

**REVIEW**

# Scientists' warning on climate change and insects

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**Handling Editor:** Jean-Philippe Lessard

**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 threats. The associated consequences are potentially severe, particularly in terms of threats to species preservation, as well as in the preservation of an

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For affiliation refer to page 22

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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

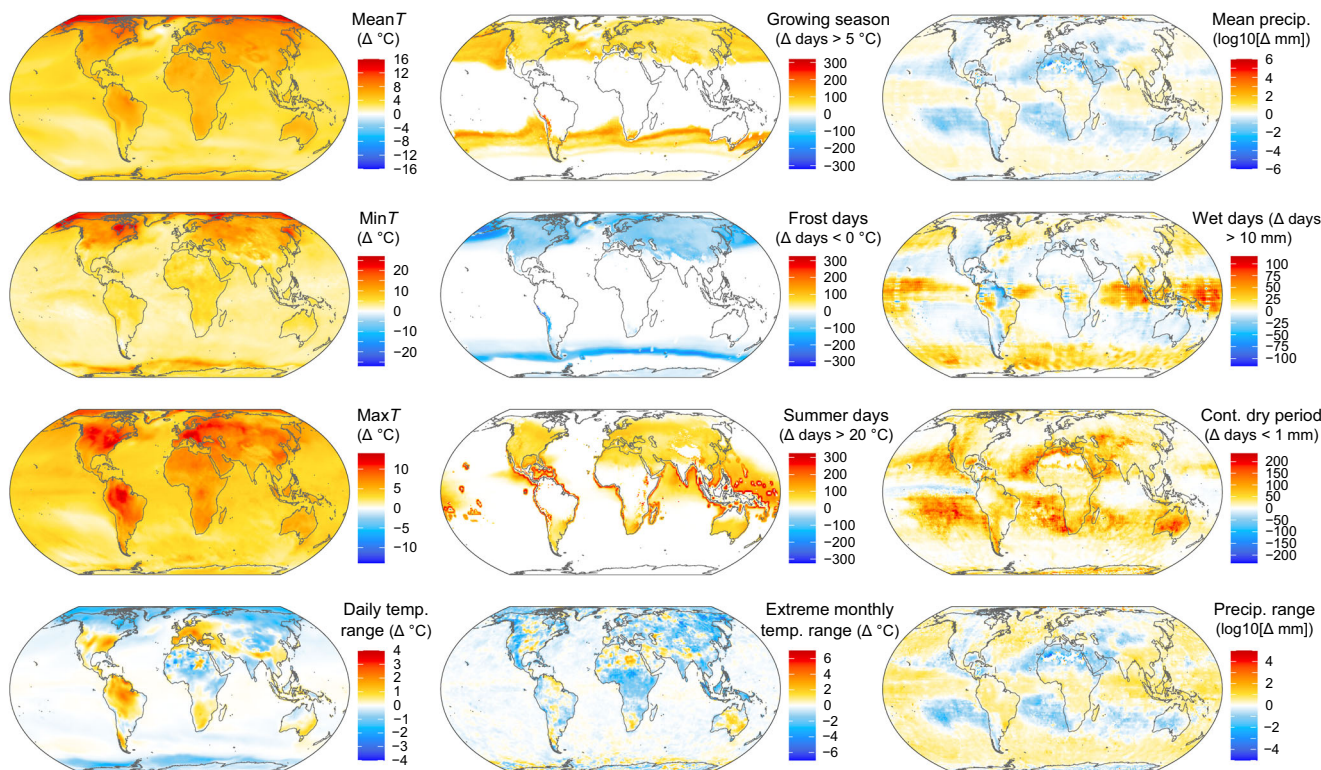
## INTRODUCTION

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 et al., 2020; Hallmann et al., 2017; Janzen & Hallwachs, 2021; Kunin, 2019; Sánchez-Bayo & Wyckhuys, 2019; van Klink et al., 2020; Wagner, 2020; Wagner 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 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; Schowalter, 2013). However, some insect species negatively affect human health and welfare by vectoring diseases or by eating our crops (Schowalter et al., 2018). In natural (unmanaged) ecosystems, abundances of pathogen and vector species are controlled through various food

**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>).

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 these 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).

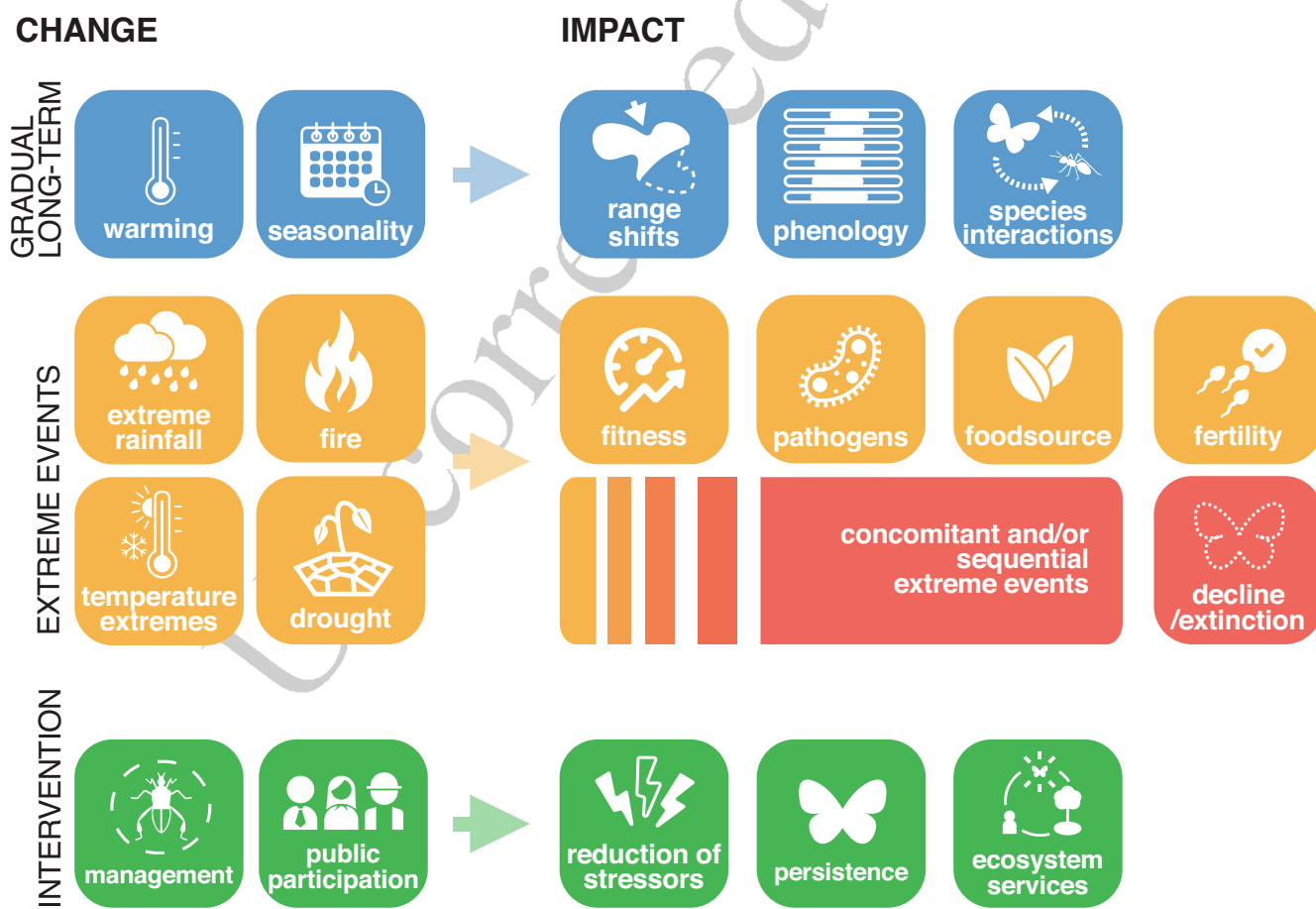
Given their generally small body size, and the fact that the vast majority of species are ectothermic (Harrison et al., 2012), insects are considered to be especially susceptible to the direct effects of changing

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 and functions provided by insects. Unfortunately, along



**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.

1 with climate change denial, other incipient forms of sci- 54  
2 entific denial are becoming more prevalent in recent 55  
3 years, including extinction denial (Lees et al., 2020). 56  
4 However, if we fail to recognize the importance of insects 57  
5 and their vitally important role in the functioning of nat- 58  
6 ural and managed terrestrial and freshwater ecosystems 59  
7 (Losey & Vaughan, 2006), or the impacts that climate 60  
8 change and other anthropogenic stressors are having on 61  
9 them, then we are essentially limiting our ability to act. 62  
10 Recognizing and acting upon the clear and striking evi- 63  
11 dence of climate change effects on insects is critical to 64  
12 support our collective efforts to build an ecologically sus- 65  
13 tainable future. 66

