). Novel interactions may arise as a result of differences among species responses and thus adaptation to warming (including their value as an interaction partner, e.g., nutritional quality), because of differential responses of spatial or temporal range, or when existing interaction partners go extinct and switches to new partners are required (Tylianakis & Morris, 2017).

Thermal tolerance mismatches may occur intraspecifically via sexual conflicts in response to different temperatures, as has been demonstrated in damselflies (Svensson et al., 2020) and whiteflies (Ma et al., 2014), or interspecifically, where tightly interacting species, such as parasitoids and their hosts, exhibit differing sensitivities to high temperatures (Abarca & Spahn, 2021; Furlong & Zalucki, 2017; Wetherington et al., 2017). This has been shown with thermal response curves for pathogen growth and host defense (Thomas & Blanford, 2003), and may lead to distinctly non-linear responses to even small temperature changes. These “thermal mismatch” effects could possibly result in a destabilization of the dynamics that could lead to the extinction of part of the system, and could create an imbalance in how mass and energy transfer in food webs (Thakur, 2020a). Studies using simulated warming to mimic natural conditions have shown that exposure to higher temperatures may also decrease the interaction strength and the fitness of each of the interacting species (Sentis et al., 2013). However, in some instances, temperature can shape insect communities directly through differences in species’ thermal performance capabilities, and not involve any effect of biotic interactions (Thierry et al., 2021).

Warmer temperatures lead to higher metabolic and feeding rates, which tends to increase the strength of trophic interactions in the short term by making consumers more dependent on their resources (Rall et al., 2012; Sentis et al., 2012). However, energetic losses often increase faster at higher temperatures than feeding rate, leading to metabolic mismatches (Bideault et al., 2021). This is especially problematic at very high temperatures, where feeding rates either asymptote or even tend to decrease (Sentis et al., 2012). This, in turn, influences biomass distribution in food chains, such as in terrestrial ecosystems where warming favored herbivore-heavy

webs (de Sassi & Tylianakis, 2012), or in some aquatic systems where it favored top-heavy (predator dominated) food chains (Kratina et al., 2012; O’Connor et al., 2009). By modeling empirical data of thermal dependence on key biological rates, Bideault et al. (2021) predicted that warming is expected to favor top-heavy webs in both terrestrial and aquatic ecosystems. This highlights how temperature can have cascading effects from physiology to species interactions and community properties. In addition, the indirect effects of high temperatures on insect communities may be mediated by changes to food web structure and stability in communities where invasive organisms are considered problematic. For example, Sentis et al. (2021) showed that experimental communities with less connectivity, shortened food chains and reduced temporal variability were more susceptible to invasions under warmer conditions. Moreover, the authors found that, under warmer conditions, in invaded communities, species diversity decreased, network connectivity increased and most top predators were lost leading to their replacement by meso-predators. Such changes in insect communities can have detrimental consequences for food web stability. This loss of predators and herbivore regulation can be further exacerbated by drought (Romo & Tylianakis, 2013). Such changes in insect communities can have detrimental consequences for food web stability.

Insects live in close association with microbial communities residing within cells, on the cuticle, inside the gastrointestinal tract or in the hemolymph. These microbiomes comprise mutualists that for instance facilitate digestion, increase immunity or aid in detoxification of plant metabolites (Feldhaar, 2011). Microbes may also host antagonists (e.g., pathogens) that are detrimental to insect health (Degli Esposti & Martinez Romero, 2017; Gurung et al., 2019). It is likely that climate-driven impacts on insect immunity will alter interactions between hosts, symbionts and pathogens. For instance, insects exposed to higher and more variable temperature regimes show higher levels of immunity than those exposed to lower and less variable temperature regimes (Bozinovic et al., 2013; Catalán et al., 2012; Van Dievel et al., 2017), whereas other studies report opposite findings (Karl et al., 2011). Mutualistic bacteria provide various ecological benefits, such as resistance to environmental stress, pathogen infections or natural enemies, yet their impact remains poorly understood at the level of ecological communities (Ferrari & Vavre, 2011; Oliver et al., 2010). Due to the reduction in size of their genome during coevolution with their hosts, mutualistic endosymbionts have little potential to cope with a changing environment, including heat stress, and can therefore be considered the Achilles heel of insects in a context of

increasing temperature (Renoz et al., 2019). Some evidence demonstrates that the interplay between insect hosts and their mutualistic and antagonistic microbial partners is temperature-dependent. For instance, gut microbiome composition can shift across seasons and is concurrent with changes in cold tolerance (Ferguson et al., 2018). Benefits or drawbacks provided by symbionts can be altered by increasing temperatures (Bensadia et al., 2006; Higashi et al., 2020; Tougeron & Iltis, 2022), in part because some symbionts reside in highly heat-sensitive organs (e.g., bacteriocytes, Shan et al., 2017) and reversely, alteration in the gut or intracellular microbial community can influence insect resistance to temperature variation (Henry & Colinet, 2018; Iltis, Tougeron, et al., 2021; Jaramillo & Castañeda, 2021). Moreover, the microbiome can be totally restructured during diapause in arthropods (Mushegian et al., 2018; Mushegian & Tougeron, 2019), but how modifications in seasonal strategies following climate change actually affect microbial communities merit further investigations.

Aquatic insects face substantially different ecophysiological problems compared with terrestrial insects, and likely will experience climate change in fundamentally different ways. Like terrestrial insects, aquatic insects are threatened by rising temperatures and changes in patterns of temperature variation, among other factors (Birrell et al., 2020). The underlying challenges, however, differ in part because water has much higher heat capacity than air, such that—at least in lotic habitats—local thermal variation is restricted in space and time relative to atmospheric fluctuations, and individuals have limited opportunities for behavioral thermoregulation. Consequently, aquatic insects have likely evolved narrower thermal performance curves (Birrell et al., 2020; Sunday et al., 2012).

Water also has a much lower oxygen capacity than air, which magnifies the difficulties of supporting aerobic respiration. Indeed, the oxygen problem may underlie low observed heat tolerances of aquatic insects: in warming waters, oxygen availability decreases modestly but demand (from metabolism) often rises rapidly, and oxygen shortage may lower heat tolerance (Frakes et al., 2021; Verberk et al., 2011; Verberk, Overgaard, et al., 2016). Consequently, aquatic ectotherms, including aquatic insects may be more sensitive to rising mean temperatures and more prone to reaching upper critical limits (Rubalcaba et al., 2020; Verberk, Durance, et al., 2016). Indeed, aquatic insects generally have lower tolerance limits to heat than terrestrial insects (Chown et al., 2015). These observations, and several recent papers, also underscore the importance of flow in delivering oxygen to the body surface (Birrell et al., 2020; Frakes et al., 2021). Low flows stemming from changes in hydrological cycles or seasonality may compound the

challenges of higher temperatures and low oxygen. Interestingly, a similar high temperature-hypoxia relationship certainly applies also to particular terrestrial insects such as leaf galls or cambium miners (Pincebourde & Casas, 2016). Many aquatic insects spend part of their lives under water as eggs, larvae, or pupae before emerging as winged, terrestrial adults. These early life stages are considered more vulnerable to heat partially because of oxygen limitation inherent to living in water (e.g., Verberk & Bilton, 2015), and also their limited mobility prevents them from behaviorally exploiting gradients in temperature and oxygen availability (eggs and pupae (Kingsolver et al., 2011)). Thus, the response of aquatic juveniles to rising temperatures will strongly affect the presence and persistence of terrestrial adults.

