



Review

The direct and indirect effects of extreme climate events on insects

Alessandro Filazzola <sup>a,b,\*</sup>, Stephen F. Matter <sup>a,c</sup>, J. Scott MacIvor <sup>b</sup>

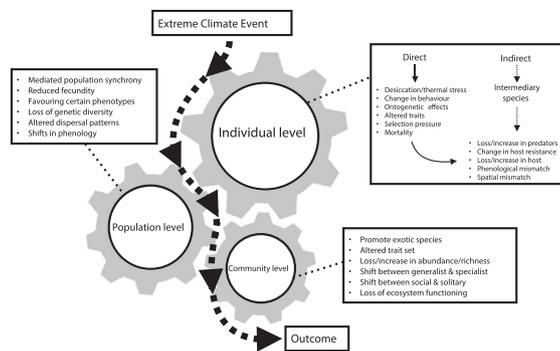
<sup>a</sup> Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada  
<sup>b</sup> Department of Biological Sciences, University of Toronto Scarborough, 1265 Military Trail, Canada  
<sup>c</sup> Department of Biological Sciences, University of Cincinnati, Cincinnati, OH 45221, United States of America



HIGHLIGHTS

- Extreme climate events are becoming more common, threatening insect biodiversity.
- Climate extremes can both directly and indirectly impact insect species.
- The effects of climate extremes can be large, but our understanding remains limited.
- Further research is needed to better predict responses with climate change.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:  
 Received 9 November 2020  
 Received in revised form 8 January 2021  
 Accepted 9 January 2021  
 Available online 15 January 2021

Editor: Jay Gan

Keywords:  
 Extreme climate event  
 Climate change  
 Entomology  
 Physiology  
 Review  
 Biodiversity

ABSTRACT

Extreme climate events are predicted to increase in the future, which will have significant effects on insect biodiversity. Research into this area has been rapidly expanding, but knowledge gaps still exist. We conducted a review of the literature to provide a synthesis of extreme climate events on insects and identify future areas of research. In our review, we asked the following questions: 1) What are the direct and indirect mechanisms that extreme climate events affect individual insects? 2) What are the effects of extreme climate events on insect populations and demography? 3) What are the implications of the extreme climate events effects on insect communities? Drought was among the most frequently described type of extreme climate event affecting insects, as well as the effects of temperature extremes and extreme temperature variation. Our review explores the factors that determine the sensitivity or resilience to climate extremes for individuals, populations, and communities. We also identify areas of future research to better understand the role of extreme climate events on insects including effects on non-trophic interactions, alteration of population dynamics, and mediation of the functional trait set of communities. Many insect species are under threat from global change and extreme climate events are a contributing factor. Biologists and policy makers should consider the role of extreme events in their work to mitigate the loss of biodiversity and delivery of ecosystem services by insects.

© 2021 Elsevier B.V. All rights reserved.

Contents

1. Introduction . . . . .	2
2. Direct effects of extreme climate events . . . . .	2
3. Indirect effects of extreme climate events . . . . .	4

\* Corresponding author at: Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada.  
 E-mail address: [alex.filazzola@utoronto.ca](mailto:alex.filazzola@utoronto.ca) (A. Filazzola).

4. Extreme climate event effects on demography and population dynamics . . . . .	4
5. Effects of extreme climate events on patterns of insect biodiversity . . . . .	5
6. Synthesis and implications . . . . .	5
Declaration of competing interest. . . . .	6
Acknowledgments . . . . .	6
References . . . . .	6

## 1. Introduction

Understanding the effects of extreme climate events is one of the biggest challenges for conservation in an era of global change. An extreme climate event is defined as a period where climate conditions surpass a threshold value from those previously observed (e.g., the 90th percentile, a once-in-a-century event) that can elicit an extreme ecological response (Smith, 2011). Climate variability has increased in recent decades and is predicted to increase further, resulting in extreme events becoming greater in duration, magnitude, and frequency (IPCC, 2014; Seneviratne et al., 2014). Extreme climate events can significantly affect ecosystem functions and services to human well-being (Du et al., 2018; Sheldon and Dillon, 2016; Zhang et al., 2013). For instance, increased duration of extreme heat days results in a decline in bumble bee diversity (Soroye et al., 2020), which are important pollinators for agriculture and natural systems (Garratt et al., 2014; Saunders, 2018). A recent meta-analysis examining extreme weather events on wildlife determined that while many species demonstrate compensatory mechanisms to mitigate negative effects, resilience was uncommon and many populations failed to recover (Neilson et al., 2020). Climate variables can create synergistic effects, having larger ecological impact than the additive effect of each variable independently (Crain et al., 2008; Roland and Matter, 2016), thereby creating “ecological surprises” where population declines are extreme (Christensen et al., 2006). Although ecological responses to extreme climate events are often negative (e.g., population declines), such effects can be small (Maxwell et al., 2019) or multiple climate variables may be antagonistic, resulting in a positive ecological response (Jackson et al., 2016). Therefore, predicting ecological responses to an extreme climate event requires understanding of the mechanisms that drive these processes.

Extreme climate events occur when one or more climate variables exceed the historic range of values in that region. We defined a climate variable as any measure of temperature or precipitation, such as maximum monthly temperature, mean annual air temperature, or total winter snowfall. Extreme weather differs from extreme climate events by occurring within significantly shorter time periods (i.e., 1–2 days). We therefore follow the IPCC categorization of extreme climate events as abnormal departures in temperature or precipitation (e.g. 1st, 5th, or 10th percentile), but not phenomena related to extreme climate (e.g. tropical cyclones, monsoons) or impacts on the physical environment, such as floods or wildfires (Field et al., 2012). An example of an extreme climate event occurred during Spring 2012 in North America when abnormally warm temperatures promoted some of the earliest plant flowering on record (Ault et al., 2013; Ellwood et al., 2013). Our review is not intended to be comprehensive of all possible climate extremes and instead will focus on some notable examples of extremes in temperature, temperature variability, and drought that are projected to increase in the future.

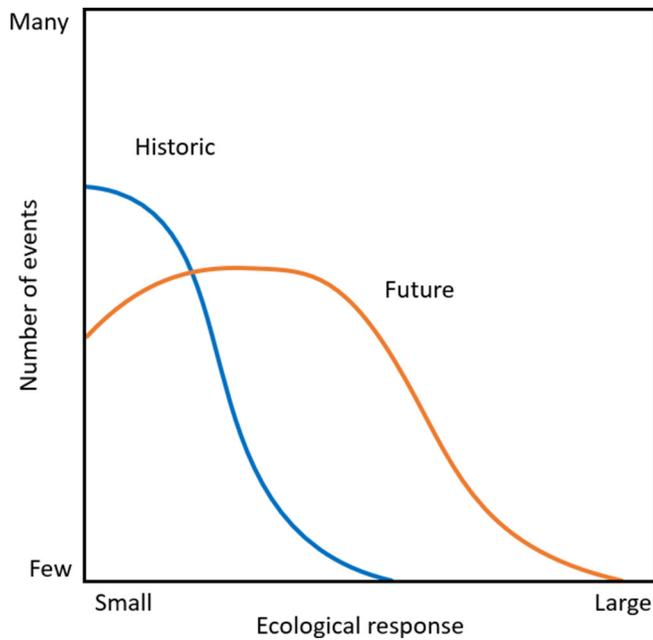
Extreme climate events can threaten insect biodiversity. Widespread declines in insects across the globe (Cardoso and Leather, 2019; Wagner, 2020) are in part caused by climate change (Maes et al., 2010; Potts et al., 2010; Sánchez-Bayo and Wyckhuys, 2019; Wilson and Maclean, 2011). Insects respond to changes in mean climate (Bale et al., 2002; Forrester, 2016; Robinet and Roques, 2010), but only more recently has research focused on the impacts of extreme climate events on insects (Forister et al., 2018; e.g., Rocha et al., 2017; Soroye

et al., 2020). Relative to other taxa, insects are expected to be more sensitive to climate change because insects are ectothermic, typically have shorter dispersal ranges and lifespans (Bale et al., 2002), have developmental timing dependent on climate-related cues (Bale and Hayward, 2010; Tobin et al., 2008), and have specialized interactions (e.g., plant-pollinator, plant-herbivore, host-parasite) with other taxa (De Palma et al., 2017; McDermott Long et al., 2017). For instance, climate variation could have indirect effects that reduce insect populations through food resources (Filazzola et al., 2020; Ogilvie et al., 2017). However, many insects are *r*-selected species with short generation times that can reproduce rapidly and thus recover quickly at the population level following an extreme event (Baudino et al., 2019; Ilg et al., 2008). Insects also have a close relationship with climate, which has been captured in studies estimating changes in distribution from recent climate change (Kerr et al., 2015; Lewthwaite et al., 2018). Consequently, insects are model indicator taxa for extreme ecological responses to climate (Kharouba et al., 2019). There is a need to synthesize the effects of extreme climate events on insects to improve our ability to predict ecological responses of climate change.