## 14 15 16 **EFFECTS OF LONG-TERM,** 17 **ANTHROPOGENIC CLIMATE** 18 **CHANGE ON INSECTS** 19

20 The effect of long term, gradual warming on insect 67  
21 declines is not always immediately apparent. Discernible 68  
22 changes in insect population dynamics, their distribu- 69  
23 tions, phenology, or abundance are usually detected after 70  
24 critical performance thresholds affecting fecundity, sur- 71  
25 vival, and other vital rates are surpassed (Harvey, 72  
26 Heinen, Gols, & Thakur, 2020). Furthermore, warming is 73  
27 occurring unequally across the biosphere and across 74  
28 time-scales, with temperate, boreal, and polar ecosystems 75  
29 at higher latitudes warming at much faster rates than 76  
30 subtropical and tropical ecosystems at lower latitudes 77  
31 (Parmesan, 2007; Post et al., 2018). Temperatures along 78  
32 tropical mountains are increasing 0.017°C per year, and 79  
33 ecosystems are already shifting upslope (Feeley 80  
34 et al., 2013). Winter is warming faster than any other sea- 81  
35 son (IPCC, 2014), and nights are becoming warmer 82  
36 worldwide (Karl et al., 1991). 83

37 In ectothermic organisms, warmer temperatures are 84  
38 generally associated with increased metabolic rates that 85  
39 may lead to increased physiological costs (Irwin & 86  
40 Lee, 2003; Williams et al., 2012). While warming stimu- 87  
41 lates growth, development, and reproduction up to some 88  
42 optimal temperature, beyond this temperature, metabolic 89  
43 costs increase disproportionately and thermal injuries 90  
44 accumulate, eventually leading to developmental failure, 91  
45 reduced fecundity, impaired dispersal capacity, and, ulti- 92  
46 mately, decreased fitness and increased mortality 93  
47 (Gilbert & Raworth, 1996). Exposure to elevated tempera- 94  
48 tures affects insect growth and development, often 95  
49 resulting in body size reductions, with negative effects on 96  
50 fecundity, longevity and dispersal, all of which can reduce 97  
51 their resilience in the face of climate change and in 98  
52 the worst-case scenarios lead to population crashes 99  
53 (Abram et al., 2017; Gardner et al., 2011; Hof et al., 2011;

Sweeney et al., 2018). As a result, climate change may 100  
reduce genetic diversity through processes including popu- 101  
lation bottlenecks, loss of genetic diversity that is not 102  
related to selection, and outbreeding or inbreeding depres- 103  
sion (Halsch et al., 2021; Pauls et al., 2013), which 104  
threatens the persistence of populations. Insect populations 105  
may display very limited genetic variation in traits associ- 106  
ated with thermal tolerance and it is concerning that in 107  
such populations, local adaptation is already lagging 108  
behind current temperatures (García-Robledo & Baer, 109  
2021a, 2021b). Studies with ants show that thermal toler- 110  
ance (or intolerance) varies across different species and 111  
under different thermal niche conditions, with tolerance or 112  
even benefits of marginally higher temperatures on colony 113  
fitness offset beyond critical thermal thresholds (Diamond 114  
et al., 2014). This paper primarily focuses on ecological 115  
responses to climate change, with less attention paid to 116  
physiological responses at the individual (=organism) level. 117  
One of the most notable phenotypic responses to warming 118  
seen in some insects are changes in body color and, in 119  
particular, a reduction in melanization (Brakefield & 120  
de Jong, 2011; Clusella-Trulas & Nielsen, 2020; Kingsolver 121  
et al., 2011; Roulin, 2014). Reduced melanization is poten- 122  
tially adaptive, as lighter individuals may be able to more 123  
effectively thermoregulate when exposed to extreme heat 124  
than darker individuals (Roulin, 2014). Consequently, 125  
phenotypic plasticity can to some extent counter other 126  
physiological stresses induced by climate change. 127

We argue that the most important outcome of climate 128  
warming is that insect communities become destabilized 129  
(Diamond et al., 2016; Pelini et al., 2014; Pureswaran 130  
et al., 2021), and that populations and even entire species 131  
may go extinct unless they alter their geographical distri- 132  
butions and/or adjust their spatial and temporal behav- 133  
ioral activity patterns and seasonal phenologies to the new 134  
climatic conditions (García-Robledo et al., 2016; Halsch 135  
et al., 2021; Harvey, Heinen, Gols, & Thakur, 2020). This 136  
leads to changes in the structure of ecological communi- 137  
ties at given locations in ways that affect species interac- 138  
tions, with potentially severe repercussions on ecosystem 139  
stability and functioning, and subsequently the provision- 140  
ing of ecosystem services. 141

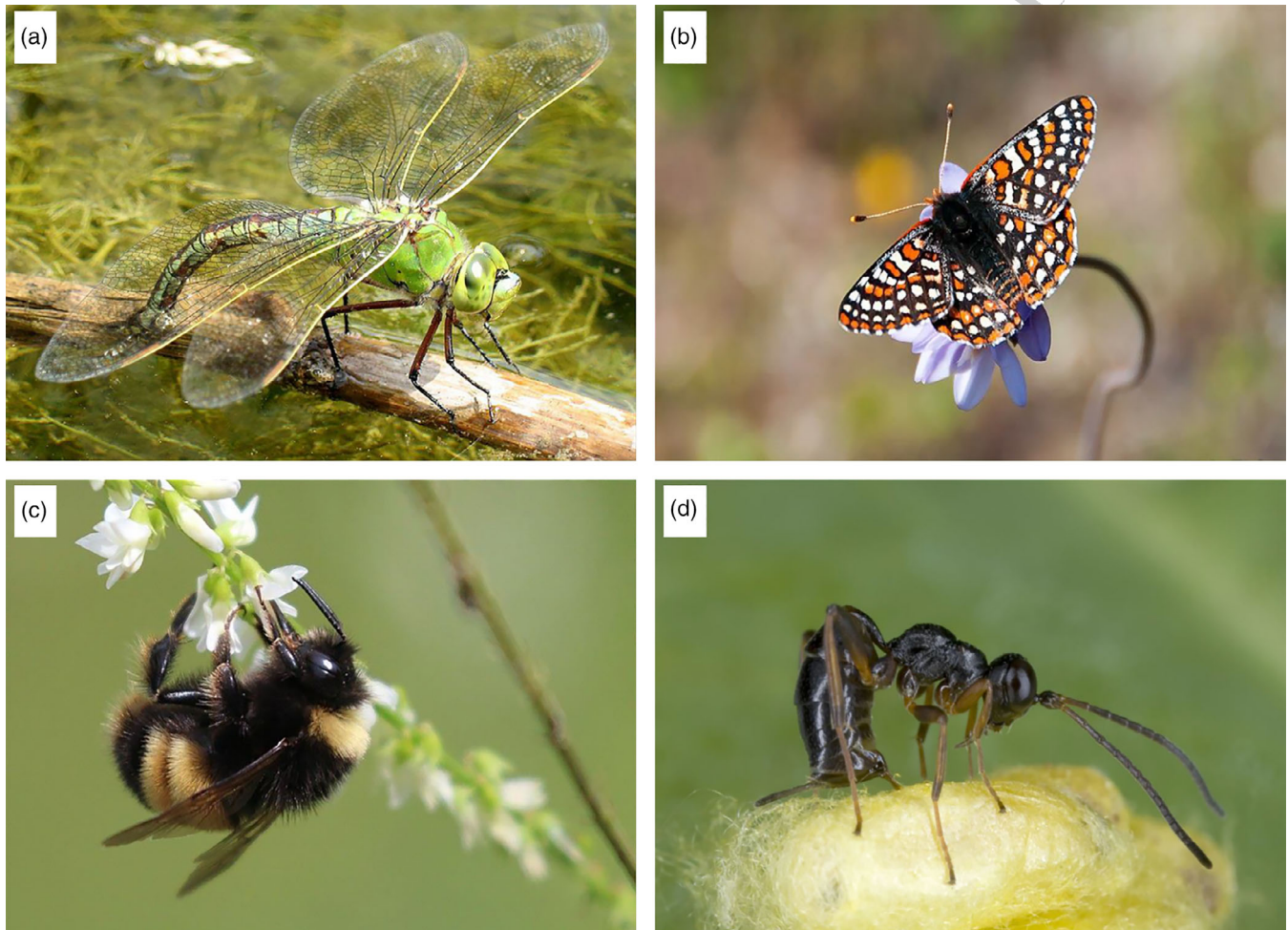
## 142 **Effect on species distributions** 143

144 Species' distributions are strongly determined by climatic 145  
factors and are labile, expanding or contracting during 146  
long-term climatic fluctuations (Hewitt, 2000). Similarly, 147  
the rapid rate of current climate warming strongly deter- 148  
mines how successfully insects are able to track climatic 149  
shifts, since they may or may not keep pace with these 150  
changes. Projections of how global warming will affect 151

1 species geographic ranges are based on bioclimatic envelope models (Vieilledent et al., 2016), the response of  
 2 insects to extreme temperatures (Sunday et al., 2014), or  
 3 simple graphical models of species elevational ranges  
 4 (Colwell et al., 2008), which calculate the potential loss of  
 5 suitable habitats. The general consensus among these different  
 6 approaches is that species at lowest latitudes or elevations  
 7 must migrate to cooler environments to avoid  
 8 extinction (Colwell et al., 2008; Sunday et al., 2011, 2014)  
 9 (Figure 3a,b). Moreover, the ability of insects to track  
 10 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



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

1 of the insect species will contract by 50% or more, whereas  
2 this drops to 18% of insects at +2°C, and 6% of insects at  
3 +1.5°C (Warren et al., 2018). Insects, like other organisms,  
4 are responding to warming by shifting their distributions  
5 poleward and to higher elevations (Grewe et al., 2013;  
6 Heiser & Schmitt, 2013; Parmesan & Yohe, 2003).  
7 However, range retractions at lower latitudes or altitudes  
8 have received less attention (but see Kerr et al., 2015;  
9 Merrill et al., 2008), as the disappearance of a population  
10 is a more gradual process. Moreover, as climate suitability  
11 continues to decline in these so-called trailing edge  
12 populations, more and more insect species, such as butter-  
13 flies, will accumulate an extinction debt (Devictor et al.,  
14 2012; Thomas et al., 2004).

