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Climate change-mediated temperature extremes and insects: From outbreaks to breakdowns

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Abstract

Insects are among the most diverse and widespread animals across the biosphere and are well-known for their contributions to ecosystem functioning and services. Recent increases in the frequency and magnitude of climatic extremes (CE), in particular temperature extremes (TE) owing to anthropogenic climate change, are exposing insect populations and communities to unprecedented stresses. However, a major problem in understanding insect responses to TE is that they are still highly unpredictable both spatially and temporally, which reduces frequency- or direction-dependent selective responses by insects. Moreover, how species interactions and community structure may change in response to stresses imposed by TE is still poorly understood. Here we provide an overview of how terrestrial insects respond to TE by integrating their organismal physiology, multitrophic, and community-level interactions, and building that up to explore scenarios for population explosions and crashes that have ecosystem-level consequences. We argue that TE can push insect herbivores and their natural enemies to and even beyond their adaptive limits, which may differ among species intimately involved in trophic interactions, leading to phenological disruptions and the structural reorganization of food webs. TE may ultimately lead to outbreak–breakdown cycles in insect communities with detrimental consequences for ecosystem functioning and resilience. Lastly, we suggest new research lines that will help achieve a better understanding of insect and community responses to a wide range of CE.

KEYWORDS
anthropogenic climate change, biodiversity, climatic extremes, heatwaves, herbivory, insect physiology, multitrophic interactions, parasitoids, predators

1 | INTRODUCTION

There is increasing evidence that a mass extinction event is in its early stages across much of the biosphere (Ceballos et al., 2017; Dirzo et al., 2014; Pievani, 2014). Well-studied species (vascular plants, vertebrates) have lost as much as 60% of genetic diversity over the past 50 years alone (Ripple et al., 2017). Recent studies are reporting that terrestrial insect biomass and/or diversity are also declining in some regions, especially in the tropics (Dirzo et al., 2014; Hallmann et al., 2017; Lister & Garcia, 2018; Sánchez-Bayo & Wyckhuys, 2019; Seibold et al., 2019; van Klink et al., 2020) although losses of many taxa are also being balanced by gains of other taxa, as recent studies have shown

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in temperate biomes (Crossley et al., 2020; Macgregor et al., 2019). Nevertheless, declining insect numbers also impact other species in food chains including insectivorous vertebrates (Lister & Garcia, 2018), and unsurprisingly, many species of insectivorous birds are also declining rapidly, especially in temperate biomes (Goulson, 2014; Hallmann et al., 2014; Rosenberg et al., 2019). By now the problem of insect declines is acknowledged as a major threat to ecosystems and human well-being (Cardoso et al., 2020). In this context they serve as a poignant proxy of the "miner's canary" (Butchart et al., 2010).

The role of anthropogenic climate change in driving declines of species and populations is the focus of many recent studies (e.g., Corcos et al., 2018; Grainger et al., 2018; Hoye et al., 2013;