The effects of extreme climate events on insects are complex. Climate change is expected to increase the severity and frequency of extreme ecological responses by insect communities in the future relative to historic patterns (Fig. 1). The response of insect communities to these events is highly species-specific, whereby some are more resilient or sensitive to climate extremes. The effects on individuals within a species are likely to scale up to the population and community levels (Fig. 2). Predicting the response of extreme climate events on insects requires understanding the effects associated with each level of ecological organization (Fig. 2). Herein, we synthesize recent studies that have explored the impacts of extreme climate events on insect communities and answer the following questions: 1) What are the direct and indirect mechanisms through which extreme climate events affect individual insects? 2) What are the effects of extreme climate events on insect populations and demography? 3) What are the implications of the extreme climate events on insect communities?

## 2. Direct effects of extreme climate events

Extremes in the maximum daily temperature can directly impact insects, including causing mortality (Fig. 2). In the last few decades, there has been an increase in hot temperature extremes and heat waves (Meehl and Tebaldi, 2004; Seneviratne et al., 2014). Globally, insects have a thermal maximum that is relatively consistent among all species and if exceeded will cause mortality from a loss of motor control (Addo-Bediako et al., 2000; Sunday et al., 2011). Insects present in hot ecosystems (e.g., tropics, deserts) are thus predicted to be the most impacted by extreme heat events in the future (Deutsch et al., 2008; Diamond et al., 2012). Recent studies indicate that hot extremes can also negatively affect temperate species such as bumble bees (Oyen et al., 2016; Soroye et al., 2020) and processionary moths (Rocha et al., 2017). Even relatively short periods of extreme heat (2 days) have been identified to reduce insect fecundity and survival (Zhu et al., 2019). In addition to exceeding thermal maxima, extreme heat induces significant stress and negatively affect insect behaviour and development (Hamblin et al., 2017; McCauley et al., 2018). In a dragonfly species (*Erythemis collocata*), heat stress caused non-lethal effects, such as



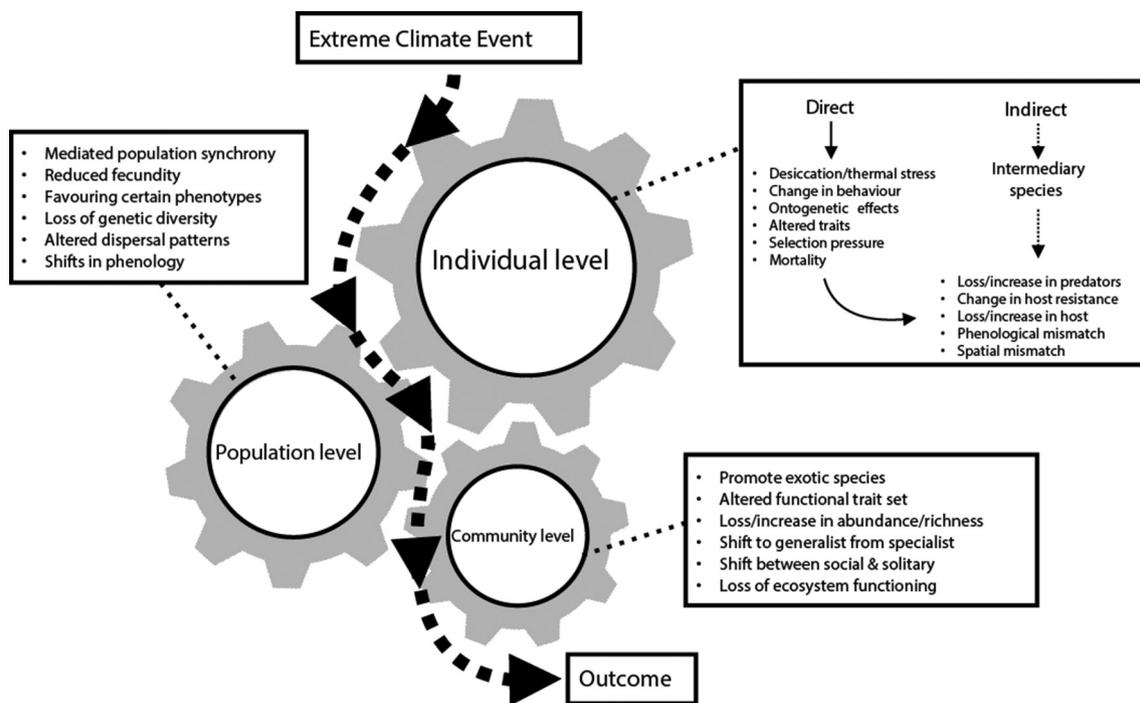
**Fig. 1.** A density distribution of the severity of ecological responses to extreme climate events. With climate change, both the frequency (area under the curve) and severity (width of curve) are expected to increase.

triggering emerging individuals to have smaller wings which affected flight performance and dispersal capacity (McCauley et al., 2018). Smaller wings is a phenotypic response that allows for better thermal regulation but at a cost to flight ability (McCauley et al., 2018). In a migratory locust (*Locusta migratoria*), heat stress disrupted ion balance that did not recover once temperatures returned to normal, causing impaired movement for affected individuals (O’Sullivan et al., 2017). A review by Abram et al. (2017) describes many behavioural responses of insects to temperature extremes including effects on foraging,

reproduction, and communication. Aquatic insects may be buffered against short-term exposures to hot air temperatures, because their thermal maxima can often be much greater than any change in water temperature (Hotaling et al., 2020). However, there can be indirect effects from heat waves other than temperature-induced mortality, such as increasing vulnerability to hypoxia for Ephemeroptera (Winter et al., 1996). Warming past a certain temperature maximum for even brief time periods can cause both lethal and non-lethal effects.

Extreme temperature variability can be equally as impactful as exceed a thermal maximum. Gradual warming provides an opportunity for insect species with high plasticity to respond, including changes in the number of instars, altering development timing, or triggering a diapause (Pavan et al., 2013; Sgrò et al., 2016). However, extreme temperature variability can be sufficiently abrupt to surpass thresholds that prevent a response. A “false spring” is an example of extreme temperature variability that occurs when an abnormally warm period triggers early spring onset in an ecosystem, that is followed by a frost event (Augsburger, 2013; Chamberlain et al., 2019). False springs can cause mortality in annual plants and damage to trees (Ault et al., 2013; Inouye, 2008), which are important resources for over-wintering insects at emergence. Although examined in plants, the direct effects of false spring on insects is largely unexplored but gaining attention (Forrest, 2016; Kharouba et al., 2014, 2018; Kudo and Ida, 2013; Rafferty et al., 2015). Similarly, extreme climate variability in autumn can have negative effects on insects. Bumble bee queens are relatively tolerant of brief cold temperatures that approach their super cooling point, but will die without entering winter diapause (Owen et al., 2013). Abnormally warm autumn temperatures can influence the decision to delay diapause and thus leave populations susceptible to mortality via a cold-temperature spike (Bale and Hayward, 2010). Research on extreme climate events is expanding, but there are still significant knowledge gaps with respect to temperature variability.

One of the more commonly explored types of extreme climate events in ecology is droughts (Forister et al., 2018; e.g., Jentsch et al., 2011; Marques et al., 2014). Drought can directly impact aquatic insects, or insects with aquatic life-stages through increased risk of desiccation.



**Fig. 2.** A conceptual framework for the effect of extreme climate events on the different ecological organizations of insects. The gears within this framework highlights the interactive nature of extreme climate events on all three ecological levels and scaling of effects from individual to community level. The text boxes each represent areas of future research, especially the role of extreme climate events in driving non-trophic interactions, mediating demographics, and altering the functional trait sets of communities.