These physical and physiological considerations may have important consequences for how climate change affects aquatic communities. Aquatic insects in temperate mountains, for example, experience wider seasonal fluctuations in temperature than do related species in tropical mountains at similar elevations. Temperate species have wider thermal breadths and, in some cases, a greater ability to acclimate to warmer temperatures (Shah et al., 2017). Such patterns have been seen in other aquatic taxa such as tadpoles (Gutiérrez-Pesquera et al., 2016) and marine ectotherms (Sunday et al., 2011). These studies suggest that tropical aquatic insects are especially vulnerable to rising temperatures (Tewksbury et al., 2008).

EFFECTS OF SHORT-TERM, UNPREDICTABLE CLIMATE EXTREMES ON INSECTS

No universal definition of extreme climatic events thus far exists (Van de Pol et al., 2017) reviewed definitions used in ecology). The term “climatic extremes” has been used to describe meteorological phenomena (e.g., heat waves, droughts, extreme rainfall events) as well as their consequential physical impacts (e.g., flooding, fires, desiccation, tornadoes, hurricanes). Furthermore, extreme climatic events can be defined by their climatological extremeness or by the extremeness of the biological impacts caused by a climate-related event. Finally, there is little consensus on the threshold for extremes (1%, 5% or 10% frequency or a certain percentile of a reference period) and how other attributes should be factored in, such as the temporal duration, magnitude, timing, spatial scale of events, or the biological level of organization it affects (Meehl & Tebaldi, 2004; Russo et al., 2014). This lack of consensus is not surprising because extremes are simply events in the tails of statistical distributions,

which for both climate factors and ecological responses are generally unimodal, making any definition of an extreme climatic event an arbitrary cutoff. Debate about the precise definition of climatic extremes, however, must not distract from the fact that a large and growing number of studies—all examining the impacts of events in the tails of their distributions—have shown that extreme climatic events have major impacts on insects. In this section, we summarize what is known about the impacts on insects of four types of extreme events: temperature extremes, droughts, rainfall events, and fire.

Heatwaves and extreme temperatures

With climate change, heatwave conditions are increasing in frequency, intensity and duration (Christidis et al., 2015; Frich et al., 2002; Meehl & Tebaldi, 2004; Perkins et al., 2012). These extreme conditions may occur in exposed micro-habitats (Gols et al., 2021), and can be especially stressful for biological functions, particularly in ectothermic species (Williams et al., 2016) (Figure 3c,d). One way to measure vulnerability to extreme heat is to compare heat tolerance limits with habitat temperatures (Hoffmann et al., 2013; Pincebourde & Casas, 2019), and such analyses have shown that terrestrial insects may frequently be exposed to lethal temperatures when they are exposed to the sun, highlighting the need for behavioral thermoregulation (Sunday et al., 2014). A methodological complication with measuring heat tolerance is that the duration of heat stress matters (Terblanche et al., 2007): prolonged exposure to mild heat stress may be equally detrimental as short exposure to intense heat, which is the typical approach used to establish heat tolerance. For example, a recent study suggests that such heat tolerance limits may underestimate actual vulnerability, as heat injury accumulates over time at temperatures below those found to be lethal in rapid ramping assays (Rezende et al., 2020, but see Dowd et al., 2015 for a rejoinder). A recent meta-analysis shows that exposure to climatic extremes (focusing on heat waves) generally harms insect fitness in terrestrial ecosystems (Thakur et al., 2021). This has led in some cases to local extinctions as observed for several French populations of the butterfly *Parnassius apollo*, which experienced extreme warmth during winter followed by cooler, normal temperatures during spring (Nakoneczny et al., 2007).

Heat stress has clear implications for survival. In addition, heat stress (even a short exposure of <1 h at 36°C) can have significant consequences for reproductive processes and fertility. Heat-induced sterility has been documented in a range of insect orders, including Diptera, Hymenoptera, Coleoptera, Hemiptera, and

Odonata (reviewed in Walsh et al., 2019). Importantly, both the characteristics of heat waves (i.e., intensity, duration, and amplitude) and the insects experiencing them can affect the outcome of these events, as susceptibility varies among ontogenetic life stages (Abarca et al., 2019; Bowler & Terblanche, 2008; Sales et al., 2021) and across taxa (e.g., Quinn et al., 1994; Verberk et al., 2018). Exposure to heat stress during development can impact adult reproductive trait expression and mating behavior (Vasudeva et al., 2021). Heat stress during adulthood also has consequences for male reproductive function and success; experimental exposure to extreme thermal conditions reduces sperm function and impairs male reproductive competitiveness (Sales et al., 2018). These consequences of heat stress can also have consequences for offspring (Hoffmann et al., 2013; Roux et al., 2010), with transgenerational damage being seen in the reproductive fitness and lifespan of sons from either fathers or sperm exposed to heatwave conditions in *Tribolium* flour beetles (Sales et al., 2018). Although heat-induced fertility impacts generally affect males more than females, females appear unable to protect stored sperm from heat-induced damage (Sales et al., 2018; Walsh, Mannion, et al., 2021; Walsh, Parratt, et al., 2021). These impacts can have potential consequences for the operational sex ratio of heat-stressed populations (Walsh, Parratt, et al., 2021). Similarly, behavioral changes in sex allocation during simulated heatwaves have also been reported (Moiroux et al., 2014). In turn, these impacts may drive changes in mating behavior (e.g., propensity for remating, Vasudeva et al., 2021) and processes linked to natural and sexual selection (Walsh, Parratt, et al., 2021). On the other hand, maternal exposure to heat can have adaptive transgenerational effects that involve e.g., tolerance and acclimation, and thus, generate thermal resistance (Zizzari & Ellers, 2014). Ultimately, insect reproductive sensitivity to heat can dictate global species distributions according to upper thermal fertility limits in both sexes (Parratt et al., 2021), indicating that climate change will have important wider impacts on insect biodiversity.

Negative effects of extreme temperature events on insects may also be linked with the stresses they induce in plants with which many insects are intimately associated (Pincebourde et al., 2017). For example, larvae of the moth *Lobesia botrana* fed on low-quality plants induced by heat stress were negatively affected in terms of development and immunity (Iltis, Louâpre, et al., 2021). The major concern is that the increasing intensity of heat waves is pushing many insect species and/or their food plants beyond their adaptive limits, exposing them to conditions that they may not have experienced in their evolutionary history, particularly given the lack of

adaptive capacity of insects to heat extremes (Harvey et al., 2021; Harvey, Heinen, Gols, & Thakur, 2020; Ma, Ma, & Pincebourde, 2021). Short-term (daily) temperature fluctuations can alter the shape of thermal performance curves, reducing the optimum and critical thermal maximum temperatures relative to those predicted using mean temperatures alone (Kingsolver & Buckley, 2018; Paaijmans et al., 2013).