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

38 As long as population losses at lower latitudes or ele-  
39 vations are compensated by range expansions at other  
40 boundaries of the range, most species may be able to per-  
41 sist (Deutsch et al., 2008). Range shifts most likely will be  
42 accompanied by loss of genetic diversity; however, not all  
43 species are able to perform such range shifts, as their  
44 capability to do so depends on several factors, including  
45 active or passive dispersal abilities, population dynamics,  
46 genetic diversity, width of the thermal safety margins,  
47 habitat availability, intra- and interspecific interactions,  
48 and co-shifting of food sources (Amundrud &  
49 Srivastava, 2020; Berg et al., 2010; Bybee et al., 2016;  
50 Deutsch et al., 2008; Hof et al., 2011; Menzel &  
51 Feldmeyer, 2021). Thus, different times of response to cli-  
52 mate change in insects are evident, and the existence of a  
53 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 extinc-  
tion, 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 ther-  
moclines. 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 ham-  
pering range expansions, especially across uneven land-  
scapes with elevational gradients (Samways et al., 2020;  
Yadav et al., 2018, 2021). It is also important to acknowl-  
edge 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  
~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 habi-  
tat 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 competi-  
tion of warm-tolerant species coming from lower eleva-  
tions, 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

1 generalist/invasive species, good dispersers, generally col- 54  
2 onizing from downstream or downslope, such as grass- 55  
3 hoppers (Yadav et al., 2018); conversely, the losers are 56  
4 often specialist species, adapted to cold habitats, among 57  
5 which some were restricted to isolated glacier-influenced 58  
6 ecosystems (Cauvy-Fraunié & Dangles, 2019). The spatial 59  
7 and temporal dynamics of the insect species assemblages 60  
8 linked to ice-related landforms is revealing a rapid turn- 61  
9 over of species with the substitution of cold-adapted spe- 62  
10 cies with more eurythermal species (Gobbi et al., 2021). 63

11 It is important to temper the primarily negative 64  
12 effects of warming on insects by also stressing that some 65  
13 species—at least transiently—may benefit in response to 66  
14 milder winters and warmer conditions that enhance sur- 67  
15 vival or voltinism (Marshall et al., 2020; Musolin, 2007; 68  
16 Tougeron et al., 2017). Winter is considered a major bio- 69  
17 logical control agent of forest and crop pests and trends 70  
18 toward warmer winters or reduced numbers of deep 71  
19 frosts are leading to increased numbers of pest outbreaks 72  
20 (Cannon, 1998; Pureswaran et al., 2019). Moreover, since 73  
21 1970 more species of generalist moths in Great Britain 74  
22 have increased in abundance than decreased in abun- 75  
23 dance (38% vs. 31%), presumably in response to warming 76  
24 (Wagner et al., 2021). Moreover, caterpillar abundances 77  
25 in cloud forests in Ecuador increased between 2001 and 78  
26 2019, because of an increase in sunny days as a result of 79  
27 climate change (Wagner et al., 2021). It needs to be 80  
28 stressed that positive responses to warming may be trans- 81  
29 sient, especially as climatic extremes are increasing, 82  
30 which imposes immense short-term stresses on insect 83  
31 populations (Harvey, Heinen, Gols, & Thakur, 2020), or 84  
32 else if warming continues unabated, pushing many spe- 85  
33 cies beyond their thermal optima for reproduction and 86  
34 survival (Buckley & Kingsolver, 2021). Effects of warming 87  
35 may also be disproportionate up the food chain, with 88  
36 more deleterious physiological effects on predators or 89  
37 parasitoids than on their prey or hosts (Jeffs & 90  
38 Lewis, 2013; Tougeron et al., 2019). Under this scenario, 91  
39 herbivores may benefit from enemy release (Moore 92  
40 et al., 2021). The net effect will still likely have negative 93  
41 consequences for food webs and communities, as the loss 94  
42 of top-down control might lead to all kind of 95  
43 unpredictable, potentially destabilizing, effects over time. 96  
44

## 45 **Effect on phenology**

46 In addition to range shifts, another well-documented aspect 100  
47 of insect response to climate change is a change in phenol- 101  
48 ogy. Elevated temperatures increase the duration of the 102  
49 growing season, which together with faster developmental 103  
50 rates allows some insect species to increase the number of 104  
51 generations in a given year (i.e., voltinism) (Bradshaw & 105  
52 106

Holzapfel, 2001). Even apparently modest temperature 54  
rises can result in increases in seasonal or annual genera- 55  
tions (Parmesan & Yohe, 2003). For example, Altermatt 56  
(2010) showed that 44 butterfly and moth species increased 57  
the number of generations after 1980 in response to rising 58  
temperatures. While warmer temperatures generally allow 59  
for extra generations in the summer, a higher voltinism 60  
may result in smaller adults being produced (Horne 61  
et al., 2015; Verberk et al., 2021). Moreover, the addition of 62  
extra generations later in the season is also affected by the 63  
overwintering strategy and photoperiod (i.e., shortening 64  
day length and the initiation of diapause), which is a domi- 65  
nant seasonality cue for many temperate insects (Lindestad 66  
et al., 2019; Marshall et al., 2020; Tougeron, 2019). Both 67  
parameters are therefore important to consider when 68  
projecting effects of climate change, and extreme tempera- 69  
tures, on patterns in insect voltinism and body size (Bale & 70  
Hayward, 2010; Forrest, 2016; Verberk et al., 2021). 71

Ecological consequences of changes in overwintering 72  
strategies, and more generally in activity timing, are still 73  
far from being well-understood (Williams et al., 2015). In 74  
some cases, an extended period of warm temperatures that 75  
promotes development may delay winter diapause induc- 76  
tion. This may create a developmental trap resulting in the 77  
production of a complete or partial additional generation 78  
in the autumn that cannot survive or enter diapause (“the 79  
lost generation hypothesis” (van Dyck et al., 2015; Kerr 80  
et al., 2020). In addition, diapause maintenance and termi- 81  
nation are disrupted because of warm winters. For exam- 82  
ple, many insects, like other organisms, require a period of 83  
chilling during diapause before they can resume develop- 84  
ment (Lehmann et al., 2017; Stålhandske et al., 2017). If a 85  
chilling cue is not received, individuals may emerge later 86  
or even not at all (Bale & Hayward, 2010; Tougeron 87  
et al., 2019). In line with this, forest experiments 88  
conducted by Fitzgerald et al. (2021) in North Carolina 89  
support the “cool-season sensitivity” hypothesis, showing 90  
that arthropods adapted to cooler conditions endured 91  
stronger negative effects of warming during warm winters. 92  
Alternatively, MacLean et al. (2017) found that exposure 93  
to warmer conditions in winter actually benefitted acorn 94  
ants by “priming” them metabolically for early activity in 95  
spring. Therefore, the effects of warmer winters on insects 96  
is likely to vary considerably among different taxa. 97

Exposure to repeated heat waves in summer, or 98  
warmer spells during winter (or both), may also generate 99  
inappropriate cues that lead insects into developmental 100  
traps (e.g., resuming development in the middle of winter) 101  
(Boggs, 2016; Forrest, 2016). For example, unseasonably 102  
warm autumn conditions are causing the wall brown but- 103  
terfly *Lasiommata megera*, to alter life-cycle decisions by 104  
breaking diapause at the end of the second generation. 105  
This makes the third generation highly susceptible to 106



1 winter mortality, and as a result the butterfly is declining  
2 rapidly across much of western Europe (van Dyck  
3 et al., 2015). In other cases, a partial or complete loss of  
4 winter diapause may result from successive years with per-  
5 missive winter temperatures, which have been shown to  
6 result in the activity of some aphid parasitoids across the  
7 entire year (Tougeron et al., 2017). Therefore, individuals  
8 that remain active throughout the winter rely on physiolog-  
9 ical and behavioral thermotolerance to survive, including  
10 rapid cold hardening, or the induction of transient and  
11 easily reversible resting stages (Diniz et al., 2017). Warmer  
12 winter conditions have also been shown to affect colony  
13 phenology in honeybees, leading to mismatches with their  
14 floral resources (Nürnberg et al., 2019). Furthermore,  
15 warmer periods in winter also stimulate colony brood  
16 rearing activity and this benefits their main parasite, inva-  
17 sive *Varroa destructor* mites (Nürnberg et al., 2019;  
18 Vercelli et al., 2021). Seasonal changes in temperature  
19 therefore also need to be placed in the context of facilitat-  
20 ing pathogens or parasites.