In desert streams, drought-driven loss of perennial water flow causes a significant change in the species composition of aquatic invertebrates favoring mesopredators over top predators that failed to recover with the return of typical precipitation levels (Bogan and Lytle, 2011). In terrestrial systems, there is also accumulating evidence that extreme drought can directly affect insects, such as increased desiccation risk for butterfly pupae (McDermott Long et al., 2017) and collembolans (Elnitsky et al., 2008). Water availability can interact with temperature extremes to impact insect species more than either variable on its own. In two African butterfly species (*Busseola fusca* and *Bicyclus anynana*), the inclusion of desiccation stress when modelling temperature extremes altered the potential suitable habitat range by more than 60% (Barton et al., 2019). Although drought effects have received significant attention in the ecological literature, a knowledge gap persists for extreme drought effects, specifically direct effects of drought on the insects themselves.

### 3. Indirect effects of extreme climate events

The resilience or sensitivity of insects to extreme climate events can be determined by interactions among species because these events can disrupt trophic structure (De Palma et al., 2017). Trophic interactions can be disrupted by climate change because of a potential mismatch in species range (Filazzola et al., 2020; Hickling et al., 2006) or in phenology (Gordo and Sanz, 2006; Singer and Parmesan, 2010). A mismatch in the co-occurrence between species can threaten interactions including plant-herbivore, plant-pollinator, or host-parasite. For instance, drought can impact insect pollinators via floral resources (Phillips et al., 2018) or floral volatiles (Burkle and Runyon, 2016; Gallagher and Campbell, 2017). Burkle and Runyon (2016) showed declines in visitation by bees, flies, and butterflies to four plant species because of extreme drought leading to reduced number of flowers, their display size, and the amount of floral volatiles. Extreme drought can also compromise the ability of plants to resist herbivory and acts as a driver in forests promoting both native and exotic phytophagous insect species (Flower et al., 2014; Gaylord et al., 2013; Stephenson et al., 2019). During the 2003 extreme drought in Western Europe, there was a significant increase in wood-boring insects because of low host-plant resistance, but a decline in defoliating species because of low nitrogen content in leaves (Rouault et al., 2006). Consequently, extreme drought can favour pest species that cause widespread tree mortality (e.g., *Agilus planipennis* – Showalter et al., 2018), but negatively impact other species from the reduced quality of food resource (Rouault et al., 2006). Extremes in climate can disrupt or facilitate trophic interactions resulting in a need to measure changes in interactions as well as the direct effects on species (Seibold et al., 2018).

Extreme climate events can also impact non-trophic interactions in communities (Filazzola et al., 2018) and is a relatively unexplored area of research for insects. Climate change is expected to alter competition dynamics among species that indirectly affect insect populations (Bale et al., 2002; Schweiger et al., 2010). For instance, exotic species can receive a competitive advantage over natives with climate (Schweiger et al., 2010). Such studies are rarely put in the context of extreme climate events (Branson, 2014; but see Staley et al., 2007). Clearly, there is a need to further explore the effects of extreme climate events while considering the complex relationships occurring in ecological communities.

### 4. Extreme climate event effects on demography and population dynamics

Extreme climate events have emergent impacts on insects at the population level (Fig. 2). Most notable are effects on population growth (Roland and Matter, 2016) caused by direct effects on survival, reproduction, fecundity, development, or dispersal (Chen et al., 2019; Kuussaari et al., 2016; Piessens et al., 2009; Salgado et al., 2020).

However, the mechanism by which extreme climate events ultimately affect population growth is complex (Boggs and Inouye, 2012). For instance, for the mosquito, *Aedes aegypti*, Chaves et al. (2014) showed that in autocorrelated environments a heat wave will decrease larval survival and induce over-compensatory fecundity leading to population outbreaks. Outbreaks of this type can have serious implications for human health because *A. aegypti* is a vector for dengue, Yellow Fever, and other diseases (Chaves et al., 2014). Not surprisingly, for species with overlapping generations, the same event can have very different effects for different stages.

Extreme climate events can produce a Moran effect (Moran, 1953) where the dynamics of populations having a similar density-dependent structure are synchronized by a strong density-independent event. Synchronized population dynamics are especially important in spatial population networks because they reduce the persistence of the species (Heino et al., 1997). The synchronizing effects of extreme climate events have been demonstrated empirically in butterfly meta-populations for *Parnassius smintheus* and *Melitaea cinxia* (Kahilainen et al., 2018; Matter and Roland, 2010).

For insects, events that extend the normal phenology can set an “ecological trap” resulting in low population growth across the overwintering period. Negative impacts happen when some or all insects attempt an additional, unsuccessful generation (Van Dyck et al., 2015). This extra-voltinism can occur when insects emerge early, develop more quickly, or continue to develop past their normal diapause stage (Forrest et al., 2019). Both additional generations and early emerging insects may be particularly susceptible to “extreme events” that are not necessarily climatically extreme but are simply outside of the conditions that the insect normally experiences.

Extreme climate events impact insect population genetics (Dillon and Lozier, 2019). The events themselves can exert strong selection, potentially favoring certain phenotypes (Grant et al., 2017; Sgrò et al., 2016). Population crashes resulting from extreme events result in a loss of genetic diversity (Jangjoo et al., 2016; Shama et al., 2011) and an increase in inbreeding, both of which increase the risk of local population extinction (Saccheri et al., 1998). In spatial population networks, crashes induced by extreme climate events can alter genetic structure, but how the effects are manifest depends on the relative effects of gene flow (dispersal) and genetic drift. In a metapopulation of the caddisfly, *Allogamus uncatus* in the Swiss Alps, the European heat wave of 2003 caused population crashes and local extinctions. Following the event there was a loss of genetic diversity within populations and an increase in differentiation among drainage habitats that presumably have limited dispersal (Shama et al., 2011). Similarly, population crashes due to extreme overwintering conditions in a spatial population network of the butterfly *Parnassius smintheus* (Roland and Matter, 2016) resulted in losses of genetic diversity (Jangjoo et al., 2020). In this system, strong patterns of genetic isolation by distance were eliminated by genetic drift associated with the crashes, but quickly re-established due to dispersal (gene flow) among subpopulations in subsequent generations (Jangjoo et al., 2020).

Extremes in climate in close successive association can negatively impact populations. Extremes are inherently defined as departures from average, but with climate change, variables (e.g., temperature, precipitation) are non-stationary resulting in extremes being constantly redefined. Overtime, a gradual warming in temperature can promote adaptation within an insect population (Bale et al., 2002; Forrest, 2016; Robinet and Roques, 2010), where a return to previously “normal” cold period could be an extreme event. Smaller populations would be particularly susceptible because they lack the genetic variability to respond to extremes in climate (Frankham, 2012; Hanski et al., 2017; e.g. Hatcher et al., 2004). Although, as observed in *Drosophila melanogaster*, extremes in temperature can sometimes result in a slower than expected loss of genetic diversity with decreasing population size (Schou et al., 2017). Depending on the timing, an extreme may not be a departure from a long-term average, but rather the

difference from a recent value (e.g., within a year) in the opposite direction. For example, species that experience acclimation to cold temperatures are typically sensitive to heat thereafter (van Dooremalen et al., 2013). Populations that are resilient to mean changes in climate could still be susceptible to extreme climate events, especially those that occur in opposite directions.

### 5. Effects of extreme climate events on patterns of insect biodiversity

Extreme climate events drive changes in insect taxonomic, functional and phylogenetic diversity, as well as turnover in community patterns that resolve distinct species compositions (Fig. 2). Despite many studies of extreme climate events on single species, or single interactions, there are fewer on impacts at the community level.