Insect microbiomes are often driven by environmental microbiomes, for instance those associated with the host plant or in the soil (Hannula et al., 2019). The effects of extreme climatic events on environmental microbiomes (Jansson & Hofmockel, 2020) may pose an additional pathway through which climate extremes may affect insect performance. For example, the bacterial endosymbiont, *Wolbachia*, is known to impact the capacity of mosquitoes to transmit a range of arboviruses and parasites, and is being actively deployed as a biocontrol agent in a number of locations globally. However, complex interactions with *Wolbachia* appear to have highly variable effects on malaria parasite infection under extreme temperatures (Murdock et al., 2014). More recently, lab studies examining thermal knockdowns have suggested that *Wolbachia* can reduce the thermal tolerance of the primary dengue vector, *Aedes aegypti* (Ware-Gilmore et al., 2021). Moreover, infection with dengue virus also reduced thermal tolerance. These results demonstrate the potential for complex effects of temperature variation (including temperature extremes) on host–microbe interactions, with impacts varying across environments. In particular, in cases where endosymbionts confer resistance to heat shock, this can allow rapid evolution of heat tolerance by the host (Harmon et al., 2009).

Extremely high temperatures are not only occurring during the daytime. Many insects are nocturnal and are sensitive to abiotic conditions that may differ significantly from those experienced by diurnal insects. Importantly, they may be highly sensitive to temperatures that deviate considerably from normal. Night warming and extremely high minimal nighttime temperatures are also threatening the persistence of some insect populations and are also affecting interspecific interactions (Higashi et al., 2020; Ma et al., 2020; Ma, Bai, et al., 2021). However, the asymmetry between night and daytime warming and extremes is thus far little studied, especially in terms of its impact on diurnal insects whose fitness-related traits, along with other overlooked behaviors such as sleep (Tougeron & Abram, 2017) or thermally-gated developmental programs such as molting, may be sensitive to heat exposure during the night. For example, successive exposure to extremely warm nights reduced adult performance (longevity and

fecundity) of the grain aphid *Sitobion avenae* over subsequent days (Zhao et al., 2014). In a study including diurnal and nocturnal ant species, ant communities from warmer habitats such as semi-deserts and subtropical dry forests were more tolerant to high temperatures than ants from cooler environments such as tropical rain and montane forests (García-Robledo et al., 2018). In all habitats, nocturnal ants displayed lower thermal tolerance than diurnal ants (García-Robledo et al., 2018). In addition, night-time warming may have distinct effects from daytime warming on top-down control of plants by herbivores (Barton & Schmitz, 2018), and could interact with other aspects of global changes such as light pollution to disrupt predator–prey interactions (Miller et al., 2017).

Considering that insects have to keep up with an increasingly variable thermal environment, which include cold and heat shocks, it is crucial to examine the cumulative impacts of fluctuating temperatures on the response of insects to thermal extremes (Hance et al., 2007; Jeffs & Leather, 2014). The cumulative effects of stressful conditions on physiological performance is becoming increasingly recognized (Cardoso et al., 2020; Didham, Barbero, et al., 2020; Didham, Basset, et al., 2020; Harvey, 2015; Kaunisto et al., 2016) and highlights the potentially much higher vulnerability of insects to stressful conditions. Climatic variability over different temporal and spatial scales may notably limit the evolutionary responses of insects to longer-term, incipient warming (Buckley & Kingsolver, 2021; Kingsolver & Buckley, 2015).

Phenotypic plasticity and bet-hedging may be critical strategies for the persistence of insect populations and species in response to immediate, intense and more or less predictable temperature changes (Sgrò et al., 2016). Phenotypic plasticity in response to thermal variation is known to protect insects by eliciting changes in a range of important biological traits (e.g., Vasudeva et al., 2021; Verberk et al., 2018). Phenotypic plasticity is expected when climatic variation is at least partially predictable, but fitness-related traits may be compromised when they are more stochastic (Liefting et al., 2009). Bet-hedging is an adaptive strategy in temporally unpredictable environments (Hopper, 1999). For instance, in environments with highly unpredictable cold and heat extreme events, it was demonstrated that several phenotypes can be expressed among the progeny of a single individual (e.g., diapausing versus active individuals, sexual versus asexual morphs) (Le Lann et al., 2021). Each of these phenotypes may have advantages over the others depending on thermal conditions. This diversified bet-hedging strategy may ensure the survival of a part of the progeny at each generation and an overall higher fitness over generations compared to thermal specialists producing a single phenotype. However, tightly

interacting insect species such as hosts and their parasitoids can respond very differently to changes in the mean and variance in temperature due to trade-offs, evolutionary history, and genetic background with parasitoids being usually more sensitive to thermal stresses (Hance et al., 2007; Le Lann et al., 2021). Moreover, phenotypic plasticity and bet-hedging in response to heat waves can depend on interactions with other species. Using an aphid–ladybeetle system, Sentis et al. (2017) experimentally investigated the effects of predators and heat shocks on aphids and showed that heat shocks inhibit phenotypic and behavioral responses to predation (and vice versa), and that such changes may alter trophic interactions.

Seasonally variable effects of climate extremes with other anthropogenic stresses

Seasonal changes in the frequency of extreme temperatures can also disrupt different stages of insect life-cycles. For instance, if diapause is not initiated because of exposure to warmer winter temperatures, there is a risk of precocious death of active stages in response to unpredictable extreme cold spells. Indeed, even as mean winter temperatures increase, the frequency and intensity of short-term cold periods is also increasing, perhaps as a result of changes in the strength of the jet stream, facilitating a breakdown in the polar vortices (Tomassini et al., 2012). Several consecutive days where temperatures are 10 or more degrees below normal during an otherwise warm winter can have negative effects on populations and modify the relative abundances of competing species (Andrade et al., 2016; Tougeron et al., 2018), due to their differences in cold tolerance (Le Lann et al., 2011). For example, cold spells occurring during winter seem to be an important factor that determines aphid-parasitoid-hyperparasitoid community composition in the following spring (Tougeron et al., 2018). Cold temperatures during winter months are critical for most insects in temperate biomes (Hahn & Denlinger, 2011), but climate change may alter the frequency of such cold events.

The impacts of climatic variability in both terrestrial and aquatic environments cannot be seen in isolation and are compounded by other stressors including habitat loss, removal of refugia, and chemical pollution (Cavallaro et al., 2019; Liess et al., 2021). Aquatic insects are especially vulnerable to pollutants; under increased temperature variability, damselflies' bioenergetic responses (balance between energy gains and losses) are more likely to be negative (Verheyen & Stoks, 2020). These impacts are further aggravated by climate change

mediated reductions in body size (Verheyen & Stoks, 2019). Similarly complex interactions are expected to occur in farmland soils or above-ground habitats, but wait to be characterized.