21 Winter conditions tend to be much more variable geo-  
22 graphically and locally than summer conditions  
23 (Bonan, 2004) and this can affect latitudinal variation in  
24 biotic processes much more strongly than conditions dur-  
25 ing the growing season. Trends toward decreasing winter  
26 snow depth, increasing numbers of winter thaws, or later  
27 snowfalls and earlier winter melts are also being observed  
28 in many temperate parts of the world under climate  
29 warming (Fontrodona Bach et al., 2018; McCabe &  
30 Wolock, 2010). The “subnivium,” defined as the physical  
31 interface between the snowpack and ground, is an impor-  
32 tant refuge that protects overwintering insect species  
33 from extremely cold temperatures by providing insula-  
34 tion during diapause (Zhu et al., 2019). During periodic  
35 thaws, or when spring melt occurs early, insects are  
36 exposed to cold temperatures on bare soils that may be  
37 lethal (Bale & Hayward, 2010; Williams et al., 2015). The  
38 absence of snow cover also subjects diapausing stages to  
39 elevated rates of moisture loss and, as a consequence,  
40 desiccation. Loss of snow cover also alters insect metabo-  
41 lism leading to a potential phenological mismatches with  
42 key resources (Renner & Zohner, 2018). Moreover, dia-  
43 pausing insects are more exposed to winter-active preda-  
44 tors when snow cover disappears for even short periods  
45 (Cooper, 2014). However, the longer-term effects of sea-  
46 sonal changes in temperature and precipitation on insect  
47 demographics are thus far little-studied.

## 50 Effect on species interactions

52 Insects, like most organisms, are embedded in complex  
53 communities, and their fate depends on interactions with

54 other species. In general, predation and other  
55 multitrophic interactions often result from long  
56 co-evolutionary processes that are specific to a particular  
57 environment under relatively stable climatic conditions.  
58 However, temperature changes may differentially affect  
59 the biology of each of the component species of a system.  
60 This has been demonstrated in multitrophic systems  
61 involving plants, their herbivores, natural enemies (para-  
62 sitoids, predators and pathogens), and hyperparasitoids  
63 (Agosta et al., 2017; Bale et al., 2002; Bannerman  
64 et al., 2011; Moore et al., 2021; Pardikes et al., 2022;  
65 Romo & Tylianakis, 2013; Schreven et al., 2017;  
66 Tougeron et al., 2018). Studies show that the effects on  
67 survival, development, and reproduction are generally  
68 negative, e.g., plants growing under conditions of  
69 extreme temperatures, increased CO<sub>2</sub>, and/or reduced  
70 rainfall could become suboptimal nutritional resources  
71 for herbivores, indirectly influencing natural enemy fit-  
72 ness and associated biocontrol services (Han et al., 2019,  
73 2022). A double negative effect may occur when tempera-  
74 ture increase promotes herbivorous pest populations  
75 while negatively impacting host plant defenses (Wang  
76 et al., 2021). Temperature increases may also induce  
77 slight shifts in feeding preference; e.g., with phytopha-  
78 gous insects feeding more on native plants versus inva-  
79 sive plants when temperature increases (Liu et al., 2021).  
80 Interactions between plants and insect pollinators are  
81 typically also known to be weakened by climate change  
82 (Tylianakis et al., 2008). The effects are likely to be even  
83 more important in higher trophic levels that depend on  
84 the host specificity and the capacity of the lower trophic  
85 levels to adapt to these changes and also because they are  
86 less numerous (Monticelli et al., 2022; Thackeray  
87 et al., 2016; van Baaren et al., 2010). These effects may be  
88 exacerbated in species-poor communities e.g., on islands  
89 or in increasingly homogeneous, chemically disrupted  
90 agro-landscapes (Raven & Wagner, 2021). Moreover,  
91 many vertebrates (e.g., small mammals, birds, reptiles,  
92 amphibians) depend on insects as food, and the loss of  
93 insects in a warming world is therefore likely to have  
94 enormous effects on broader ecological communities.

95 One major consequence of changes in the distribution  
96 and phenology described above is the occurrence of  
97 potential spatial and temporal mismatches among  
98 interacting species. Differential responses between tro-  
99 phic levels may, for instance, decouple the timing of gen-  
100 erations among interacting species (Damien &  
101 Tougeron, 2019; Gérard et al., 2020; Thackeray  
102 et al., 2016). This may be especially prevalent among spe-  
103 cialized species that are constrained by the responses of  
104 their prey or hosts, or in species that already have narrow  
105 environmental niches (Damien & Tougeron, 2019;  
106 Tylianakis et al., 2008). The mismatch between insect

1 food availability in spring and the breeding success of  
2 long-distance migratory birds is a well-studied example  
3 (Both et al., 2006). These mismatches may subsequently  
4 destabilize and reduce the efficacy of crucial interactions  
5 such as between plants and pollinators (Peralta  
6 et al., 2020), or herbivores and natural enemies (Bale  
7 et al., 2002; Harvey, 2015; Singer & Parmesan, 2010).  
8 Mismatches may be countered by strong selective pres-  
9 sure leading to readjustments in the phenology, distribu-  
10 tion, or physiology of interacting species (Klapwijk  
11 et al., 2010; Schleuning et al., 2020). Moreover, climate  
12 warming may lead to formation of new interactions  
13 among species that were previously disassociated in space  
14 or time (Shah et al., 2020). Novel interactions may arise  
15 as a result of differences among species responses and  
16 thus adaptation to warming (including their value as an  
17 interaction partner, e.g., nutritional quality), because of  
18 differential responses of spatial or temporal range, or  
19 when existing interaction partners go extinct and  
20 switches to new partners are required (Tylianakis &  
21 Morris, 2017).

22 Thermal tolerance mismatches may occur intraspe-  
23 cifically via sexual conflicts in response to different tem-  
24 peratures, as has been demonstrated in damselflies  
25 (Svensson et al., 2020) and whiteflies (Ma et al., 2014), or  
26 interspecifically, where tightly interacting species, such  
27 as parasitoids and their hosts, exhibit differing sensitivi-  
28 ties to high temperatures (Abarca & Spahn, 2021;  
29 Furlong & Zalucki, 2017; Wetherington et al., 2017). This  
30 has been shown with thermal response curves for patho-  
31 gen growth and host defense (Thomas & Blanford, 2003),  
32 and may lead to distinctly non-linear responses to even  
33 small temperature changes. These “thermal mismatch”  
34 effects could possibly result in a destabilization of the  
35 dynamics that could lead to the extinction of part of the  
36 system, and could create an imbalance in how mass and  
37 energy transfer in food webs (Thakur, 2020a). Studies  
38 using simulated warming to mimic natural conditions  
39 have shown that exposure to higher temperatures may  
40 also decrease the interaction strength and the fitness of  
41 each of the interacting species (Sentis et al., 2013).  
42 However, in some instances, temperature can shape  
43 insect communities directly through differences in spe-  
44 cies’ thermal performance capabilities, and not involve  
45 any effect of biotic interactions (Thierry et al., 2021).

46 Warmer temperatures lead to higher metabolic and  
47 feeding rates, which tends to increase the strength of tro-  
48 phic interactions in the short term by making consumers  
49 more dependent on their resources (Rall et al., 2012;  
50 Sentis et al., 2012). However, energetic losses often  
51 increase faster at higher temperatures than feeding rate,  
52 leading to metabolic mismatches (Bideault et al., 2021).  
53 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 bio-  
mass 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 ter-  
restrial and aquatic ecosystems. This highlights how tem-  
perature can have cascading effects from physiology to  
species interactions and community properties. In addi-  
tion, 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 communi-  
ties 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 con-  
nectivity increased and most top predators were lost lead-  
ing to their replacement by meso-predators. Such  
changes in insect communities can have detrimental con-  
sequences 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.