Rasmann et al., 2014). Evidence suggests that rapid climatic shifts have been a key factor in previous mass extinction episodes (Joachimski et al., 2012; Maslin & Lewis, 2015). Although multiple factors are involved in recent insect declines, climate change is certainly among them (Sánchez-Bayo & Wyckhuys, 2019; Soroye et al., 2020; Wagner, 2020). Like other ectotherms, insects are highly susceptible to abiotic changes in the environment. Many insects have life cycles that vary seasonally, such as annual species that overwinter as eggs or pupae, and larval or adult stages that are active in spring and summer. Evidence is accumulating that insects are responding to warming in different ways, such as through shifts in their geographic (both latitude and elevation) ranges, changes in
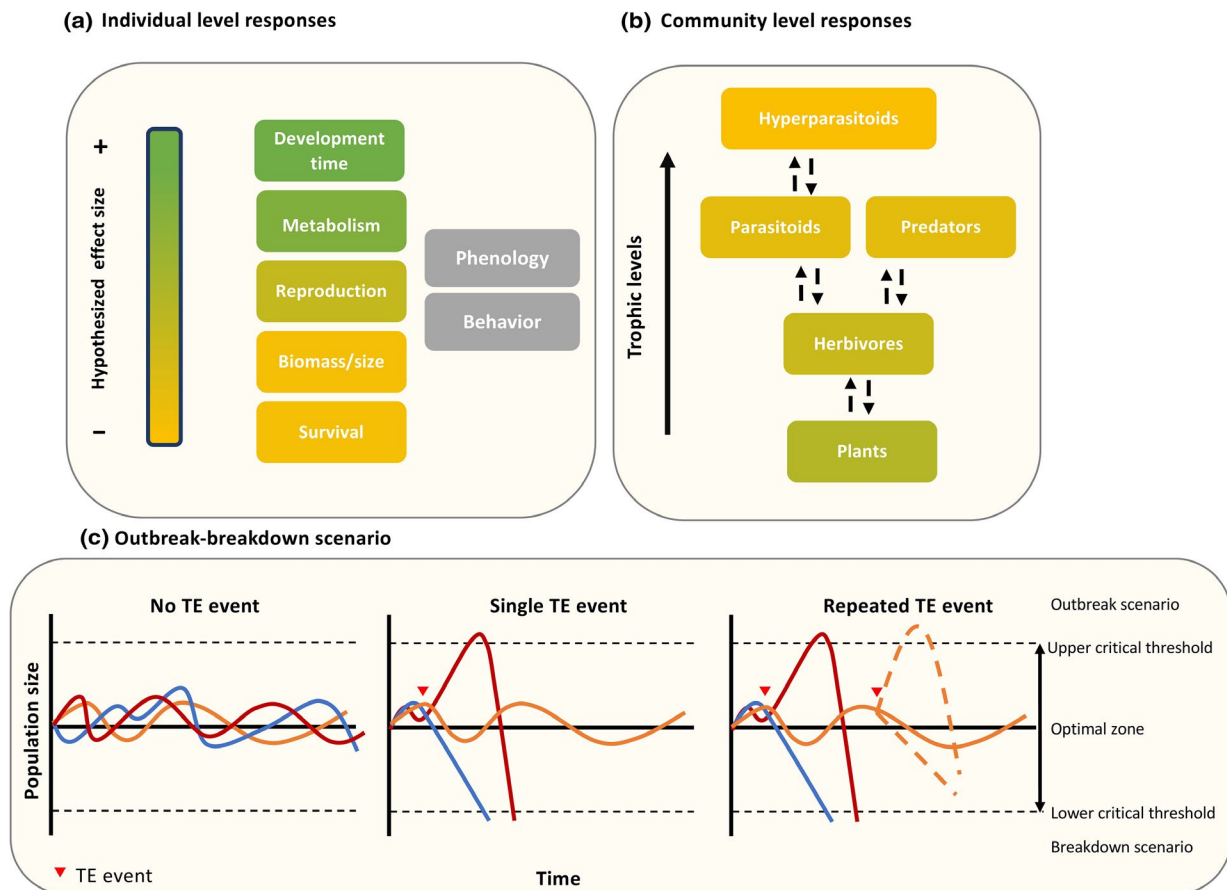

FIGURE 1 Overview of insect responses to temperature extremes (TE). In (a) species attributes are given that are potentially affected by TE. Color coding, from green (positive) to yellow (negative) or gray (undefined) depicts the hypothesized effect size of exposure to TE. In (b) an example is given of a simple insect food web with their interactions (dashed lines). Evidence suggests that species higher in the food chain are more negatively affected by TE than species lower in the food chain (depicted by the different color gradients). In (c) examples are given of insect population outbreak and breakdown scenarios in response to single or sequential TE events. In the left panel, we show three coexisting insect species (indicated by three line colors) exhibiting seasonal fluctuations in their population dynamics. The middle panel presents an outbreak event of an insect species (red line) followed by its breakdown in response to a single TE event (red triangle). Outbreaks occur when a population reaches or crosses an upper threshold (considerably above the carrying capacity, which approximates the upper threshold) and subsequently leads to its breakdown. A key assumption here is that the outbreaking insect overexploits its main food resource leading to its population crash (see main text for details). In response to a single TE event, breakdowns may also occur in insect species (blue line) when its population size becomes very small, and close to its lower critical threshold. The insect species that is less affected (orange line) by a single TE event could still face an outbreak-to-breakdown scenario or a direct breakdown (shown by dashed lines) when another TE event takes place (second red triangle). Such scenarios (right panel) are likely to depend on the abiotic characteristics of the sequential TE event, and potential maladaptation in the (orange line) insect species during the first TE event