Insects are not equally affected by extremes in climate. Given the temporal nature of extreme climate events, species active at different times (e.g., spring-active vs. summer-active) within communities will be affected differently, with consequences for diversity and ecosystem functioning (e.g. phenological mismatch between bees and flowers, Kudo and Ida, 2013). Unusually dry springs reduce early-blooming flower densities that provide essential forage for bumble bee queens. This in turn, increases colony failure and decreases the number of workers in summer, thereby reducing the abundance and (to a lesser extent) diversity of bees in the local environment (Thomson, 2016). What flowers remain after an extreme climate event also impacts queen nesting success as homogenous pollen diets (with some exceptions) lead to smaller colonies containing smaller workers, and thus higher rates of nest failure (Watrous et al., 2019). Social insects may therefore be more susceptible to extreme climate events early in the season when colonies are getting established. By contrast, non-social insects may be largely unaffected by an early extreme climate event because it provides a longer period for recovery. Comparing the response of tropical and temperate flies, each were observed to be tolerant of heat extremes, but only the temperate species could tolerate cold extremes (Chen et al., 1990). Insects globally share a similar thermal maximum, suggesting tropical species are no better adapted to extreme heat than temperate species (Addo-Bediako et al., 2000; Sunday et al., 2011). Conversely, temperate species are threatened by both extremes in temperature and temperature variability. For instance, in temperate climates, univoltine reproduction is the most common (Wallace and Anderson, 1996) and this single generation would be susceptible to extreme temperature variability such as a false spring or abnormal freeze-thaw events. Multivoltine species that experience an extreme climate event would have an opportunity for the population to recover within the same year through multiple instances of reproduction (Chase and Knight, 2003; Gerisch et al., 2012). The evolutionary history of a species will therefore play a significant role in determining the response or vulnerability to an extreme climate event.

Insect species within a community may respond differently to extreme climate events because of variation in functional traits that facilitate survival, despite acute changes in their environment. These traits are often phylogenetically constrained and so shifts in patterns in taxonomic, functional, and phylogenetic diversity are possible and drive spatially distinct communities. Schowalter et al. (1999) manipulated drought conditions on desert shrubs in New Mexico, demonstrating no significant difference in insect species richness (>40 taxa identified) between drought-stressed or control bushes, despite significant species turnover resulting in distinct communities. This result was driven by drought-stressed plants that produced significantly more flowers, whereas irrigated shrubs produced more biomass, each condition supporting different suites of insect taxa. Similarly, drought along a spatial gradient promoted the abundance of xeric butterfly species over mesic species with little change to the overall number of individuals (Debinski et al., 2013). Distinct communities may result from extreme climate events with little effect on taxonomic diversity. Prolonged stressors, however, will ultimately lead to declines or extinction of

maladapted taxa. Lastly, community turnover resulting from extreme climate events, may also manifest along an environmental gradient, where effects are exacerbated at one end. Extreme climate events such as drought may be buffered in cities due to supplemental irrigation that alter patterns in insect communities from outside the city inwards (e.g. greater beetle and ant diversity in urban vs non-urban; Bang and Faeth, 2011).

Some insect communities can resist extreme climate events through idiosyncratic responses among species to alternating extremes (e.g. drought-resilient vs. drought-sensitive species) (Burkle and Runyon, 2016; Stephenson et al., 2019). Extreme drought can, however, exceed the tolerance of the insect community if it persists substantially beyond historic patterns. For example, the 2014 drought in California was the most severe in over 100 years (Robeson, 2015) and significantly lowered butterfly diversity at high elevation sites because of a shorter flight window (Forister et al., 2018). In another example, Lindberg et al. (2002) showed that in soil micro-invertebrate communities facing drought conditions, collembolan abundance and diversity declined, and drought was more important in structuring insect communities than was irrigation. Persistent species will have functional traits that, for example, help resist drought. Since functional traits are often phylogenetically conserved, extreme climate events should drive declines in functional and phylogenetic diversity, especially when these events are persistent but variable in frequency and alter insect reproductive fitness (Colinet et al., 2015).

### 6. Synthesis and implications

We present a conceptual figure that summarizes the effects of extreme climate events on insects across the different organizational units in ecology (Fig. 2). In this figure, we highlight the significant and complex effects of extreme climate events on ecosystems. These are key areas where research is limited, especially on mediation of population synchrony, ontogenetic effects, and the promotion of exotic species. Correlations among population sizes of a species have been proposed to follow correlations with local climate conditions, i.e., the Moran effect (Moran, 1953), but recent work suggests this approach is overly reductionist and that there is a need for better understanding of climate change effects on dispersal and species interactions (Hansen et al., 2020). Similarly, the effects of extreme climate events on ontogeny is another topic to explore further. Within our review, we highlighted notable examples of climate driven changes to insect development, such as warmer temperatures reducing the number of caterpillar instars (Pavan et al., 2013) or the wing size of dragonflies (McCauley et al., 2018). However, these are rarely tested through the lens of extreme climate events that could increase deleterious effects. Lastly, extreme climate events are expected to promote exotic species by increasing the susceptibility of a community to invasion (Diez et al., 2012; Jiménez et al., 2011). While these effects have been rarely examined in insects, the potential impacts could be significant, such as drought facilitating pest species like the Emerald Ash Borer (*Agilus planipennis* – Showalter et al., 2018).

The sensitivity or resilience of a species is dependent on factors such as physiological characteristics, interactions between species, and life-history strategies. Some traits of insect species could provide resilience to multiple forms of extreme climate events, such as desiccation (i.e., drought) and cold tolerance (e.g., extreme cold events) because they have the same physiological mechanisms. At the population level, density-dependent feedbacks could rapidly recover a population following an extreme event if other characteristics of the habitat, such as food resources, remain abundant (Neilson et al., 2020). However, there is no “one-size fits all” set of traits that allows a species to be immune to all events. There are many different forms of extreme climate events, despite our focus on temperature extremes, temperature variability, and drought. A central component to a species’ ability to resist an extreme climate event is plasticity and tolerance to variability.

Additionally, certain life-stages that are more vulnerable to climate extremes because they lack the capacity for a plastic response, such as reducing reproductive output or extending winter diapause. Genetic variation is thus a key component of resilience at the population level. For instance, populations with genetic polymorphisms of phosphoglucose isomerase (PGI), have been identified to have greater thermal adaptation and resilience to climate extremes for the butterfly *Lycaena tityrus* (Karl et al., 2008) and the beetle *Chrysomela aeneicollis* (Dahlhoff and Rank, 2000). At the community level, assemblages that are more diverse are likely to be more resilient to extreme climate events because different species can capitalize on opposite ends of the gradient. Connecting the effects of extreme climate events across these levels of ecological organization will allow for more accurate predictions for insect communities.

Extreme climate events are expected to increase in the future and insects are expected to be strongly affected. Research in experimental biology has made excellent progress identifying limits in insect physiology, but these are often restricted to laboratory, greenhouse, and mesocosm studies that ignore the complexity of ecological communities. Measuring the response of insect communities to extreme climate events in the field are often restricted to opportunistic studies because by inherently these events are rare (although increasing). Further research is needed, and we identified potential research gaps understanding the role of extreme climate events in driving non-trophic interactions, mediating demographics, and altering the trait sets of communities. Additionally, knowledge of insect biodiversity is relatively crude, and baselines might not exist to compare responses to extreme climate events in many environments. Long-term population monitoring would be an effective tool to assist in quantifying the response of insect biodiversity to extreme climate events. Better understanding of extreme climate events on insect communities can allow proper management to maintain the delivery of ecosystem services and support global biodiversity.

### Declaration of competing interest

There are no conflicts of interest to declare with this study.

### Acknowledgments

We thank Dr. Jens Roland for comments on an earlier draft that helped improve the manuscript. This research was funded by a Killam Post-Doctoral Fellowships and an NSERC Post-Doctoral Fellowship awarded to AF.