Drought

Drought is another climatic extreme that threatens insects. In several different regions, the duration and intensity of prolonged (acute) droughts is increasing and is concomitant with above average temperatures, heat waves and often fire (Dai, 2011; Williams et al., 2022). Pulsed droughts, on the other hand, may also be prolonged but are briefly broken by intense rainfall events (Harris et al., 2018). Both types of drought can have directly negative physiological effects on insects, or induce effects on plant communities and insects that depend on them for food and shelter up to the terminal end of the food chain (Gutbrodt et al., 2011; Han et al., 2022; Jactel et al., 2012; Ploughe et al., 2019).

The effect of drought stress on insects is complex and depends on multiple factors. For instance, insects feeding on trees may respond to drought quite differently than insects feeding on smaller plants such as forbs, sedges and grasses (Gely et al., 2021). During the summer, drought episodes can decrease herbivorous insect populations on small plants because these are more prone to water stress, and this in turn will lead to a scarcity in food resources that in turn has severe consequences in terms of population dynamics and of interspecific interactions. For example, one consequence of desiccation (and thereby loss) of plant tissues is an increase in competition for hosts or prey among higher trophic levels. By contrast, insects feeding on trees are often “buffered” against drought, owing to the fact that trees contain much greater root and shoot biomass and can generally endure more intense periods of drought than smaller plants. Nevertheless, drought stress can still generate chemical, physiological, and chemical changes in plants, irrespective of their mass (Anderegg et al., 2015; Gely et al., 2020; Jactel et al., 2012).

Drought stress can alter foliar and root concentrations of primary metabolites (e.g., nutrients, such as amino acids and sugars) and secondary metabolites (e.g., defensive allelochemicals) and this can affect the growth and development of insect herbivores (Han et al., 2016; Sconiers & Eubanks, 2017). A recent review (Gely et al., 2020) provided a framework that linked water stress from increased drought severity to insect performance. They predicted that different herbivore guilds will show different but predictable responses to drought stress with most guilds being negatively affected, many

wood borers being a favorable exception, at least in the short term. There have been a few whole-forest drought manipulation experiments. Insect responses to an experimental drought in a tropical rainforest of North Queensland, Australia, showed variable responses among different feeding guilds (Gely, 2021). In the experimentally droughted area, there was significantly more wood borer damage to trees than in the control area (Gely et al., 2021). Many ant species in Australian rainforests take nectar from extrafloral nectaries whereas some also rely on aphid honeydew. Food sources are reduced in areas under drought, and stable isotope analysis indicates that many ant species are becoming increasingly predatory (Gely, 2021), which will have impacts on food webs in these forests.

Droughts can affect reproduction, as some insect eggs require water for development (Rohde et al., 2017). Similarly, drought can change plant signaling and the quality of floral rewards for pollinators leading to reductions in pollinator attraction and plant reproduction (Descamps et al., 2018; Rering et al., 2020). Even a single severe drought can alter plant-insect communities. Following a severe drought in 1995 in the United Kingdom, the total abundance of butterflies increased, but this was accompanied by substantial changes in community composition, particularly in more northerly, wetter sites. Specialist, vulnerable species were lost while generalist, widespread species increased, likely because of enhanced opportunities for recruitment from the larger regional populations. A year later, communities had yet to return to equilibrium (De Palma et al., 2017), signifying that episodic droughts can lead to greater extinction risk, likely both in terms of species and genetic diversity. A similar finding was reported for butterflies in Arizona (Wagner & Balowitz, 2021). Single, severe droughts may push the last remaining ephemeral populations toward extinction, with a concomitant loss of genetic diversity.

While the physiological and ecological mechanisms associated with responses to extreme drought are multi-faceted and not well understood, the consequences are increasingly apparent. A recent mega-drought in western North America had negative and long-lasting effects on montane butterfly communities that were comparable in magnitude to the combined effects of decades of habitat loss and degradation at lower elevations (Halsch et al., 2021). In the case of dragonflies in the Cape Floristic Region, which is subject to periodic droughts, adults, even among localized endemic species, temporarily use artificial ponds to pull through periods of extreme drought (Deacon et al., 2019). In the same region, dragonfly adults remained faithful to the pond margins and continued to forage there until rains returned, while water beetles soon departed from ponds

when major droughts continued (Jooste et al., 2020). These responses indicate that freshwater insects can have different behavioral responses to periodic droughts. Conversely, less volant taxa and insect which have historically evolved in perennially humid to wet communities, such as the faunas of cloud and rain forests would be expected to be especially challenged by droughts (Janzen & Hallwachs, 2021; Wagner, 2020). Climatic extremes, like drought, generate “winners” and “losers” among insects, based on changes in plant quality and non-linear effects up the food chain, although, when put into the context of other anthropogenic stresses, the longer-term prognosis for insects is negative (Harvey, Heinen, Gols, & Thakur, 2020).

Extreme rainfall, floods

Climate warming is also leading to an increase in the frequency and intensity of rainfall events, such as those occurring during thunderstorms and hurricanes (Armal et al., 2018; Brooks, 2013; Frame et al., 2020; Guhathakurta et al., 2011). Extreme rainfall and accompanying flooding can have both direct and indirect effects on insects. The direct effects constitute displacement and drowning. Heavy rainfall dislodges insects from plants with small or less well-attached species being particularly vulnerable (Beirne, 1970; Chen, Harvey, et al., 2019; Moran et al., 1987). Indirectly, insects can be affected by rainfall and flooding through changes in the abiotic environment. Flooding and subsequent soil waterlogging induces a number of alterations in important soil physico-chemical properties like soil pH, redox potential and oxygen level that in turn can lead to hypoxia or anoxia (Ashraf, 2012), affecting soil-dwelling insects in particular. Insects, including many soil-dwelling and riparian insects have evolved various mechanisms to withstand short-term hypoxia or anoxia (Harrison et al., 2018; Hoback & Stanley, 2001; Woods & Lane, 2016), but these capacities can be exceeded by longer-term soil flooding. Wet soil may also force subterranean insects to the soil surface where they are more vulnerable to attack by their natural enemies (Beirne, 1970).

Changes in soil conditions can lead to changes in above-ground primary and secondary plant metabolism that affects the performance of insects feeding on them (Ayres, 1993). At the same time, rain changes microclimatic conditions such as temperature and humidity which are both important environmental variables affecting insect performance. The sudden drop in temperature during heavy downpours may reduce feeding activity and thus extend development time (Chen, Harvey, et al., 2019). Increased humidity may favor conditions for

growth of some insects (e.g., aphids and grasshoppers), but it also may promote infection with pathogenic viruses and fungi (Beirne, 1970). Other indirect effects of extreme rainfall on insects can occur through disturbance of the insect's habitat. Flooding occurring in the aftermath of extreme rainfall events may cause the death of small forbs and increase tree mortality. The effects of this on insects are not always negative, as some insects thrive on the woody debris left after severe storms, the regrowth of shoots, or by colonizing new plants (Gandhi et al., 2007 and references within).