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Insects live in close association with microbial com-  
munities residing within cells, on the cuticle, inside the  
gastrointestinal tract or in the hemolymph. These  
microbiomes comprise mutualists that for instance facili-  
tate 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 find-  
ings (Karl et al., 2011). Mutualistic bacteria provide vari-  
ous ecological benefits, such as resistance to  
environmental stress, pathogen infections or natural ene-  
mies, 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

1 genome during coevolution with their hosts, mutualistic  
2 endosymbionts have little potential to cope with a chang-  
3 ing environment, including heat stress, and can therefore  
4 be considered the Achilles heel of insects in a context of  
5 increasing temperature (Renoz et al., 2019). Some evidence  
6 demonstrates that the interplay between insect hosts and  
7 their mutualistic and antagonistic microbial partners is  
8 temperature-dependent. For instance, gut microbiome  
9 composition can shift across seasons and is concurrent  
10 with changes in cold tolerance (Ferguson et al., 2018).  
11 Benefits or drawbacks provided by symbionts can be  
12 altered by increasing temperatures (Bensadia et al., 2006;  
13 Higashi et al., 2020; Tougeron & Iltis, 2022), in part  
14 because some symbionts reside in highly heat-sensitive  
15 organs (e.g., bacteriocytes, Shan et al., 2017) and reversely,  
16 alteration in the gut or intracellular microbial community  
17 can influence insect resistance to temperature variation  
18 (Henry & Colinet, 2018; Iltis, Tougeron, et al., 2021;  
19 Jaramillo & Castañeda, 2021). Moreover, the microbiome  
20 can be totally restructured during diapause in arthropods  
21 (Mushegian et al., 2018; Mushegian & Tougeron, 2019),  
22 but how modifications in seasonal strategies following cli-  
23 mate change actually affect microbial communities merit  
24 further investigations.

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

39 Water also has a much lower oxygen capacity than  
40 air, which magnifies the difficulties of supporting aerobic  
41 respiration. Indeed, the oxygen problem may underlie  
42 low observed heat tolerances of aquatic insects: in  
43 warming waters, oxygen availability rises modestly but  
44 demand (from metabolism) often rises rapidly, and  
45 oxygen shortage may lower heat tolerance (Frakes  
46 et al., 2021; Verberk et al., 2011; Verberk, Overgaard,  
47 et al., 2016). Consequently, aquatic ectotherms, including  
48 aquatic insects may be more sensitive to rising mean tem-  
49 peratures and more prone to reaching upper critical  
50 limits (Rubalcaba et al., 2020; Verberk, Durance,  
51 et al., 2016). Indeed, aquatic insects generally have lower  
52 tolerance limits to heat than terrestrial insects (Chown  
53 et al., 2015). These observations, and several recent

papers, also underscore the importance of flow in deliver- 54  
ing oxygen to the body surface (Birrell et al., 2020; Frakes 55  
et al., 2021). Low flows stemming from changes in hydro- 56  
logical cycles or seasonality may compound the chal- 57  
lenges of higher temperatures and low oxygen. 58  
Interestingly, a similar high temperature-hypoxia rela- 59  
tionship certainly applies also to particular terrestrial 60  
insects such as leaf gallers or cambium miners 61  
(Pincebourde & Casas, 2016). Many aquatic insects spend 62  
part of their lives under water as eggs, larvae, or pupae 63  
before emerging as winged, terrestrial adults. These early 64  
life stages are considered more vulnerable to heat par- 65  
tially because of oxygen limitation inherent to living in 66  
water (e.g., Verberk & Bilton, 2015), and also their lim- 67  
ited mobility prevents them from behaviorally exploiting 68  
gradients in temperature and oxygen availability (eggs 69  
and pupae (Kingsolver et al., 2011). Thus, the response of 70  
aquatic juveniles to rising temperatures will strongly 71  
affect the presence and persistence of terrestrial adults. 72

73 These physical and physiological considerations may  
74 have important consequences for how climate change  
75 affects aquatic communities. Aquatic insects in temperate  
76 mountains, for example, experience wider seasonal fluc-  
77 tuations in temperature than do related species in tropi-  
78 cal mountains at similar elevations. Temperate species  
79 have wider thermal breadths and, in some cases, a  
80 greater ability to acclimate to warmer temperatures  
81 (Shah et al., 2017). Such patterns have been seen in other  
82 aquatic taxa such as tadpoles (Gutiérrez-Pesquera  
83 et al., 2016) and marine ectotherms (Sunday et al., 2011).  
84 These studies suggest that tropical aquatic insects are  
85 especially vulnerable to rising temperatures (Tewksbury  
86 et al., 2008). 87

## 88 89 **EFFECTS OF SHORT-TERM, 90 UNPREDICTABLE CLIMATE 91 EXTREMES ON INSECTS**

92 No universal definition of extreme climatic events thus  
93 far exists (Van de Pol et al., 2017) reviewed definitions  
94 used in ecology). The term “climatic extremes” has been  
95 used to describe meteorological phenomena (e.g., heat  
96 waves, droughts, extreme rainfall events) as well as their  
97 consequential physical impacts (e.g., flooding, fires, desic-  
98 cation, tornadoes, hurricanes). Furthermore, extreme cli-  
99 matic events can be defined by their climatological  
100 extremeness or by the extremeness of the biological  
101 impacts caused by a climate-related event. Finally, there  
102 is little consensus on the threshold for extremes (1%, 5%  
103 or 10% frequency or a certain percentile of a reference  
104 period) and how other attributes should be factored in,  
105 such as the temporal duration, magnitude, timing, spatial  
106

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 (Nakonieczny 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 has similar 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 males (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

1 waves is pushing many insect species and/or their food  
2 plants beyond their adaptive limits, exposing them to  
3 conditions that they may not have experienced in their  
4 evolutionary history, particularly given the lack of adap-  
5 tive capacity of insects to heat extremes (Harvey  
6 et al., 2021; Harvey, Heinen, Gols, & Thakur, 2020; Ma,  
7 Ma, & Pincebourde, 2021). Short-term (daily) tempera-  
8 ture fluctuations can alter the shape of thermal perfor-  
9 mance curves, reducing the optimum and critical  
10 thermal maximum temperatures relative to those  
11 predicted using mean temperatures alone (Kingsolver &  
12 Buckley, 2018; Paaijmans et al., 2013).

13 Insect microbiomes are often driven by environmen-  
14 tal microbiomes, for instance that associated with the  
15 host plant or in the soil (Hannula et al., 2019). The effects  
16 of extreme climatic events on environmental  
17 microbiomes (Jansson & Hofmockel, 2020) may pose an  
18 additional pathway through which climate extremes may  
19 affect insect performance. For example, the bacterial  
20 endosymbiont, *Wolbachia*, is known to impact the capac-  
21 ity of mosquitoes to transmit a range of arboviruses and  
22 parasites, and is being actively deployed as a “biocontrol  
23 agent” in a number of locations globally. However, the  
24 complex interactions with *Wolbachia* appear to have  
25 highly variable effects on malaria parasite infection  
26 under extreme temperatures (Murdock et al., 2014). More  
27 recently, lab studies examining thermal knockdowns  
28 have suggested that *Wolbachia* can reduce the thermal  
29 tolerance of the primary dengue vector, *Aedes aegypti*  
30 (Ware-Gilmore et al., 2021). Moreover, infection with  
31 dengue virus also reduced thermal tolerance. These  
32 results demonstrate the potential for complex effects of  
33 temperature variation (including temperature extremes)  
34 on host–microbe interactions, with impacts varying  
35 across environments. In particular, in cases where endo-  
36 symbionts confer resistance to heat shock, this can allow  
37 rapid evolution of heat tolerance by the host (Harmon  
38 et al., 2009).

39 Extremely high temperatures are not only occurring  
40 during the daytime. Many insects are nocturnal and are  
41 sensitive to abiotic conditions that may differ signifi-  
42 cantly from those experienced by diurnal insects.  
43 Importantly, they may be highly sensitive to tempera-  
44 tures that deviate considerably from normal. Night  
45 warming and extremely high minimal nighttime temper-  
46 atures are also threatening the persistence of some insect  
47 populations and are also affecting interspecific interac-  
48 tions (Higashi et al., 2020; Ma et al., 2020; Ma, Bai,  
49 et al., 2021). However, the asymmetry between night and  
50 daytime warming and extremes is thus far little studied,  
51 especially in terms of its impact on diurnal insects whose  
52 fitness-related traits, along with other overlooked behav-  
53 iors such as sleep (Tougeron & Abram, 2017) or

thermally-gated developmental programs such as  
54 molting, may be sensitive to heat exposure during the  
55 night. For example, successive exposure to extremely  
56 warm nights reduced adult performance (longevity and  
57 fecundity) of the grain aphid *Sitobion avenae* over subse-  
58 quent days (Zhao et al., 2014). In a study including  
59 diurnal and nocturnal ant species, ant communities from  
60 warmer habitats such as semi-desert and subtropical dry  
61 forests were more tolerant to high temperatures than ants  
62 from cooler environments such as tropical rain and mon-  
63 tane forests (García-Robledo et al., 2018). In all habitats,  
64 nocturnal ants displayed lower thermal tolerance than  
65 diurnal ants (García-Robledo et al., 2018). In addition,  
66 night-time warming may have distinct effects from day-  
67 time warming on top-down control of plants by herbi-  
68 vores (Barton & Schmitz, 2018), and could interact with  
69 other aspects of global changes such as light pollution to  
70 disrupt predator–prey interactions (Miller et al., 2017).  
71

72 Considering that insects have to keep up with an  
73 increasingly variable thermal environment, which include  
74 cold and heat shocks, it is crucial to examine the cumula-  
75 tive impacts of fluctuating temperatures on the response of  
76 insects to thermal extremes (Hance et al., 2007; Jeffs &  
77 Leather, 2014). The cumulative effects of stressful condi-  
78 tions on physiological performance is becoming increas-  
79 ingly recognized (Cardoso et al., 2020; Didham et al., 2020;  
80 Harvey, 2015; Kaunisto et al., 2016) and highlights the  
81 potentially much higher vulnerability of insects to stressful  
82 conditions. Climatic variability over different temporal  
83 and spatial scales may notably limit the evolutionary  
84 responses of insects to longer-term, incipient warming  
85 (Buckley & Kingsolver, 2021; Kingsolver & Buckley, 2015).