seasonal and/or diel growth, and activity patterns and related processes like seasonal voltinism (Chen et al., 2011; Parmesan, 2006; Tobin et al., 2008). These involve not only direct responses of insects to changes in temperature, but also indirect responses, that is, how responses affect other species intimately involved in trophic interactions with them (Chen, Donner et al., 2019; Chen, Gols et al., 2019; Gillespie et al., 2012; Harvey, 2015; Robinson et al., 2017). Consequently, these effects can simplify food webs and hamper the functioning of ecosystems (Cramer et al., 2001; Pelini et al., 2015; Wardle et al., 2011).

Thus far most studies of climate change effects on biodiversity and insects have focused primarily on longer term (i.e., decadal) time scales. However, embedded within long-term warming are climatic extremes (hereafter CE), such as temperature extremes (hereafter TE), severe droughts, and heavy precipitation events, as well as attendant events such as floods and fire, that occur over a comparatively short duration of days or weeks. Importantly, CE have increased in frequency, duration, and intensity over the past two decades (Christidis et al., 2015; Mazdiyasni & AghaKouchak, 2015; Meehl & Tebaldi, 2004; Palmer, 2014). CE are gaining increased attention for their effects on biodiversity at all levels of organization (Harris et al., 2018; Isbell et al., 2015; Reusch et al., 2005). A major concern is that the increasing intensity of CE, such as TE experienced during heatwaves, is pushing many insect species to or beyond their adaptive limits (Agosta et al., 2018; Soroye et al., 2020), exposing them to conditions that they may have rarely experienced in their evolutionary history.

Given the wide breadth of the field, this review focuses on insect responses to TE. Following the IPCC definition of CE, we define TE as "rare temperature events which would be as rare or rarer than the 10th or 90th percentile of probability density functions estimated from temperature observations over a period of time (usually 20–25 years)" (IPCC, 2018). We examine the biological, physiological, and ecological effects of TE on insects from an organismal, multitrophic, and community-level perspective (Figure 1). By bridging these different scales, we develop a framework to suggest how TE will increase the frequency of insect outbreak and breakdown events. More specifically, in section one, we discuss the effects of TE on insect physiology, development, reproduction, and behavior. In section two, we discuss TE in a multitrophic framework, beginning with plant–insect interactions and moving up in the food chain by including the third (and fourth) trophic level ([hyper] parasitoids and predators). In section three, we describe the effects of TE on community-level processes. In section four, we synthesize the previous three sections by formulating "outbreak," "breakdown," and sequential "outbreak to breakdown"' scenarios based on the insect responses to TE and its legacies. Finally, we highlight future research avenues for improving our understanding of insect responses from organismal- to community-level aspects within our outbreak–breakdown framework by proposing a number of research questions to advance insect biology in a world with increasing TE.