### References

- Abram, P.K., Boivin, G., Moiroux, J., Brodeur, J., 2017. Behavioural effects of temperature on ectothermic animals: unifying thermal physiology and behavioural plasticity. *Biol. Rev.* 92, 1859–1876. <https://doi.org/10.1111/brv.12312>.
- Addo-Bediako, A., Chown, S.L., Gaston, K.J., 2000. Thermal tolerance, climatic variability and latitude. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 267, 739–745. <https://doi.org/10.1098/rspb.2000.1065>.
- Augsburger, C.K., 2013. Reconstructing patterns of temperature, phenology, and frost damage over 124 years: spring damage risk is increasing. *Ecology* 94, 41–50. <https://doi.org/10.1890/12-0200.1>.
- Ault, T.R., Henebry, G.M., de Beurs, K.M., Schwartz, M.D., Betancourt, J.L., Moore, D., 2013. The false spring of 2012, earliest in North American record. *Eos, Trans. Am. Geophys. Union* 94, 181–182. <https://doi.org/10.1002/2013EO200001>.
- Bale, J.S., Hayward, S.A.L., 2010. Insect overwintering in a changing climate. *J. Exp. Biol.* 213, 980–994.
- Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E.G., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A.D., Whittaker, J.B., 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Glob. Chang. Biol.* 8, 1–16. <https://doi.org/10.1046/j.1365-2486.2002.00451.x>.
- Bang, C., Faeth, S.H., 2011. Variation in arthropod communities in response to urbanization: seven years of arthropod monitoring in a desert city. *Landsc. Urban Plan.* 103, 383–399. <https://doi.org/10.1016/j.landurbplan.2011.08.013>.
- Barton, M.G., Terblanche, J.S., Sinclair, B.J., 2019. Incorporating temperature and precipitation extremes into process-based models of African lepidoptera changes the predicted distribution under climate change. *Ecol. Model.* 394, 53–65. <https://doi.org/10.1016/j.ecolmodel.2018.12.017>.
- Baudino, F., Werenkraut, V., Ruggiero, A., 2019. Rapid recovery of the beetle richness–elevation relationship and its environmental correlates after a major volcanic event in northwestern Patagonia, Argentina. *Insect Conserv. Divers.* <https://doi.org/10.1111/icad.12395> n/a.
- Bogan, M.T., Lytle, D.A., 2011. Severe drought drives novel community trajectories in desert stream pools. *Freshw. Biol.* 56, 2070–2081. <https://doi.org/10.1111/j.1365-2427.2011.02638.x>.
- Boggs, C.L., Inouye, D.W., 2012. A single climate driver has direct and indirect effects on insect population dynamics. *Ecol. Lett.* <https://doi.org/10.1111/j.1461-0248.2012.01766.x>.
- Branson, D.H., 2014. Influence of a large late summer precipitation event on food limitation and grasshopper population dynamics in a northern Great Plains grassland. *Environ. Entomol.* 37, 686–695. [https://doi.org/10.1603/0046-225X\(2008\)37\[686:IOALLS\]2.0.CO;2](https://doi.org/10.1603/0046-225X(2008)37[686:IOALLS]2.0.CO;2).
- Burkle, L.A., Runyon, J.B., 2016. Drought and leaf herbivory influence floral volatiles and pollinator attraction. *Glob. Chang. Biol.* 22, 1644–1654. <https://doi.org/10.1111/gcb.13149>.
- Cardoso, P., Leather, S.R., 2019. Predicting a global insect apocalypse. *Insect Conserv. Divers.* 12, 263–267. <https://doi.org/10.1111/icad.12367>.
- Chamberlain, C.J., Cook, B.L., García de Cortázar-Atauri, I., Wolkovich, E.M., 2019. Rethinking false spring risk. *Glob. Chang. Biol.* 25, 2209–2220. <https://doi.org/10.1111/gcb.14642>.
- Chase, J.M., Knight, T.M., 2003. Drought-induced mosquito outbreaks in wetlands. *Ecol. Lett.* 6, 1017–1024. <https://doi.org/10.1046/j.1461-0248.2003.00533.x>.
- Chaves, L.F., Scott, T.W., Morrison, A.C., Takada, T., 2014. Hot temperatures can force delayed mosquito outbreaks via sequential changes in *Aedes aegypti* demographic parameters in autocorrelated environments. *Acta Trop.* 129, 15–24. <https://doi.org/10.1016/j.actatropica.2013.02.025>.
- Chen, C.-P., Lee, R.E., Denlinger, D.L., 1990. A comparison of the responses of tropical and temperate flies (Diptera: Sarcophagidae) to cold and heat stress. *J. Comp. Physiol. B.* 160, 543–547. <https://doi.org/10.1007/BF00258982>.
- Chen, C., Harvey, J.A., Biere, A., Gols, R., 2019. Rain downpours affect survival and development of insect herbivores: the specter of climate change? *Ecology* 100, e02819. <https://doi.org/10.1002/ecy.2819>.
- Christensen, M.R., Graham, M.D., Vinebrooke, R.D., Findlay, D.L., Paterson, M.J., Turner, M.A., 2006. Multiple anthropogenic stressors cause ecological surprises in boreal lakes. *Glob. Chang. Biol.* 12, 2316–2322. <https://doi.org/10.1111/j.1365-2486.2006.01257.x>.
- Colinet, H., Sinclair, B.J., Vernon, P., Renault, D., 2015. Insects in fluctuating thermal environments. *Annu. Rev. Entomol.* 60, 123–140. <https://doi.org/10.1146/annurev-ento-010814-021017>.
- Crain, C.M., Kroeker, K., Halpern, B.S., 2008. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecol. Lett.* 11, 1304–1315. <https://doi.org/10.1111/j.1461-0248.2008.01253.x>.
- Dahlhoff, E.P., Rank, N.E., 2000. Functional and physiological consequences of genetic variation at phosphoglucose isomerase: heat shock protein expression is related to enzyme genotype in a montane beetle. *Proc. Natl. Acad. Sci.* 97, 10056 LP–10061. <https://doi.org/10.1073/pnas.160277697>.
- De Palma, A., Dennis, R.L.H., Brereton, T., Leather, S.R., Oliver, T.H., 2017. Large reorganizations in butterfly communities during an extreme weather event. *Ecography (Cop.)* 40, 577–585. <https://doi.org/10.1111/ecog.02228>.
- Debinski, D.M., Caruthers, J.C., Cook, D., Crowley, J., Wickham, H., 2013. Gradient-based habitat affinities predict species vulnerability to drought. *Ecology* 94, 1036–1045.
- Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., Martin, P.R., 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl. Acad. Sci.* 105, 6668 LP–6672. <https://doi.org/10.1073/pnas.0709472105>.
- Diamond, S.E., Sorger, D.M., Hulcr, J., Pelini, S.L., Del Toro, I., Hirsch, C., Oberg, E., Dunn, R.R., 2012. Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants. *Glob. Chang. Biol.* 18, 448–456. <https://doi.org/10.1111/j.1365-2486.2011.02542.x>.
- Diez, J.M., D'Antonio, C.M., Dukes, J.S., Grosholz, E.D., Olden, J.D., Sorte, C.J., Blumenthal, D.M., Bradley, B.A., Early, R., Ibáñez, I., Jones, S.J., Lawler, J.J., Miller, L.P., 2012. Will extreme climatic events facilitate biological invasions? *Front. Ecol. Environ.* 10, 249–257. <https://doi.org/10.1890/110137>.
- Dillon, M.E., Lozier, J.D., 2019. Adaptation to the abiotic environment in insects: the influence of variability on ecophysiology and evolutionary genomics. *Curr. Opin. Insect Sci.* 36, 131–139. <https://doi.org/10.1016/j.cois.2019.09.003>.
- van Dooremalen, C., Berg, M.P., Ellers, J., 2013. Acclimation responses to temperature vary with vertical stratification: implications for vulnerability of soil-dwelling species to extreme temperature events. *Glob. Chang. Biol.* 19, 975–984. <https://doi.org/10.1111/gcb.12081>.
- Du, L., Mikle, N., Zou, Z., Huang, Y., Shi, Z., Jiang, L., McCarthy, H.R., Liang, J., Luo, Y., 2018. Global patterns of extreme drought-induced loss in land primary production: identifying ecological extremes from rain-use efficiency. *Sci. Total Environ.* 628–629, 611–620. <https://doi.org/10.1016/j.scitotenv.2018.02.114>.
- Ellwood, E.R., Temple, S.A., Primack, R.B., Bradley, N.L., Davis, C.C., 2013. Record-breaking early flowering in the eastern United States. *PLoS One* 8, e53788.
- Elnitsky, M.A., Benoit, J.B., Denlinger, D.L., Lee, R.E., 2008. Desiccation tolerance and drought acclimation in the Antarctic collembolan *Cryptopygus antarcticus*. *J. Insect Physiol.* 54, 1432–1439. <https://doi.org/10.1016/j.jinsphys.2008.08.004>.
- Field, C.B., Barros, V., Stocker, T.F., Dahe, Q., 2012. Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation: Special Report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