86 Phenotypic plasticity and bet-hedging may be critical  
87 strategies for the persistence of insect populations and  
88 species in response to immediate, intense and more or  
89 less predictable temperature changes (Sgrò et al., 2016).  
90 Phenotypic plasticity in response to thermal variation is  
91 known to protect insects by eliciting changes in a range  
92 of important biological traits (e.g., Vasudeva et al., 2021;  
93 Verberk et al., 2018). Phenotypic plasticity is expected  
94 when climatic variation is at least partially predictable,  
95 but fitness-related traits may be compromised when they  
96 are more stochastic (Liefting et al., 2009). Bet-hedging is  
97 an adaptive strategy in temporally unpredictable environ-  
98 ments (Hopper, 1999). For instance, in environments  
99 with highly unpredictable cold and heat extreme events,  
100 it was demonstrated that several phenotypes can be  
101 expressed among the progeny of a single individual  
102 (e.g. diapausing versus active individuals, sexual versus  
103 asexual morphs) (Le Lann et al., 2021). Each of these  
104 phenotypes may have advantages over the others  
105 depending on thermal conditions. This diversified  
106 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

1 performance. They predicted that different herbivore  
2 guilds will show different but predictable responses to  
3 drought stress with most guilds being negatively affected,  
4 many wood borers being a favorable exception, at least in  
5 the short term. There have been a few whole-forest  
6 drought manipulation experiments. Insect responses to  
7 an experimental drought in a tropical rainforest of North  
8 Queensland, Australia, showed variable responses among  
9 different feeding guilds (Gely, 2021). In the experimen-  
10 tally droughted area, there was significantly more wood  
11 borer damage to trees than in the control area (Gely  
12 et al., 2021). Many ant species in Australian rainforests  
13 take nectar from extrafloral nectaries whereas some also  
14 rely on aphid honeydew. Food sources are reduced in  
15 areas under drought, and stable isotope analysis indicates  
16 that many ant species are becoming increasingly preda-  
17 tory (Gely, 2021), which will have impacts on food webs  
18 in these forests.

19 Droughts can affect reproduction, as some insect eggs  
20 require water for development (Rohde et al., 2017).  
21 Similarly, drought can change plant signaling and the qual-  
22 ity of floral rewards for pollinators leading to reductions in  
23 pollinator attraction and plant reproduction (Descamps  
24 et al., 2018; Rering et al., 2020). Even a single severe  
25 drought can alter plant-insect communities. Following the  
26 severe drought of 1995 in the United Kingdom, the total  
27 abundance of butterflies increased, but this was accompa-  
28 nied by substantial changes in community composition,  
29 particularly in more northerly, wetter sites. Specialist, vul-  
30 nerable species were lost while generalist, widespread spe-  
31 cies increased, likely because of enhanced opportunities for  
32 recruitment from the larger regional populations. A year  
33 later, communities had yet to return to equilibrium  
34 (De Palma et al., 2017), signifying that episodic drought can  
35 lead to greater extinction risk, likely both in terms of species  
36 and genetic diversity. A similar finding was reported for  
37 butterflies in Arizona (Wagner & Balowitz, 2021). Single,  
38 severe droughts may push the last remaining ephemeral  
39 populations toward extinction, with a concomitant loss of  
40 genetic diversity.

41 While the physiological and ecological mechanisms  
42 associated with responses to extreme drought are  
43 multi-faceted and not well understood, the consequences  
44 are increasingly apparent. A recent mega-drought in  
45 western North America had negative and long-lasting  
46 effects on montane butterfly communities that were com-  
47 parable in magnitude to the combined effects of decades  
48 of habitat loss and degradation at lower elevations  
49 (Halsch et al., 2021). In the case of dragonflies in the  
50 Cape Floristic Region, which is subject to periodic  
51 droughts, adults, even among localized endemic species,  
52 temporarily use artificial ponds to pull through periods of  
53 extreme drought (Deacon et al., 2019). In the same

region, dragonfly adults remain faithful to the pond mar- 54  
gins and continue to forage there until rains return, while 55  
water beetles soon depart from ponds when major 56  
droughts continue (Jooste et al., 2020). These responses 57  
indicate that freshwater insects can have different behav- 58  
ioral responses to periodic droughts. Conversely, less 59  
volant taxa and insect which have historically evolved in 60  
perennially humid to wet communities, such as the 61  
faunas of cloud and rain forests would be expected to be 62  
especially challenged by droughts (Janzen & 63  
Hallwachs, 2021; Wagner, 2020). Climatic extremes, like 64  
droughts, generate “winners” and “losers” among insects, 65  
based on changes in plant quality and non-linear effects 66  
up the food chain, although, when put into the context of 67  
other anthropogenic stresses, the longer-term prognosis 68  
for insects is negative (Harvey, Heinen, Gols, & 69  
Thakur, 2020). 70

## 71 Extreme rainfall, floods 72

73 Climate warming is also leading to an increase in the fre- 74  
quency and intensity of rainfall events, such as those 75  
occurring during thunderstorms and hurricanes (Armal 76  
et al., 2018; Brooks, 2013; Frame et al., 2020; 77  
Guhathakurta et al., 2011). Extreme rainfall and accompa- 78  
nying flooding can have both direct and indirect effects on 79  
insects. The direct effects constitute displacement and 80  
drowning. Heavy rainfall dislodges insects from plants 81  
with small or less well-attached species being particularly 82  
vulnerable (Beirne (1970) and references within, Moran 83  
et al. (1987), Chen, Harvey, et al. (2019)). Indirectly, 84  
insects can be affected by rainfall and flooding through 85  
changes in the abiotic environment. Flooding and subse- 86  
quent soil waterlogging induces a number of alterations in 87  
important soil physicochemical properties like soil pH, 88  
redox potential and oxygen level that in turn can lead to 89  
hypoxia or anoxia (Ashraf, 2012), affecting soil-dwelling 90  
insects in particular. Insects, including many soil-dwelling 91  
and riparian insects have evolved various mechanisms to 92  
withstand short-term hypoxia or anoxia (Harrison et al., 93  
2018; Hoback & Stanley, 2001; Woods & Lane, 2016), but 94  
these capacities can be exceeded by longer-term soil 95  
flooding. Wet soil may also force subterranean insects to 96  
the soil surface where they are more vulnerable to attack 97  
by their natural enemies (Beirne, 1970). 98

99 Changes in soil conditions can lead to changes in 100  
above-ground primary and secondary plant metabolism 101  
that affects the performance of insects feeding on them 102  
(Ayres, 1993). At the same time, rain changes microcli- 103  
matic conditions such as temperature and humidity 104  
which are both important environmental variables affect- 105  
ing insect performance. The sudden drop in temperature 106

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 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 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 rain 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 policy 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,



1 it is important to consider not only that burning has dif-  
2 ferential ecological effects based on ecosystem sensitivity  
3 or dependency on fire, but also the variant spatial distri-  
4 bution of fire across these different landscapes in terms  
5 of extent (i.e., 10 vs. 10,000 ha<sup>2</sup>), fire frequency, fuel loads  
6 within fire perimeters, and distance to refuges (Pryke &  
7 Samways, 2012a). For example, some fire-resistant plants  
8 with tightly packed leaf bases have been shown to pro-  
9 vide refuges for insects and other arthropods even during  
10 intense fires (Brennan et al., 2011). The importance of  
11 these refuges in the resilience of insect communities  
12 needs further investigation.

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

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

## 43 INSECT CONSERVATION UNDER 44 CLIMATE WARMING AND 45 CLIMATIC EXTREMES

46  
47 In our paper, we have highlighted individual and popula-  
48 tion and community-level responses to climate change,  
49 but landscape or ecosystem consequences have remained  
50 largely undiscussed, whereas at these levels the conse-  
51 quences are most influential. The balance should there-  
52 fore shift toward these effects in terms of policy-making,  
53 scientific research, and conservation approaches. Indeed,

54 the effects of climate change on insects are numerous  
55 and often lineage-specific. They may vary across life  
56 stage, physiological state, as well as across local biotic  
57 and abiotic conditions and, thus, appear to be idiosyn-  
58 cratic. Of course, many research topics seem idiosyncratic  
59 until we begin to understand them better. If we want to  
60 understand and mitigate the impacts of extreme climatic  
61 events, and climate change in general, on insect biology  
62 and insect decline, we need more research (and associ-  
63 ated funding and political will) on the impacts of climate  
64 change not only on the basic biology of insects, but also  
65 on integrative aspects at the scale of the ecosystem  
66 (Hof, 2021). The decline in insect abundance and biomass  
67 we are now facing—and can expect in the future given  
68 the effects of climate change described above and still  
69 other stressors—will have far-reaching community-level  
70 effects due to the fact that insects form the major part of  
71 the second trophic level in many ecosystems. As insects  
72 provide a critical contribution to ecosystem functioning  
73 and hence ecosystem services, loss of insect biomass,  
74 abundance, and diversity will therefore disrupt trophic  
75 cascades, including declines of flowering plants and ero-  
76 sion of terrestrial food webs (Wilson, 1987). For example,  
77 the large number of insects during the breeding season  
78 are a crucial component of nestling diets of many bird  
79 species, and a decline in insect availability can severely  
80 reduce nestling survival and fitness (Tallamy &  
81 Shriver, 2021). Likewise, losses in biomass of up to 80%  
82 in important pollinator taxa will inevitably have disrupt-  
83 tive consequences for pollination (Hallmann et al., 2017,  
84 2021). Extreme climatic events affect many insect species  
85 in the community simultaneously, exacerbating the dis-  
86 ruptive ecological consequences.