2 | ECO-PHYSIOLOGICAL AND DEVELOPMENTAL RESPONSES TO TE

2.1 | Effects of TE on insect ecophysiology

Insects, like other small other ectotherms, exhibit traits that reflect long-term evolutionary responses to small-scale local conditions (microclimates) that may deviate considerably from large-scale macroclimatic conditions (Angilletta, 2009; Pincebourde & Casas, 2015). However, larger organisms or those that are able to disperse rapidly may be able to track more optimal microclimates better than smaller or less motile organisms, including many insects. Therefore, it is important to understand the physiological and ecological responses of insects to microclimate, particularly as these may change dramatically during TE. Ambient temperature plays a major role in the regulation of physiological functions in insects such as respiration, immunity, metabolism, growth and reproduction, and, in turn, these factors affect biological characteristics such as behavior, locomotion, dispersal, longevity, and survival (Adamo et al., 2012; reviewed by González-Tokman et al., 2020; Huey et al., 2012; Kingsolver et al., 2015; Roitberg & Mangel, 2016; Figure 1a). Insects have evolved physiological strategies that enable them to adapt to seasonal changes in temperatures and warmer conditions. For example, adaptations to warming include temporal shifts from periods of activity to quiescence via diapause and/or aestivation (Bale et al., 2002; Masaki, 1980; Salman et al., 2019) or by increasing the number of generations per year (Altermatt, 2010). Clearly, many insects can evolutionarily respond to warming that occurs over an extended period of time (e.g., many years or decades). However, TE expose insects to conditions that may impose immense (temporary) physiological stresses that well exceed those occurring under more gradual warming (Colinet et al., 2015).

Physiological responses of insects to heat exposure were recently reviewed by Colinet et al. (2015) and González-Tokman et al. (2020). In summary, thermal changes are first perceived and processed at the neurological level, that is, sensing changes in temperature followed by the control of appropriate behavioral, metabolic, and developmental responses. For example, high temperatures increase the production of biogenic amines, of which some are neurotransmitters that control behavior and metabolism, as well as the production of hormones which also play an important role in the regulation of physiological processes. Metabolic rates and oxygen demands increase with increasing temperature resulting in the production of more free radicals and the formation of toxic products which trigger a defensive response (e.g., production of antioxidants). Behavioral and physiological thermoregulation are measurements to mitigate the potential adverse effects of exposure to high temperatures. The responses so far refer to moderate increases in temperature. When temperatures further increase, insects, like other higher organisms, produce heat shock proteins that protect denaturation of other proteins that do not function normally at higher temperatures. Eventually, neural performance is impaired affecting muscular function or is shut down completely (reversible coma) just before the insect dies. The effect of temperature on any of these processes

may vary inter- and intraspecifically and may even may be life-stage specific (see also section below; González-Tokman et al., 2020).

Many insects exhibit limited ability to thermoregulate when exposed to TE because their body temperatures closely approximate ambient temperature (Huey et al., 1999; Kingsolver et al., 2011; Woods, 2013). Exposure to extreme heat induces thermal stresses on insects and can push many species toward or even beyond critical adaptive thresholds (Agosta et al., 2018; Fischer et al., 2014; Iserbyt & Rasmont, 2012; Kingsolver et al., 2013). Moreover, the ability to deal with exposure to TE may depend on the timing of a TE event during the growing season. For instance, insect tolerance to heat exposure often increases in insects that previously have been exposed to short periods of high temperatures (Colinet et al., 2015), a process referred to as "heat hardening." Consequently, an incidence of a TE early in the growing season may have stronger consequences than a TE occurring later in the season, as early in the season, insects have not experienced hardening yet. Furthermore, there is considerable intraspecific genetic variation in heat tolerance within insect species (Colinet et al., 2015). For example, the large cabbage white butterfly (*Pieris brassicae*) has a wide distribution and is adapted to a broad range of climates across the Palearctic that vary from hot, dry semi-tropical to cool temperate or even boreal climates with short summers. Held and Spieth (1999) found that populations of *P. brassicae* from southern Spain undergo pupal aestivation in summer when exposed to high temperatures and long day length and do not initiate winter diapause under warm temperatures and shorter day length. This phenological response is presumably a local adaptation to extremely hot conditions in southern Spain that reduce food availability (brassicaceous plants) during summer. By contrast, populations of *P. brassicae* in other countries with less extreme climates do not aestivate in summer and diapause in winter (Held & Spieth, 1999).