- Filazzola, A., Liczner, A.R.A.R., Westphal, M., Lortie, C.J., 2018. The effect of consumer pressure and abiotic stress on positive plant interactions are mediated by extreme climatic events. *New Phytol.* 217, 140–150. <https://doi.org/10.1111/nph.14778>.
- Filazzola, A., Matter, S.F., Roland, J., 2020. Inclusion of trophic interactions increases the vulnerability of an alpine butterfly species to climate change. *Glob. Chang. Biol.* 26, 2867–2877. <https://doi.org/10.1111/gcb.15068>.
- Flower, A., Gavin, D.G., Heyerdahl, E.K., Parsons, R.A., Cohn, G.M., 2014. Drought-triggered western spruce budworm outbreaks in the interior Pacific Northwest: a multi-century dendrochronological record. *For. Ecol. Manag.* 324, 16–27. <https://doi.org/10.1016/j.foreco.2014.03.042>.
- Forister, M.L., Fordyce, J.A., Nice, C.C., Thorne, J.H., Waetjen, D.P., Shapiro, A.M., 2018. Impacts of a millennium drought on butterfly faunal dynamics. *Clim. Chang. Resp.* 5, 3. <https://doi.org/10.1186/s40665-018-0039-x>.
- Forrest, J.R.K., 2016. Complex responses of insect phenology to climate change. *Curr. Opin. Insect Sci.* 17, 49–54. <https://doi.org/10.1016/j.cois.2016.07.002>.
- Forrest, J.R.K., Cross, R., CaraDonna, P.J., 2019. Two-year bee, or not two-year bee? How voltinism is affected by temperature and season length in a high-elevation solitary bee. *Am. Nat.* 193, 560–574. <https://doi.org/10.1086/701826>.
- Frankham, R., 2012. How closely does genetic diversity in finite populations conform to predictions of neutral theory? Large deficits in regions of low recombination. *Heredity (Edinb.)* 108, 167–178. <https://doi.org/10.1038/hdy.2011.66>.
- Gallagher, M.K., Campbell, D.R., 2017. Shifts in water availability mediate plant–pollinator interactions. *New Phytol.* 215, 792–802. <https://doi.org/10.1111/nph.14602>.
- Garratt, M.P.D., Coston, D.J., Truslove, C.L., Lappage, M.G., Polce, C., Dean, R., Biesmeijer, J.C., Potts, S.G., 2014. The identity of crop pollinators helps target conservation for improved ecosystem services. *Biol. Conserv.* 169, 128–135. <https://doi.org/10.1016/j.biocon.2013.11.001>.
- Gaylord, M.L., Kolb, T.E., Pockman, W.T., Plaut, J.A., Yezzer, E.A., Macalady, A.K., Pangle, R.E., McDowell, N.G., 2013. Drought predisposes piñon–juniper woodlands to insect attacks and mortality. *New Phytol.* 198, 567–578. <https://doi.org/10.1111/nph.12174>.
- Gerisch, M., Dziöck, F., Schanowski, A., Ilg, C., Henle, K., 2012. Community resilience following extreme disturbances: the response of ground beetles to a severe summer flood in a Central European lowland stream. *River Res. Appl.* 28, 81–92. <https://doi.org/10.1002/rra.1438>.
- Gordo, O., Sanz, J.J., 2006. Temporal trends in phenology of the honey bee *Apis mellifera* (L.) and the small white *Pieris rapae* (L.) in the Iberian Peninsula (1952–2004). *Ecol. Entomol.* 31, 261–268. <https://doi.org/10.1111/j.1365-2311.2006.00787.x>.
- Grant, P.R., Grant, B.R., Huey, R.B., Johnson, M.T.J., Knoll, A.H., Schmitt, J., 2017. Evolution caused by extreme events. *Philos. Trans. R. Soc. B Biol. Sci.* 372, 20160146. <https://doi.org/10.1098/rstb.2016.0146>.
- Hamblin, A.L., Youngsteadt, E., López-Urbe, M.M., Frank, S.D., 2017. Physiological thermal limits predict differential responses of bees to urban heat-island effects. *Biol. Lett.* 13, 20170125. <https://doi.org/10.1098/rsbl.2017.0125>.
- Hansen, B.B., Grøtan, V., Herfindal, I., Lee, A.M., 2020. The Moran effect revisited: spatial population synchrony under global warming. *Ecography (Cop.)* 43, 1591–1602. <https://doi.org/10.1111/ecog.04962>.
- Hanski, I., Schulz, T., Wong, S.C., Ahola, V., Ruokolainen, A., Ojanen, S.P., 2017. Ecological and genetic basis of metapopulation persistence of the Glanville fritillary butterfly in fragmented landscapes. *Nat. Commun.* 8, 14504. <https://doi.org/10.1038/ncomms14504>.
- Hatcher, P.E., Wilkinson, M.J., Albani, M.C., Hebbert, C.A., 2004. Conserving marginal populations of the food plant (*Impatiens noli-tangere*) of an endangered moth (*Eustroma reticulatum*) in a changing climate. *Biol. Conserv.* 116, 305–317. [https://doi.org/10.1016/S0006-3207\(03\)00200-3](https://doi.org/10.1016/S0006-3207(03)00200-3).
- Heino, M., Kaitala, V., Ranta, E., Lindström, J., 1997. Synchronous dynamics and rates of extinction in spatially structured populations. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 264, 481–486. <https://doi.org/10.1098/rspb.1997.0069>.
- Hickling, R., Roy, D.B., Hill, J.K., Fox, R., Thomas, C.D., 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Glob. Chang. Biol.* 12, 450–455. <https://doi.org/10.1111/j.1365-2486.2006.01116.x>.
- Hotaling, S., Shah, A.A., McGowan, K.L., Tronstad, L.M., Giersch, J.J., Finn, D.S., Woods, H.A., Dillon, M.E., Kelley, J.L., 2020. Mountain stoneflies may tolerate warming streams: evidence from organismal physiology and gene expression. *Glob. Chang. Biol.* 26, 5524–5538.
- Ilg, C., Dziöck, F., Foeckler, F., Follner, K., Gerisch, M., Glaeser, J., Rink, A., Schanowski, A., Scholz, M., Deichner, O., Henle, K., 2008. Long-term reactions of plants and macroinvertebrates to extreme floods in floodplain grasslands. *Ecology* 89, 2392–2398. <https://doi.org/10.1890/08-0528.1>.
- Inouye, D.W., 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89, 353–362. <https://doi.org/10.1890/06-2128.1>.
- IPCC, 2014. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva, Switzerland.
- Jackson, M.C., Loewen, C.J.G., Vinebrooke, R.D., Chimimba, C.T., 2016. Net effects of multiple stressors in freshwater ecosystems: a meta-analysis. *Glob. Chang. Biol.* 22, 180–189. <https://doi.org/10.1111/gcb.13028>.
- Jangjoo, M., Matter, S.F., Roland, J., Keyghobadi, N., 2016. Connectivity rescues genetic diversity after a demographic bottleneck in a butterfly population network. *Proc. Natl. Acad. Sci.* 113, 10914 LP–10919. <https://doi.org/10.1073/pnas.1600865113>.
- Jangjoo, M., Matter, S.F., Roland, J., Keyghobadi, N., 2020. Demographic fluctuations lead to rapid and cyclic shifts in genetic structure among populations of an alpine butterfly, *Parnassius smintheus*. *J. Evol. Biol.* 33, 668–681. <https://doi.org/10.1111/jeb.13603>.