87 Perhaps more indirectly, but equally disruptive, will be  
88 the effect of large-scale insect decline at the ecosystem  
89 level. Significant losses of insect abundance and diversity  
90 may threaten ecosystem resilience through reduced func-  
91 tional diversity (Antão et al., 2020; Jonsson &  
92 Malmqvist, 2000; Seymour et al., 2020). Functional redun-  
93 dancy provides “insurance” against the loss of a few species  
94 (Naeem et al., 2012; Naeem & Li, 1997). With the current  
95 estimated rates of insect decline, functional diversity may  
96 quickly approach the lower threshold of full functional  
97 niche occupancy, meaning that further loss will jeopardize  
98 ecosystem functioning. In addition to knowledge about  
99 how species respond to climate extremes (response traits),  
100 we also need to know how they affect ecosystem processes  
101 (effect traits), in order to understand how community attri-  
102 butes are related to ecosystem function and resilience  
103 (de Bello et al., 2021; Suding et al., 2008).

104 This response-to-effect trait framework is increasingly  
105 adopted by land managers as it can guide landscape  
106 actions and local measures to preserve insect functional

1 diversity. Among the conservation approaches that can  
2 be undertaken, we can consider direct and relatively local  
3 approaches aimed at reducing the effects of climate  
4 change on insect biodiversity through appropriate envi-  
5 ronmental management, and global policy approaches  
6 involving the general public. It is clear that climate  
7 change is harmful to insects and biological processes  
8 involving insects at the individual, population, commu-  
9 nity, and ecosystem levels. We need to act now to mini-  
10 mize these impacts; we know how to do it, but the  
11 decision-making and requisite funding keep getting  
12 pushed down the road or onto the shoulders of future  
13 generations.

## 16 Management approaches

17  
18 To protect insects from climate change, and climatic  
19 extremes, it is necessary to go beyond traditional surveys  
20 that record insect presence-absence and understand their  
21 physiological and behavioral tolerance to environmental  
22 extremes. Insects have both physiological and behavioral  
23 thermoregulation capacities that can prevent exposure to  
24 harmful temperatures (Abram et al., 2017) or buffer them  
25 against the damaging effects of extreme temperatures  
26 once exposed (Ma, Ma, & Pincebourde, 2021). The envi-  
27 ronmental elements that can act on them, and that can  
28 be manipulated, are at both the landscape (macro scale)  
29 and at the micro-habitat level (microclimates), but it is  
30 important to know how management fits with the main-  
31 tenance of other ecosystem services, as well as how each  
32 individual taxon may respond (Oliver & Morecroft, 2014;  
33 Tougeron et al., 2022). The conservation implications of  
34 microclimatic diversity at fine scales are just beginning to  
35 be explored—but a general conclusion from studies to  
36 date is that insects will be more resilient to climate  
37 change when they consist of intact communities with  
38 high structural complexity and high levels of plant spe-  
39 cies diversity, which together will generate diverse micro-  
40 climatic refugia (Pincebourde et al., 2016; Woods  
41 et al., 2015). Microclimates can be influenced by land-  
42 scape properties (Oliver & Morecroft, 2014). For instance,  
43 hedgerows, woodlots, sown vegetation, and flower strips  
44 may represent microclimatic refuges for agrobiodiversity  
45 in the face of extreme climatic events (Lenoir et al., 2017;  
46 Thakur et al., 2020). The windbreak and antifreeze roles  
47 of hedges has been widely studied and confirmed in agri-  
48 cultural landscapes. Wooded and closed areas generally  
49 have lower temperature amplitudes than open areas over  
50 a daily scale but are also colder on average, which can  
51 affect insect thermoregulatory abilities (Alford  
52 et al., 2017; Tougeron et al., 2016). Similarly, field-level  
53 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 spe-  
cies 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 facilitat-  
ing 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 com-  
plex environments. This result agrees with the studies  
performed in mountain areas by Brighenti et al. (2021)  
and Tampucci, Gobbi, et al. (2017), 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, under-  
standing 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 sug-  
gest that they already contain climate change refugia;  
thus, these agencies need tools to detect and prioritize cli-  
mate change refugia for management. Moreover, the role  
of mammalian ecosystem engineers, which can quite dra-  
matically influence the structure and composition of habi-  
tats, 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 habitat, by flooding, salt

1 intrusion, and erosion of dune crests and cliff faces.  
2 Inland, ecological resilience can be gained by insuring  
3 that large-scale networks of conservation corridors over  
4 various elevations are in place so that not only is more  
5 habitat available, simply reducing the risk of population  
6 loss through more land area being available, but also  
7 because there is a greater chance that refuges are avail-  
8 able (Samways & Pryke, 2016).

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

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

32 Prescribed burning is used in many countries to man-  
33 age forests and woodlands. Where the effects of fire are  
34 confined to relatively small areas, recolonization by  
35 ground-dwelling invertebrates from adjacent unburned  
36 areas can be rapid, with communities returning to nor-  
37 mal by the following season (Nunes et al., 2000, 2006),  
38 and fires can also enhance habitat diversity (see *Fire*).  
39 One potential solution to climate-driven changes on  
40 insect assemblages is to counter the effects of extreme  
41 fires with prescribed, managed fires in ecosystems that  
42 rely on fire to maintain healthy structure and function.  
43 In doing so, burning ameliorates effects of future fires by  
44 increasing pyrodiversity: as fire moves across a region,  
45 the resulting landscape includes a fine-scale mosaic of  
46 burned and unburned patches, creating not only refugia  
47 for insects, but conditions that promote spatial heteroge-  
48 neity of resources and enhanced conditions for insect  
49 communities (Kim & Holt, 2012; Koltz et al., 2018;  
50 Ponisio et al., 2016). In longleaf pine ecosystems where  
51 regular application of prescribed fire is extensively used,  
52 juvenile and non-flying insects have been shown to climb  
53 into the canopy where microclimate conditions are more

favorable for their survival (Dell et al., 2017). Land man-  
agement 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 biodi-  
versity (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 anthropo-  
genic stresses that do not necessarily operate indepen-  
dently (Harvey, Heinen, Gols, & Thakur, 2020; Wagner  
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 can and 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 pesti-  
cides 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 trans-  
formative 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 prod-  
uct growth to ecological economics with a circular econ-  
omy; and stabilize the human population.

It must be stressed that halting upward trends in ris-  
ing carbon dioxide concentrations and global surface  
temperatures will take decades, if not more, and there-  
fore 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, is a promising start. Agreements such as these  
should, however, have clearly delineated goals within a

1 strict time-frame, and should strive for immediate imple- 54  
2 mentation and a much higher degree of accountability. 55  
3 The current division between land set aside for nature 56  
4 reserves and land assigned to agricultural production or 57  
5 urban development, is far from balanced, and this 58  
6 urgently needs to be addressed by regional governing 59  
7 bodies. Existing natural areas need to be strictly pre- 60  
8 served; our planet can no longer afford to lose more pris- 61  
9 tine habitat. We need to rethink and revise agriculture, 62  
10 with a strong emphasis on ecological intensification of 63  
11 production systems. We can ecologically improve agricul- 64  
12 tural lands, through optimization of the ecological 65  
13 matrix, and the creation of networks by interspersing cor- 66  
14 ridors and stepping stones of habitat within the agricul- 67  
15 tural landscape. This will not only benefit insect species 68  
16 diversity via the provisioning of habitat, but also might 69  
17 serve a crucial role in mitigation of negative effects of cli- 70  
18 matic change and extremes on insects through the crea- 71  
19 tion of climate refugia. Industrial agriculture in its 72  
20 current form is not sustainable for the preservation of 73  
21 biodiversity. Unguided pesticide application and over-use 74  
22 of industrial fertilizers have many non-target side effects 75  
23 and pollute our ecosystems (Bernhardt et al., 2017); 76  
24 whenever possible, their use should be avoided and 77  
25 replaced with environmentally sound alternatives. More 78  
26 strategic and targeted approaches need to be adopted to 79  
27 ensure the productivity of the agricultural system, while 80  
28 minimizing the detrimental effects of excess fertilizer and 81  
29 pesticide inputs on (insect) biodiversity. Ecological inten- 82  
30 sification of the agricultural landscape has been unequiv- 83  
31 ocaly shown to benefit both agricultural yield and 84  
32 diversity (Gurr et al., 2016). The concept of ecological 85  
33 intensification should be further extended and incorpo- 86  
34 rated into our landscape and city planning. Road verges, 87  
35 public green spaces, and local gardens can form impor- 88  
36 tant habitats and *refugia*, which will benefit insects and 89  
37 related animals, especially under climate change and cli- 90  
38 matic extremes.