Poff et al. (2018) measured the response of stream-dwelling insects to an extreme flooding event in a mountainous area in northern Colorado. The resilience of the aquatic insects in response to this event depended on life history traits of the insects: taxa with mobile larvae and terrestrial adult stages, at the time of the event, were more persistent than those without these specific life stages (84% vs. 25% taxa persistence). Some species were extirpated altogether. After the floodwaters retreated, genetic diversity declined in some species but increased in others, suggesting rapid recolonization by some species (Poff et al., 2018). Similarly, the soil microarthropod community (Collembola and Acari) of a grassland in the floodplain of the Saale river in Germany recovered in terms of species richness and density within 3 months after a severe summer flooding (González-Macé & Scheu, 2018). These results suggest that communities are, to some extent, resilient to these extreme disturbances. Not all members of a community are equally resilient, however, and the genetic diversity of populations may change in response to these events. Some desert stream insects exhibit adaptive behavior to escape flooding and use rainfall preceding flash floods as a cue to crawl vertically away from the stream (Lytle & White, 2007). However, this flood avoidance behavior was only found in insects originating from populations collected in streams where rain is a reliable predictor of imminent flooding (Lytle & White, 2007). A recent study showed that in a protected Costa Rican tropical forest, parasitism frequency correlated negatively with precipitation anomalies (i.e., extreme wet events), suggesting a weakening of trophic interaction strength (Salcido et al., 2020). On Barro Colorado Island (BCI, Panama), the variation in the ambient temperature and precipitation appear to affect the populations of certain species of assassin bugs (Lucas et al., 2016). Entomologists also observed that populations of some large Saturniidae showed a significant increase over time (Basset et al., 2017). The peaks in saturniid abundance were most conspicuous with increasing average precipitation on BCI (Anderson-Teixeira et al., 2015). These studies contrast with recent findings indicating insect decline in both tropical and temperate regions. We clearly lack sufficient insect

monitoring data (Basset & Lamarre, 2019) to either refute or support claims of global insect decline with respect to tropical regions (Janzen & Hallwachs, 2019). How communities may respond to unpredictable and recurring extreme rainfall and flooding events, and how this may affect community structure and functioning, especially when they increase in frequency and intensity, is largely unknown.

Fire

Droughts and modified patterns of precipitation have led to alterations in global fire regimes in terms of extent, duration, seasonality, and severity (Jain et al., 2021; Nimmo et al., 2021). While fire is a lethal threat to many animals, the scientific community is only beginning to consider it as an integral component of climate change and an evolving force affecting the response of organisms to it (Nimmo et al., 2021; Whelan, 1995). Results from studies on how fire affects insects vary due to differences in weather, burn intensity, focal taxa studied, and season of burn (Banza et al., 2021; Dell et al., 2017; Pryke & Samways, 2012a, 2012b; Saunders et al., 2021; Swengel, 2001). Arthropods possess complex life histories, and responses are typically taxon-specific (Joern & Laws, 2013), which limits the body of literature on invertebrate responses to fire, and hinders the capacity to propose effective conservation policies in response to extreme fire events (Saunders et al., 2021). More mechanistic studies are crucially needed to ameliorate our ability to anticipate the consequences of changing fire regimes.

Many of the insect taxa associated with early successional series and fire-adapted communities require periodic burns for their persistence. Indeed, many wood boring beetles and their natural enemies may be attracted to fires. The impact of fire on arthropods varies from negative to neutral to positive with some taxa being highly vulnerable, e.g., Araneae, while others are not, e.g., Coleoptera (Kral et al., 2017). Strong recovery of the herbaceous understory can boost general arthropod abundance (Campbell et al., 2007). Even for species that are fire-dependent, positive effects of fires can be reversed when fire regimes are dramatically altered. For example, localized decreased species richness and/or abundance after fires have been observed in South Africa (Pryke & Samways, 2012a) and Australia (Andersen & Müller, 2000), although in South Africa at least there can be rapid recovery as, e.g., pollinators expand outward from fire refugia (Adedjoja et al., 2019). In any investigation, it is important to consider not only that burning has differential ecological effects based on ecosystem sensitivity

or dependency on fire, but also the variant spatial distribution of fire across these different landscapes in terms of extent (i.e., 10 vs. 10,000 ha²), fire frequency, fuel loads within fire perimeters, and distance to refuges (Pryke & Samways, 2012a). For example, some fire-resistant plants with tightly packed leaf bases have been shown to provide refuges for insects and other arthropods even during intense fires (Brennan et al., 2011). The importance of these refuges in the resilience of insect communities needs further investigation.

Alterations in fire regimes due to global change are likely to be complex; for example, these changes can contribute to phenological asynchronies in herbivore–enemy interactions. Parasitoids have latent post-fire recovery and temporal changes of seasonal burns may affect the availability of holometabolous hosts at specific life stages (Koltz et al., 2018). Similarly, Dell et al. (2019) found that frequent fire resulted in a loss of specialized trophic interactions, and this pushed trophic webs toward generalization, including increases in the abundance of generalist feeding Orthoptera and Lepidoptera. As a result, shorter burn regimes can generate periodic pest outbreaks. If these (and other orders) are more efficient at dispersing during large wildfires, and more rapidly recolonize post-burn, they could affect community structure and function. Fires may also have far-reaching consequences for aquatic insects, especially those that rely on terrestrial environments during part of their life cycle. For example, the eggs of some lentic taxa lie dormant in topsoil layers, making them particularly vulnerable (Blanckenberg et al., 2019).

Since little is known about longer-term effects of climatic extremes and related events on insects, one effective method to measure demographic changes is to utilize technological advances in insect identification, such as eDNA metabarcoding (Jinbo et al., 2011). This would be extremely useful immediately in the weeks, months, and years after an extreme event, such as fire.

INSECT CONSERVATION UNDER CLIMATE WARMING AND CLIMATIC EXTREMES

In this paper, we have highlighted individual, population, and community-level responses to climate change, but landscape or ecosystem consequences have remained largely undiscussed, whereas at these levels the consequences are most influential. The balance should therefore shift toward these effects in terms of policy-making, scientific research, and conservation approaches. Indeed, the effects of climate change on insects are numerous and often lineage-specific. They may vary across life

stage, physiological state, as well as across local biotic and abiotic conditions and, thus, appear to be idiosyncratic. Of course, many research topics seem idiosyncratic until we begin to understand them better. If we want to understand and mitigate the impacts of extreme climatic events, and climate change in general, on insect biology and insect declines, we need more research (and associated funding and political will) on the impacts of climate change not only on the basic biology of insects, but also on integrative aspects at the scale of the ecosystem (Hof, 2021). The decline in insect abundance and biomass we are now facing—and can expect in the future given the effects of climate change described above and still other stressors—will have far-reaching community-level effects due to the fact that insects form the major part of the second trophic level in many ecosystems. As insects provide a critical contribution to ecosystem functioning and hence ecosystem services, loss of insect biomass, abundance, and diversity will therefore disrupt trophic cascades, including declines of flowering plants and the erosion of terrestrial food webs (Wilson, 1987). For example, the large number of insects during the breeding season are a crucial component of nestling diets of many bird species, and a decline in insect availability can severely reduce nestling survival and fitness (Tallamy & Shriver, 2021). Likewise, losses in biomass of up to 80% in important pollinator taxa will inevitably have disruptive consequences for pollination (Hallmann et al., 2017, 2021). Extreme climatic events affect many insect species in the community simultaneously, exacerbating the disruptive ecological consequences.