- Jentsch, A., Kreyling, J., Elmer, M., Gellesch, E., Glaser, B., Grant, K., Hein, R., Lara, M., Mirzæ, H., Nadler, S.E., Nagy, L., Otieno, D., Pritsch, K., Rascher, U., Schädler, M., Schloter, M., Singh, B.K., Stadler, J., Walter, J., Wellstein, C., Wöllecke, J.,
- Beierkuhnlein, C., 2011. Climate extremes initiate ecosystem-regulating functions while maintaining productivity. *J. Ecol.* 99, 689–702. <https://doi.org/10.1111/j.1365-2745.2011.01817.x>.
- Jiménez, M.A., Jaksic, F.M., Armesto, J.J., Gaxiola, A., Meserve, P.L., Kelt, D.A., Gutiérrez, J.R., 2011. Extreme climatic events change the dynamics and invasibility of semi-arid annual plant communities. *Ecol. Lett.* 14, 1227–1235. <https://doi.org/10.1111/j.1461-0248.2011.01693.x>.
- Kahilainen, A., van Nouhuys, S., Schulz, T., Saastamoinen, M., 2018. Metapopulation dynamics in a changing climate: increasing spatial synchrony in weather conditions drives metapopulation synchrony of a butterfly inhabiting a fragmented landscape. *Glob. Chang. Biol.* 24, 4316–4329. <https://doi.org/10.1111/gcb.14280>.
- Karl, I., Schmitt, T., Fischer, K., 2008. Phosphoglucose isomerase genotype affects life-history traits and cold stress resistance in a copper butterfly. *Funct. Ecol.* 22, 887–894.
- Kerr, J.T., Pindar, A., Galpern, P., Packer, L., Potts, S.G., Roberts, S.M., Rasmont, P., Schweiger, O., Colla, S.R., Richardson, L.L., Wagner, D.L., Gall, L.F., Sikes, D.S., Pantoja, A., 2015. Climate change impacts on bumblebees converge across continents. *Science (80-. )* 349, 177–180. <https://doi.org/10.1126/science.1227031>.
- Kharouba, H., Vellend, M., Sarfraz, R.M., Myers, J.H., 2014. The effects of experimental warming on the timing of a plant–insect herbivore interaction. *J. Anim. Ecol.* 84, 785–796.
- Kharouba, H.M., Ehrhén, J., Gelman, A., Bolmgren, K., Allen, J.M., Travers, S.E., Wolkovich, E.M., 2018. Global shifts in the phenological synchrony of species interactions over recent decades. *Proc. Natl. Acad. Sci.* 115, 5211 LP–5216. <https://doi.org/10.1073/pnas.1714511115>.
- Kharouba, H.M., Lewthwaite, J.M.M., Guralnick, R., Kerr, J.T., Vellend, M., 2019. Using insect natural history collections to study global change impacts: challenges and opportunities. *Philos. Trans. R. Soc. B Biol. Sci.* 374, 20170405. <https://doi.org/10.1098/rstb.2017.0405>.
- Kudo, G., Ida, T.Y., 2013. Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology* 94, 2311–2320. <https://doi.org/10.1890/12-2003.1>.
- Kuussaari, M., Rytteri, S., Heikkinen, R.K., Heliölä, J., von Bagh, P., 2016. Weather explains high annual variation in butterfly dispersal. *Proc. R. Soc. B Biol. Sci.* 283, 20160413. <https://doi.org/10.1098/rspb.2016.0413>.
- Lewthwaite, J.M.M., Angert, A.L., Kembel, S.W., Goring, S.J., Davies, T.J., Mooers, A.Ø., Sperling, F.A.H., Vamosi, S.M., Vamosi, J.C., Kerr, J.T., 2018. Canadian butterfly climate debt is significant and correlated with range size. *Ecography (Cop.)* 41, 2005–2015. <https://doi.org/10.1111/ecog.03534>.
- Lindberg, N., Engtsson, J.B., Persson, T., 2002. Effects of experimental irrigation and drought on the composition and diversity of soil fauna in a coniferous stand. *J. Appl. Ecol.* 924–936.
- Maes, D., Titeux, N., Hortal, J., Anselin, A., Declere, K., De Knijf, G., Fichet, V., Luoto, M., 2010. Predicted insect diversity declines under climate change in an already impoverished region. *J. Insect Conserv.* 14, 485–498. <https://doi.org/10.1007/s10841-010-9277-3>.
- Marques, S., Primo, A., Martinho, F., Azeiteiro, U., 2014. Shifts in estuarine zooplankton variability following extreme climate events: a comparison between drought and regular years. *Mar. Ecol. Prog. Ser.* 499, 65–76.
- Matter, S.F., Roland, J., 2010. Effects of experimental population extinction for the spatial population dynamics of the butterfly *Parnassius smintheus*. *Oikos* 119, 1961–1969. <https://doi.org/10.1111/j.1600-0706.2010.18666.x>.
- Maxwell, S.L., Butt, N., Maron, M., McAlpine, C.A., Chapman, S., Ullmann, A., Segan, D.B., Watson, J.E.M., 2019. Conservation implications of ecological responses to extreme weather and climate events. *Divers. Distrib.* 25, 613–625. <https://doi.org/10.1111/ddi.12878>.
- McCauley, S.J., Hammond, J.I., Mabry, K.E., 2018. Simulated climate change increases larval mortality, alters phenology, and affects flight morphology of a dragonfly. *Ecosphere* 9, e02151. <https://doi.org/10.1002/ecs2.2151>.
- McDermott Long, O., Warren, R., Price, J., Brereton, T.M., Botham, M.S., Franco, A.M.A., 2017. Sensitivity of UK butterflies to local climatic extremes: which life stages are most at risk? *J. Anim. Ecol.* 86, 108–116. <https://doi.org/10.1111/1365-2656.12594>.
- Meehl, G.A., Tebaldi, C., 2004. More intense, more frequent, and longer lasting heat waves in the 21st century. *Science (80-. )* 305, 994 LP–997. <https://doi.org/10.1126/science.1098704>.
- Moran, P.A.P., 1953. *The statistical analysis of the Canadian Lynx cycle*. *Aust. J. Zool.* 1, 291–298.
- Neilson, E.W., Lamb, C.T., Konkolic, S.M., Peers, M.J.L., Majchrzak, Y.N., Doran-Myers, D., Garland, L., Martinig, A.R., Boutin, S., 2020. There's a storm a-coming: ecological resilience and resistance to extreme weather events. *Ecol. Evol.* <https://doi.org/10.1002/ece3.6842> n/a.
- O'Sullivan, J.D.B., MacMillan, H.A., Overgaard, J., 2017. Heat stress is associated with disruption of ion balance in the migratory locust, *Locusta migratoria*. *J. Therm. Biol.* 68, 177–185.
- Ogilvie, J.E., Griffin, S.R., Gezon, Z.J., Inouye, B.D., Underwood, N., Inouye, D.W., Irwin, R.E., 2017. Interannual bumble bee abundance is driven by indirect climate effects on floral resource phenology. *Ecol. Lett.* 20, 1507–1515. <https://doi.org/10.1111/ELE.12854>.
- Owen, E.L., Bale, J.S., Hayward, S.A.L., 2013. Can winter-active bumblebees survive the cold? Assessing the cold tolerance of *Bombus terrestris* audax and the effects of pollen feeding. *PLoS One* 8, e80061.
- Oyen, K.J., Giri, S., Dillon, M.E., 2016. Altitudinal variation in bumble bee (*Bombus*) critical thermal limits. *J. Therm. Biol.* 59, 52–57. <https://doi.org/10.1016/j.jtherbio.2016.04.015>.
- Pavan, F., Floreani, C., Barro, P., Zandigiacomo, P., Dalla Montà, L., 2013. Occurrence of two different development patterns in *Lobesia botrana* (Lepidoptera: Tortricidae) larvae during the second generation. *Agric. For. Entomol.* 15, 398–406. <https://doi.org/10.1111/afe.12027>.