39 Specific levels of action to directly protect insects can 91  
40 range from global political interventions to that of indi- 92  
41 vidual choices and behavior. Although the conservation 93  
42 of biodiversity is a systemic challenge, every person can 94  
43 play a role through their individual actions (see next 95  
44 section). Seen through the eye of an insect, even small 96  
45 individual actions can make a huge difference. In this 97  
46 context, it is necessary to invest in popularizing the role 98  
47 of insects in ecosystems. Interesting experiments like 99  
48 the use of charismatic species prove useful for public 100  
49 awareness. Children should also be taught in elementary 101  
50 classes the vitally important role that insects play 102  
51 in a healthy, functioning biosphere (Oberhauser & 103  
52 Guiney, 2009). Also, scientific progress alone is unlikely 104  
53 to result in desirable outcomes (Wyckhuys et al., 2022) 105  
106

and needs to be paired with enabling policies, broad 54  
awareness-raising, and stakeholder education. The evi- 55  
dence is clear and the onus is on governing bodies to act 56  
now. With species and habitats being lost every day, a 57  
refusal or delay to act is not a wise choice. 58  
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## Individual choices and behavior: What can you do? 61 62

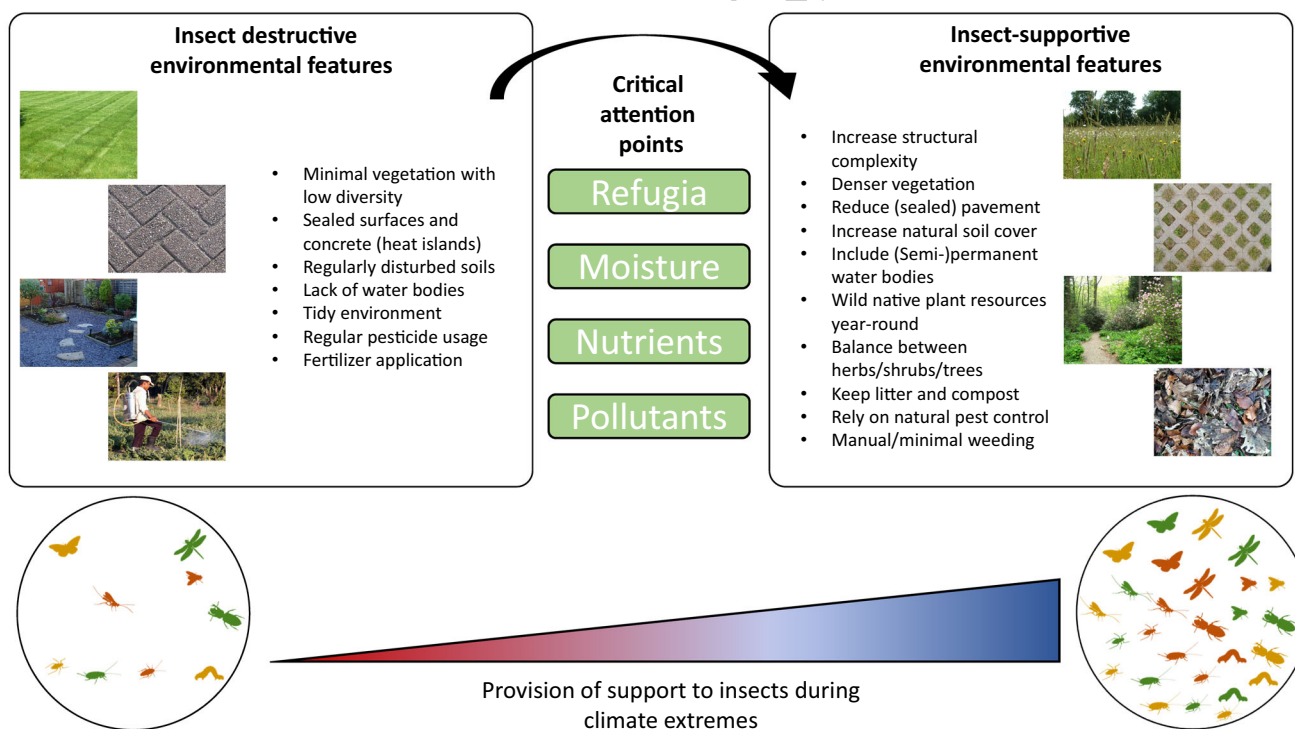
63  
64 Although the most impactful actions are those that should 65  
66 be implemented by governing institutions, decisions made 67  
68 at smaller scales by individuals can still make a large dif- 69  
70 ference for insect conservation (Cosquer et al., 2012; 71  
72 MacDonald et al., 2015). This is especially relevant in the 73  
74 context of climatic extremes. Most people live in cities, 75  
76 which because of a lack of primary resources and suitable 77  
78 habitats can be a hostile place for many organisms 79  
80 (Bugnot et al., 2019; Parris et al., 2018). Furthermore, cit- 81  
82 ies, which are dominated by concrete, tend to form strong 83  
84 heat islands, which can exacerbate the effects of climate 85  
86 extremes, especially those associated with rising tempera- 87  
88 tures (Ramamurthy & Bou-Zeid, 2017). The high propor- 89  
90 tions of sealed soil surface area may also increase the local 91  
92 impact of precipitation extremes. It has become evident 93  
94 that individuals can and are willing to play an important 95  
96 role in making cities more suited to insect life and other 97  
98 wildlife (MacDonald et al., 2015). Fortunately, the solu- 99  
100 tions are generally low-cost. A good place to start is in 101  
102 your garden or balcony, but even an appropriately 103  
104 designed windowsill can be relevant. Three ingredients are 105  
106 essential to insect survival in the face of climatic extremes; 107  
108 suitable microclimate refugia, access to a water source, 109  
110 nutrition, and absence of pesticides (Deguines et al., 2020). 111  
112 Many urban gardens are sealed-off and neatly organized. 113  
114 None of the insects' primary requirements for reproduc- 115  
116 tion and survival are met in most gardens. The solutions, 117  
118 however, are remarkably simple. Sealed areas in a garden, 119  
120 as well as traditionally well-maintained lawns should be 121  
122 reduced to a minimum. Exposed soil, and the plants that 123  
124 grow in it provide the most important microclimate needs, 125  
126 a source of moisture, and nutrients. The choice of what to 127  
128 grow and where also makes a difference. A highly diverse 129  
130 mixture of native plants provides the most heterogeneous 131  
132 habitat, and supports the highest diversity of interactions. 133  
134 Cultivated plant varieties should be avoided as, although 135  
136 they may appear highly attractive, they often provide little 137  
138 nutritional rewards for insects. Pollinators appear to prefer 139  
140 gardens made up primarily of native plants with a few 141  
142 exotics present (Salisbury et al., 2015) Many urban and 143  
144 suburban gardeners rely heavily on pesticides, paying little 145  
146 attention to the label, ignoring recommended application 147  
148 rates and possible collateral damage. Pesticide use should 149  
150

1 be avoided altogether. Sowing native wildflower mixtures,  
 2 even in pots, can play a role in fulfilling the basic needs of  
 3 local insect diversity. Mowing should be limited, prefera-  
 4 bly until after the flowering season and peak of insect  
 5 abundance. Leaving plant material, such as leaf litter,  
 6 standing senescing biomass, and a compost pile are other  
 7 potential microrefugia that can make a difference.  
 8 Insect-friendly gardening reduces individual carbon foot-  
 9 prints and increases the rewards in the form of floral  
 10 abundance, which is appreciated by insects and (most)  
 11 humans alike. An insect-friendly garden is a beautiful gar-  
 12 den, but a beautiful garden is not necessarily an  
 13 insect-friendly one. We all can make a difference for the  
 14 preservation of insect diversity, especially in cities, through  
 15 the choices we make (Figure 4).

in both temperate and tropical ecosystems. Whereas attrib- 54  
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18 **SUMMARY**

20 Over the past several decades, increasing evidence is show-  
 21 ing that many insect taxa are experiencing rapid declines



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

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 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.

### ACKNOWLEDGMENTS

We dedicate this paper to the memory of Edward O. Wilson and Tom Lovejoy, and to co-authors Matthew J. G. Gage and Simon Leather, who passed away during the process of its preparation.

### CONFLICT OF INTEREST

The authors declare no conflict of interest.

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**How to cite this article:** Harvey, Jeffrey A., Kévin Tougeron, Rieta Gols, Robin Heinen, Mariana Abarca, Paul K. Abram, Yves Basset, et al. 2022. "Scientists' Warning on Climate Change and Insects." *Ecological Monographs* e1553. <https://doi.org/10.1002/ecm.1553>