Perhaps more indirectly, but equally disruptive, will be the effects of large-scale insect decline at the ecosystem level. Significant losses of insect abundance and diversity may threaten ecosystem resilience through reduced functional diversity (Antão et al., 2020; Jonsson & Malmqvist, 2000; Seymour et al., 2020). Functional redundancy provides “insurance” against the loss of a few species (Naeem et al., 2012; Naeem & Li, 1997). With the current estimated rates of insect decline, functional diversity may quickly approach the lower threshold of full functional niche occupancy, meaning that further losses will jeopardize ecosystem functioning. In addition to knowledge about how species respond to climate extremes (response traits), we also need to know how they affect ecosystem processes (effect traits), in order to understand how community attributes are related to ecosystem functioning and resilience (de Bello et al., 2021; Suding et al., 2008).

This response-to-effect trait framework is increasingly adopted by land managers as it can guide landscape actions and local measures to preserve insect functional diversity. Among the conservation approaches that can be undertaken, we can consider direct and relatively local

approaches aimed at reducing the effects of climate change on insect biodiversity through appropriate environmental management, and global policy approaches involving the general public. It is clear that climate change is harmful to insects and biological processes involving insects at the individual, population, community, and ecosystem levels. We need to act now to minimize these impacts; we know how to do it, but the decision-making and requisite funding keep getting pushed down the road or onto the shoulders of future generations.

Management approaches

To protect insects from climate change, and climatic extremes, it is necessary to go beyond traditional surveys that record insect presence-absence and understand their physiological and behavioral tolerance to environmental extremes. Insects have both physiological and behavioral thermoregulation capacities that can prevent exposure to harmful temperatures (Abram et al., 2017) or buffer them against the damaging effects of extreme temperatures once exposed (Ma, Ma, & Pincebourde, 2021). The environmental elements that can act on them, and that can be manipulated, are at both the landscape (macro scale) and at the micro-habitat level (microclimates), but it is important to know how management fits with the maintenance of other ecosystem services, as well as how each individual taxon may respond (Oliver & Morecroft, 2014; Tougeron et al., 2022). The conservation implications of microclimatic diversity at fine scales are just beginning to be explored—but a general conclusion from studies to date is that insects will be more resilient to climate change when they consist of intact communities with high structural complexity and high levels of plant species diversity, which together will generate diverse microclimatic refugia (Pincebourde et al., 2016; Woods et al., 2015). Microclimates can be influenced by landscape properties (Oliver & Morecroft, 2014). For instance, hedgerows, woodlots, sown vegetation, and flower strips may represent microclimatic refuges for agrobiodiversity in the face of extreme climatic events (Lenoir et al., 2017; Thakur et al., 2020). The windbreak and antifreeze roles of hedges has been widely studied and confirmed in agricultural landscapes. Wooded and closed areas generally have lower temperature amplitudes than open areas over a daily scale but are also colder on average, which can affect insect thermoregulatory abilities (Alford et al., 2017; Tougeron et al., 2016). Similarly, field-level crop diversification and cover cropping has been shown to be promising (Pan et al., 2020). Mountains and other sites of topographic complexity may provide microhabitat diversity to animals challenged by climate change

(Forister et al., 2021; Halsch et al., 2021; Loarie et al., 2009). Importantly, it is necessary to understand the extent to which landscape properties can affect insect tolerance to thermal extremes.

Little attention has thus far been paid to identifying climate refugia, at least over short temporal scales. Demonstrating the occurrence and role of some habitat types or landforms in slowing the declines of some species during contemporary climate change could have great impact on active climate-adaptation strategies. Despite the recognized importance of climate change refugia, the ability to quantify their potential for facilitating species persistence remains elusive. Keppel et al. (2015) developed a flexible framework for prioritizing refugia, based on their potential to maintain biodiversity in the face of climate change. For instance, the highest-capacity climate-change refugia in Tasmanian plants is primarily in cool, wet, and topographically complex environments. This result agrees with studies performed in mountain areas by Brighenti et al. (2021), Tampucci, Gobbi, et al. (2017), and Tampucci, Azzoni, et al. (2017) that demonstrated the role of several cold rocky landforms (i.e., a surface mantle of rocky debris and interiors composed of ice and rock; e.g., glaciers, rock glaciers, debris-covered glaciers, ice-core moraines) as potential warm-stage refugia for cold-adapted aquatic and ground-dwelling insect species. However, understanding how the area and isolation of refugia mediate changes in taxonomic, functional, and phylogenetic insect diversity caused by climate change is a key step in prioritizing the conservation of specific refugial sites that optimize conservation value. For instance, the access to such climate refugia through potential dispersal corridors can rescue insect diversity (Thakur, 2020b). As pointed out by Morelli et al. (2016), the physical and ecological diversity of landscapes managed by public agencies suggest that they already contain climate change refugia; thus, these agencies need tools to detect and prioritize climate change refugia for management. Moreover, the role of mammalian ecosystem engineers, which can quite dramatically influence the structure and composition of habitats, can also generate localized refugia which benefit insects during climatic extremes (Thakur et al., 2020). Thus, management strategies that prioritize conservation of large vertebrates will benefit smaller organisms, including insects. One of the crucial factors dealing with extreme climatic and weather events is to understand the functional value of the topographic landscape. At sea level, increasingly impactful high tides inevitably will lead to direct loss of coastal habitats, by flooding, salt intrusion, and erosion of dune crests and cliff faces. Inland, ecological resilience can be gained by ensuring that large-scale networks of conservation corridors over

various elevations are in place so that not only is more habitat available, simply reducing the risk of population loss through more land area being available, but also because there is a greater chance that refuges are available (Samways & Pryke, 2016).

The transformation of industrial agriculture toward agroecology also allows to bring structural diversity in the landscape that can lead to a better resilience of insect communities, but also of their biodiversity and the ecosystem services they provide, e.g., biological control (Altieri et al., 2015).

For freshwater insects there are several management options to alleviate the impact of climate warming. These include measures to improve or safeguard water oxygenation by ensuring flow or improving water quality, since low levels of oxygenation may exacerbate heat stress for these insects. Given that pesticidal pollutants amplify climate change impacts in aquatic settings (e.g., Verheyen & Stoks, 2020) with cascading effects over space and time (Brühl et al., 2021), their phase-down should rapidly be pursued. Locally, warming can further be mitigated by increasing shading or increasing groundwater tables (e.g., by reducing drainage in catchments), which restores the influence of cool, ground water. A combination of these measures over larger spatial scales will also result in a mosaic of different thermal regimes and this landscape heterogeneity may help aquatic insects find temporary refuge from heat events.