- Phillips, B.B., Shaw, R.F., Holland, M.J., Fry, E.L., Bardgett, R.D., Bullock, J.M., Osborne, J.L., 2018. Drought reduces floral resources for pollinators. *Glob. Chang. Biol.* 24, 3226–3235. <https://doi.org/10.1111/gcb.14130>.
- Piessens, K., Adriaens, D., Jacquemyn, H., Honnay, O., 2009. Synergistic effects of an extreme weather event and habitat fragmentation on a specialised insect herbivore. *Oecologia* 159, 117–126. <https://doi.org/10.1007/s00442-008-1204-x>.
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* <https://doi.org/10.1016/j.tree.2010.01.007>.
- Rafferty, N.E., CaraDonna, P.J., Bronstein, J.L., 2015. Phenological shifts and the fate of mutualisms. *Oikos* 124, 14–21. <https://doi.org/10.1111/oik.01523>.
- Robeson, S.M., 2015. Revisiting the recent California drought as an extreme value. *Geophys. Res. Lett.* 42, 6771–6779. <https://doi.org/10.1002/2015GL064593>.
- Robinet, C., Roques, A., 2010. Direct impacts of recent climate warming on insect populations. *Integr. Zool.* 5, 132–142. <https://doi.org/10.1111/j.1749-4877.2010.00196.x>.
- Rocha, S., Kerdelhué, C., Ben Jamaa, M.L., Dhahri, S., Burban, C., Branco, M., 2017. Effect of heat waves on embryo mortality in the pine processionary moth. *Bull. Entomol. Res.* 107, 583–591. <https://doi.org/10.1017/S0007485317000104>.
- Roland, J., Matter, S.F., 2016. Pivotal effect of early-winter temperatures and snowfall on population growth of alpine *Parnassius smintheus* butterflies. *Ecol. Monogr.* 86, 412–428. <https://doi.org/10.1002/ecm.1225>.
- Rouault, G., Candau, J.-N., Lieutier, F., Nageleisen, L.-M., Martin, J.-C., Warzée, N., 2006. Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. *Ann. For. Sci.* 63, 613–624.
- Saccheri, I., Kuussaari, M., Kankare, M., Vikman, P., Fortelius, W., Hanski, I., 1998. Inbreeding and extinction in a butterfly metapopulation. *Nature* 392, 491–494. <https://doi.org/10.1038/33136>.
- Salgado, A.L., DiLeo, M.F., Saastamoinen, M., 2020. Narrow oviposition preference of an insect herbivore risks survival under conditions of severe drought. *Funct. Ecol.* <https://doi.org/10.1111/1365-2435.13587> n/a.
- Sánchez-Bayo, F., Wyckhuys, K.A.G., 2019. Worldwide decline of the entomofauna: a review of its drivers. *Biol. Conserv.* 232, 8–27. <https://doi.org/10.1016/j.biocon.2019.01.020>.
- Saunders, M.E., 2018. Insect pollinators collect pollen from wind-pollinated plants: implications for pollination ecology and sustainable agriculture. *Insect Conserv. Divers.* 11, 13–31. <https://doi.org/10.1111/icad.12243>.
- Schou, M.F., Loeschcke, V., Bechsgaard, J., Schlötterer, C., Kristensen, T.N., 2017. Unexpected high genetic diversity in small populations suggests maintenance by associative overdominance. *Mol. Ecol.* 26, 6510–6523. <https://doi.org/10.1111/mec.14262>.
- Schowalter, T.D., Lightfoot, D.C., Whitford, W.G., 1999. Diversity of arthropod responses to host-plant water stress in a desert ecosystem in southern New Mexico. *Am. Midl. Nat.* 142, 281–290. [https://doi.org/10.1674/0003-0031\(1999\)142\[0281:DOARTH\]2.0.CO;2](https://doi.org/10.1674/0003-0031(1999)142[0281:DOARTH]2.0.CO;2).
- Schweiger, O., Biesmeijer, J.C., Bommarco, R., Hickler, T., Hulme, P.E., Klotz, S., Kühn, I., Moora, M., Nielsen, A., Ohlemüller, R., Petanidou, T., Potts, S.G., Pyšek, P., Stout, J.C., Sykes, M.T., Tscheulin, T., Vilà, M., Walthers, G.-R., Westphal, C., Winter, M., Zobel, M., Settele, J., 2010. Multiple stressors on biotic interactions: how climate change and alien species interact to affect pollination. *Biol. Rev.* 85, 777–795. <https://doi.org/10.1111/j.1469-185X.2010.00125.x>.
- Seibold, S., Cadotte, M.W., MacIvor, J.S., Thorn, S., Müller, J., 2018. The necessity of multitrophic approaches in community ecology. *Trends Ecol. Evol.* 33, 754–764. <https://doi.org/10.1016/j.tree.2018.07.001>.
- Seneviratne, S.I., Donat, M.G., Mueller, B., Alexander, V. L., 2014. No pause in the increase of hot temperature extremes. *Nat. Clim. Chang.* 4, 161–163. <https://doi.org/10.1038/nclimate2145>.
- Sgrò, C.M., Terblanche, J.S., Hoffmann, A.A., 2016. What can plasticity contribute to insect responses to climate change? *Annu. Rev. Entomol.* 61, 433–451. <https://doi.org/10.1146/annurev-ento-010715-023859>.
- Shama, L.N.S., Kubow, K.B., Jokela, J., Robinson, C.T., 2011. Bottlenecks drive temporal and spatial genetic changes in alpine caddisfly metapopulations. *BMC Evol. Biol.* 11, 278. <https://doi.org/10.1186/1471-2148-11-278>.
- Sheldon, K.S., Dillon, M.E., 2016. Beyond the mean: biological impacts of cryptic temperature change. *Integr. Comp. Biol.* 56, 110–119. <https://doi.org/10.1093/icb/icw005>.
- Showalter, D.N., Villari, C., Herms, D.A., Bonello, P., 2018. Drought stress increased survival and development of emerald ash borer larvae on coevolved Manchurian ash and implicates phloem-based traits in resistance. *Agric. For. Entomol.* 20, 170–179.
- Singer, M.C., Parmesan, C., 2010. Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Philos. Trans. R. Soc. B Biol. Sci.* 365, 3161–3176. <https://doi.org/10.1098/rstb.2010.0144>.
- Smith, M.D., 2011. An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. *J. Ecol.* 99, 656–663. <https://doi.org/10.1111/j.1365-2745.2011.01798.x>.
- Soroye, P., Newbold, T., Kerr, J., 2020. Climate change contributes to widespread declines among bumble bees across continents. *Science* (80-. ) 367, 685 LP–688. <https://doi.org/10.1126/science.aax8591>.
- Staley, J.T., Mortimer, S.R., Morecroft, M.D., Brown, V.K., Masters, G.J., 2007. Summer drought alters plant-mediated competition between foliar- and root-feeding insects. *Glob. Chang. Biol.* 13, 866–877. <https://doi.org/10.1111/j.1365-2486.2007.01338.x>.
- Stephenson, N.L., Das, A.J., Amperssee, N.J., Bulaon, B.M., Yee, J.L., 2019. Which trees die during drought? The key role of insect host-tree selection. *J. Ecol.* 107, 2383–2401. <https://doi.org/10.1111/1365-2745.13176>.
- Sunday, J.M., Bates, A.E., Dulvy, N.K., 2011. Global analysis of thermal tolerance and latitude in ectotherms. *Proc. R. Soc. B Biol. Sci.* 278, 1823–1830. <https://doi.org/10.1098/rspb.2010.1295>.
- Thomson, D.M., 2016. Local bumble bee decline linked to recovery of honey bees, drought effects on floral resources. *Ecol. Lett.* 19, 1247–1255. <https://doi.org/10.1111/ele.12659>.
- Tobin, P.C., Nagarkatti, S., Loeb, G., Saunders, M.C., 2008. Historical and projected interactions between climate change and insect voltinism in a multivoltine species. *Glob. Chang. Biol.* 14, 951–957. <https://doi.org/10.1111/j.1365-2486.2008.01561.x>.
- Van Dyck, H., Bonte, D., Puls, R., Gotthard, K., Maes, D., 2015. The lost generation hypothesis: could climate change drive ectotherms into a developmental trap? *Oikos* 124, 54–61. <https://doi.org/10.1111/oik.02066>.
- Wagner, D.L., 2020. Insect declines in the anthropocene. *Annu. Rev. Entomol.* 65, 457–480. <https://doi.org/10.1146/annurev-ento-011019-025151>.
- Wallace, J.B., Anderson, N.H., 1996. Habitat, life history, and behavioral adaptations of aquatic insects. *Introd. Aquat. Insects North Am.* 3, 41–73.
- Watrous, K.M., Duennes, M.A., Woodard, S.H., 2019. Pollen diet composition impacts early nesting success in queen bumble bees *Bombus impatiens* Cresson (Hymenoptera: Apidae). *Environ. Entomol.* 48, 711–717. <https://doi.org/10.1093/ee/nvz043>.
- Wilson, R.J., Maclean, I.M.D., 2011. Recent evidence for the climate change threat to Lepidoptera and other insects. *J. Insect Conserv.* 15, 259–268. <https://doi.org/10.1007/s10841-010-9342-y>.
- Winter, A., Ciborowski, J.J.H., Reynoldson, T.B., 1996. Effects of chronic hypoxia and reduced temperature on survival and growth of burrowing mayflies (Hexagenia limbata) (Ephemeroptera: Ephemeridae). *Can. J. Fish. Aquat. Sci.* 53, 1565–1571.
- Zhang, Y., Peng, C., Li, W., Fang, X., Zhang, T., Zhu, Q., Chen, H., Zhao, P., 2013. Monitoring and estimating drought-induced impacts on forest structure, growth, function, and ecosystem services using remote-sensing data: recent progress and future challenges. *Environ. Rev.* 21, 103–115. <https://doi.org/10.1139/er-2013-0006>.
- Zhu, L., Wang, L., Ma, C.-S., 2019. Sporadic short temperature events cannot be neglected in predicting impacts of climate change on small insects. *J. Insect Physiol.* 112, 48–56. <https://doi.org/10.1016/j.jinsphys.2018.12.003>.