Prescribed burning is used in many countries to manage forests and woodlands. Where the effects of fire are confined to relatively small areas, recolonization by ground-dwelling invertebrates from adjacent unburned areas can be rapid, with communities returning to normal by the following season (Nunes et al., 2000, 2006), and fires can also enhance habitat diversity (see Fire). One potential solution to climate-driven changes on insect assemblages is to counter the effects of extreme fires with prescribed, managed fires in ecosystems that rely on fire to maintain healthy structure and function. In doing so, burning ameliorates effects of future fires by increasing pyrodiversity: as fire moves across a region, the resulting landscape includes a fine-scale mosaic of burned and unburned patches, creating not only refugia for insects, but conditions that promote spatial heterogeneity of resources and enhanced conditions for insect communities (Kim & Holt, 2012; Koltz et al., 2018; Ponisio et al., 2016). In longleaf pine ecosystems where regular application of prescribed fire is extensively used, juvenile and non-flying insects have been shown to climb into the canopy where microclimate conditions are more favorable for their survival (Dell et al., 2017). Land management practices that have excluded burning on fire-evolved landscapes have created high fuel loads

which result in extreme fire events, eroding pyrodiversity and resulting in concomitant reductions in insect biodiversity (Berlinck & Batista, 2020; Ponisio et al., 2016).

Ultimately, management of habitats across various scales in response to climate change and climatic extremes needs to consider that insects face numerous anthropogenic stresses that do not necessarily operate independently (Harvey, Heinen, Gols, & Thakur, 2020; Wagner, Fox, et al., 2021). For example, systemic insecticides translocate to (extra-)floral nectar or honeydew (Calvo-Agudo et al., 2019), negatively impacting a broad suite of flower visitors and thereby deepen population-level impacts of both stochastic or climate-related events. These diverse stressors interact and therefore should not be mitigated in isolation. Thus, it is vitally important that factors such as habitat loss and fragmentation, invasive species, intensive agricultural practices, various forms of pollution (e.g., synthetic pesticides and fertilizer), and other stresses are fully integrated into conservation management approaches (Harvey, Heinen, Armbrecht, et al., 2020; Hof, 2021; Pryke & Samways, 2012a). Only in this way will declines in insects be stabilized or reversed.

Policy making and public participation

It is pertinent to the preservation of insect diversity and all biodiversity, in general, that drastic changes are made in the way humans see and treat our resource-limited planet. We need a massive-scale mobilization with transformative action to address the climate crisis. We echo the call made by Ripple et al. (2021) to change course in six areas, including a progressive reduction (and eventual elimination) in the use of fossil fuels; curbing short-lived air pollutants such as black carbon (soot), methane, and hydrofluorocarbons; restoring and permanently protecting Earth's ecosystems to restore biodiversity and accumulate carbon; switching to mostly plant-based diets; moving away from indefinite gross domestic product growth to ecological economics with a circular economy; and stabilize the human population.

It must be stressed that halting upward trends in rising carbon dioxide concentrations and global surface temperatures will take decades, if not more, and therefore requires an immediate enforcement of efforts to halt the drivers of climate change at the global level. The Paris Agreement, along with COPs 1-26, which are global efforts to tackle the climate problem with 196 partner countries, a promising start. Agreements such as these should, however, have clearly delineated goals within a strict time-frame, and should strive for immediate implementation and a much higher degree of accountability. The current division between land set aside for nature

reserves and land assigned to agricultural production or urban development, is far from balanced, and this urgently needs to be addressed by regional governing bodies. Existing natural areas need to be strictly preserved; our planet can no longer afford to lose more pristine habitat. We need to rethink and revise agriculture, with a strong emphasis on ecological intensification of production systems. We can ecologically improve agricultural lands, through optimization of the ecological matrix, and the creation of networks by interspersing corridors and stepping stones of habitat within the agricultural landscape. This will not only benefit insect species diversity via the provisioning of habitat, but also might serve a crucial role in mitigation of negative effects of climatic change and extremes on insects through the creation of climate refugia. Industrial agriculture in its current form is not sustainable for the preservation of biodiversity. Unguided pesticide application and over-use of industrial fertilizers have many non-target side effects and pollute our ecosystems (Bernhardt et al., 2017); whenever possible, their use should be avoided and replaced with environmentally sound alternatives. More strategic and targeted approaches need to be adopted to ensure the productivity of the agricultural system, while minimizing the detrimental effects of excess fertilizer and pesticide inputs on (insect) biodiversity. Ecological intensification of the agricultural landscape has been unequivocally shown to benefit both agricultural yield and diversity (Gurr et al., 2016). The concept of ecological intensification should be further extended and incorporated into our landscape and city planning. Road verges, public green spaces, and local gardens can form important habitats and *refugia*, which will benefit insects and related animals, especially under climate change and climatic extremes.

Specific levels of action to directly protect insects can range from global political interventions to that of individual choices and behavior. Although the conservation of biodiversity is a systemic challenge, every person can play a role through their individual actions. Seen through the eye of an insect, even small individual actions can make a huge difference. In this context, it is necessary to invest in popularizing the role of insects in ecosystems. Interesting experiments like the use of charismatic species prove useful for public awareness. Children should also be taught in elementary classes the vitally important role that insects play in a healthy, functioning biosphere (Oberhauser & Guiney, 2009). Also, scientific progress alone is unlikely to result in desirable outcomes (Wyckhuys et al., 2022) and needs to be paired with enabling policies, broad awareness-raising, and stakeholder education. The evidence is clear and the onus is on governing bodies to act now. With species and habitats being lost every day, a refusal or delay to act is not a wise choice.

Individual choices and behavior: What can you do?

Although the most impactful actions are those that should be implemented by governing institutions, decisions made at smaller scales by individuals can still make a large difference for insect conservation (Cosquer et al., 2012; MacDonald et al., 2015). This is especially relevant in the context of climatic extremes. Most people live in cities, which because of a lack of primary resources and suitable habitats can be a hostile place for many organisms (Bugnot et al., 2019; Parris et al., 2018). Furthermore, cities, which are dominated by concrete, tend to form strong heat islands, which can exacerbate the effects of climate extremes, especially those associated with rising temperatures (Ramamurthy & Bou-Zeid, 2017). The high proportions of sealed soil surface area may also increase the local impact of precipitation extremes. It has become evident that individuals can and are willing to play an important role in making cities more suited to insect life and other wildlife (MacDonald et al., 2015). Fortunately, the solutions are generally low-cost. A good place to start is in your garden or balcony, but even an appropriately designed windowsill can be relevant. Four ingredients are essential for insect survival in the face of climatic extremes: suitable microclimate refugia; access to a water source; sufficient nutrition; absence of pesticides (Deguines et al., 2020). Many urban gardens are sealed-off and neatly organized. None of insects' primary requirements for reproduction and survival are met in most gardens. The solutions, however, are remarkably simple. Sealed areas in a garden, as well as traditionally well-maintained lawns, should be reduced to a minimum. Exposed soil, and the plants that grow in it, provide the most important microclimate needs, sources of moisture, and nutrients. The choice of what to grow and where also makes a difference. A highly diverse mixture of native plants provides the most heterogeneous habitat, and supports the highest diversity of interactions. Cultivated plant varieties should be avoided, as although they may appear highly attractive, they often provide little nutritional rewards for insects. Pollinators appear to prefer gardens made up primarily of native plants with a few exotics present (Salisbury et al., 2015). Many urban and suburban gardeners rely heavily on pesticides, paying little attention to the label, ignoring recommended application rates and possible collateral damage. Pesticide use should be avoided altogether. Sowing native wildflower mixtures, even in pots, can play a role in fulfilling the basic needs of local insect diversity. Mowing should be limited, preferably until after the flowering season and hence peak of insect abundance. Leaving plant material, such as leaf litter, standing senescing biomass, and a compost pile are other

potential microrefugia that can make a difference. Insect-friendly gardening reduces individual carbon footprints and increases the rewards in the form of floral abundance, which is appreciated by insects and (most) humans alike. An insect-friendly garden is a beautiful garden, but a beautiful garden is not necessarily an insect-friendly one. We all can make a difference for the preservation of insect diversity, especially in cities, through the choices we make (Figure 4).

SUMMARY

Over the past several decades, increasing evidence is showing that many insect taxa are experiencing rapid declines in both temperate and tropical ecosystems. Whereas attribution to any specific factor in explaining these declines is elusive, there is little doubt among most researchers that human-induced climate change is playing an important role. Here it is crucial to distinguish between the effects of more gradual, incipient warming and the effects of short-term

exposure to climatic extremes, the latter of which pushes many species to (and beyond) their thermal tolerance. However, placing overemphasis on any single factor is also problematic. It is important to recognize that habitat loss and fragmentation, chemical and organic pollution, invasive species and other human-mediated changes to the environment, which are broadly connected to human land use, are currently recognized as the main drivers of the declines of insects and other invertebrate and vertebrate taxa as well. Importantly, climate change will amplify the effects of other factors, in particular human land use, and hamper the ability of insects to avoid or adapt to multiple anthropogenic stresses. This is because migration to new habitats tracking climatic changes will not be possible if land use has already converted these places into unsuitable habitat. Similarly, land use can pose great barriers to dispersal. Species do not exist in isolation, but communities and ecosystems are characterized by a bewildering array of multitrophic interactions that embody a labyrinth of complexity. Warming may differentially affect species in food webs, leading to phenological mismatches or the loss of key resources. The loss of

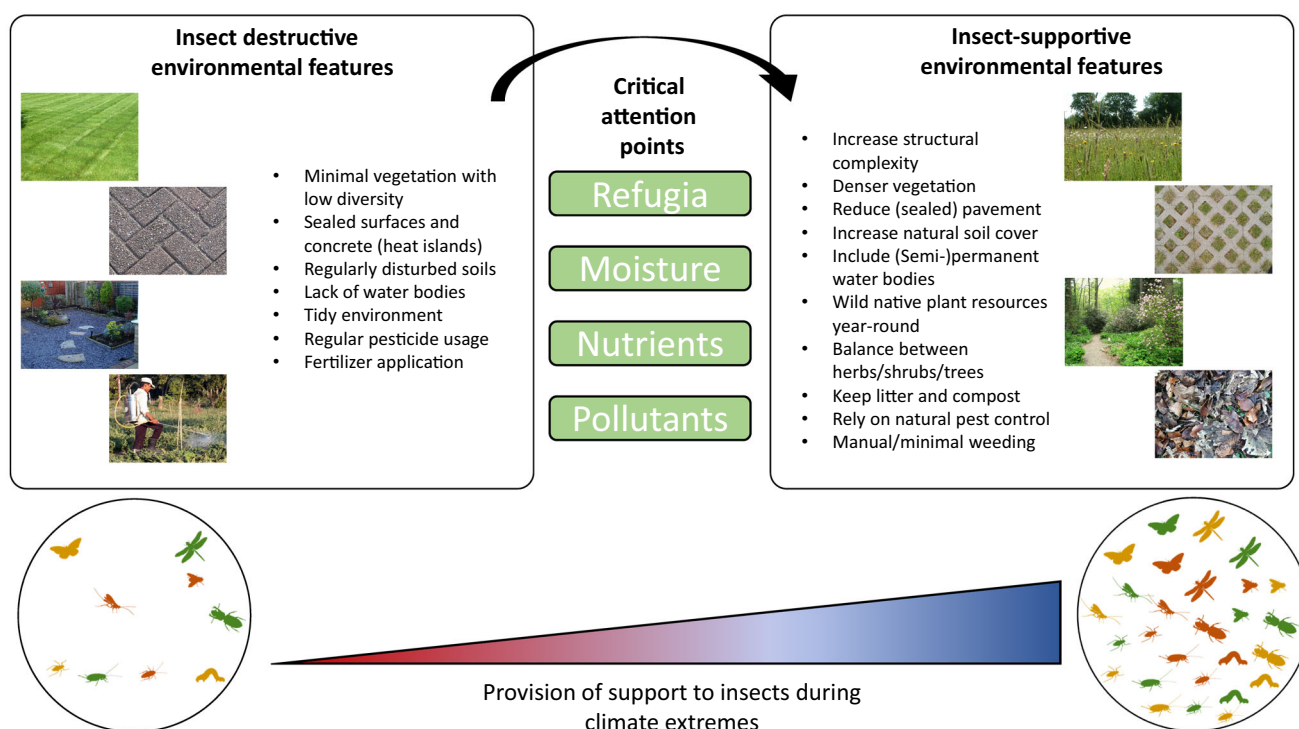


FIGURE 4 Local environmental characteristics can either harm or benefit insects (left panel) and this is especially notable when insects are exposed to climatic extremes such as droughts and heatwaves. Intensively managed landscapes often lead to the simplification of habitats, reducing plant diversity and thus limiting access to key resources for insects. This ultimately results in declining insect diversity. Ecologically targeted management strategies (right panel) can rectify this by paying particular attention to several criteria that enhance ecological communities from the bottom-up, with attention paid to both soil and above-ground processes, which benefits a wide range of insects across different trophic levels. Images: Wikimedia commons. Users: Lawn: Paul Frederickson CC BY-SA 2.5; pavement: Michiel1972 CC BY-SA 3.0; garden: Flute flute CC BY-SA 3.0; pesticide: Roy Bateman CC BY-SA 3.0; flower meadow: Ian Knox CC BY-SA 2.0; open pavement: Titus Tscharnkte CC BY-SA 3.0; tree/shrub/herb vegetation: Daderot CC BY-SA 3.0; leaf litter: Ceridwen CC BY-SA 2.0.

insects also works its way up the food chain, and may be playing an important role in the widespread decline of their consumers, such as insectivorous birds in temperate biomes. The broader ecosystem-level effects of insect decline and the role played by climate warming thus need further attention. By conserving insect communities, and by restoring the ecological balance in farming landscapes, human welfare can be improved and substantial downstream societal benefits can be reaped. Given that climate change continues unabated and climatic extremes in particular pose an immediate, short-term threat to insects, with long-term consequences for ecosystems, it is essential to also consider the importance of managing and restoring habitats that make them as “climate-proof” as possible and enable insects to find refuges in which they can “ride out” extreme climatic events. At larger scales, corridors should be maintained that enable insects to disperse over time to more climatically suitable habitats. Most importantly, there are means of safeguarding insect populations for posterity, and we need to take the initiative to implement them. Our contribution to the scientists’ warning series thus highlights the increasing threat that climate change and attendant short-term climatic extremes pose to insects and other ectotherms in terrestrial and freshwater ecosystems.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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DATA AVAILABILITY STATEMENT

No data were collected for this study.

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