Physiological sensitivity to climate change may differ quite significantly between insects living in temperate and tropical ecosystems. The climate variability hypothesis (CVH) predicts that there is a positive relationship between the thermal tolerance range and the level of climatic variability experienced by an organism across latitudes or along elevational gradients (Bozinovic et al., 2011; Dobzhansky, 1950; Janzen, 1967; Stevens, 1989). Based on the CVH, it is generally assumed that temperate insects are more sensitive to short-term, stochastic TE than to longer term more gradual increases in mean temperature. This is because most temperate species are well-adapted to seasonal changes in temperature (cold winters and warm summers) which is reflected in their life cycles that are often tightly coordinated with seasonally changing temperatures. Tropical insects are sensitive to both TE and longer term warming because most species (at least at lower elevations) are adapted to narrower temperature regimes than their temperate counterparts, given that tropical temperatures are relatively stable over time (Colinet et al., 2015; Deutsch et al., 2008). For this reason, many tropical insects synchronize their life cycles more with precipitation cycles (e.g., rainy and dry seasons) than with temperature. Importantly, the majority of tropical insects live close to their thermal limits already and as such are vulnerable to even modest warming (Deutsch

et al., 2008; Lister & Garcia, 2018; Pincebourde & Casas, 2015). Polato et al. (2018), for example, found that tropical montane insects in three clades exhibited significantly lower thermal tolerances and dispersal abilities than temperate species. They suggested that this is possibly due to a climate warming-induced reduction in the variation of seasonal temperatures occurring in tropical montane habitats. These results show that species-rich tropical montane ecosystems are highly vulnerable to climate change (Polato et al., 2018).

The assumption that tropical insects are more vulnerable to warming depends mainly on macroclimatic data (Deutsch et al., 2008) and rarely accounts for seasonal activity patterns of temperate insects (Johansson et al., 2020). In fact, differences in thermal tolerance between tropical and temperate insects became minimal when temperatures during the period of insect's developmental stages were incorporated into models (Johansson et al., 2020). Moreover, a major problem in understanding insect responses to warming in temperate biomes is that although TE are occurring more often, they are still highly unpredictable, reducing frequency- or direction-dependent selective responses by the insects. In response to TE, insects may respond by either increasing or reducing physical activity or by seeking cooler microclimates—such as burrowing into the soil or moving to lower parts of their food plants—where they experience less thermal stress (Hemmings & Andrew, 2017). These microclimates act as transient refuges where the insects can "ride out" extreme conditions until they pass (Thakur et al., 2020).

The question is to what extent do species differ in their ability to deal with TE? There is evidence that some species are better adapted to cope with TE than others, and that some species will even thrive, at least transiently, under these conditions (Harris et al., 2018; Ma et al., 2015; Økland & Bjørnstad, 2006). Populations of species that lack this ability may become maladapted to a given environment (often measured via trait responses) potentially leading to negative growth and a population size that is far from its carrying capacity. Moreover, it can ultimately lead to the local extinction of populations (Brady et al., 2019; Morris & Lundberg, 2011). Maladaptation in insect populations during and after TE is likely to depend on two factors: (a) thermal safety margins ($T_{optimal} - T_{environment}$, where $T_{optimal}$ is the optimal temperature for an insect species, and $T_{environment}$ is the ambient temperature), and (b) the frequency of sequential CE of different kinds. Narrow thermal safety margins imply that insects have lower physiological flexibility to adjust to TE (Kingsolver et al., 2013; Sgrò et al., 2016). These insects are therefore more likely to exhibit thermal maladaptation, and their survival may depend on their ability to relocate to more favorable thermal environments (Chapman et al., 2015). Those species with broader thermal safety margins could also become maladapted if populations are sequentially exposed to CE with very different abiotic conditions (e.g., to an extreme hot period followed by an extreme wet period), especially when the genetic correlations between extreme and non-extreme environmental states are weak (Chevin & Hoffmann, 2017). An insect can only prevent maladaptation when it is able to exhibit biochemical adaptation to a wide range of environments including various types of extreme and non-extreme environments. This is

mainly possible with "jack-of-all-trades, and master of none" insects (Angilletta, 2014). Insects with such a strategy are unlikely to dominate in any environment but are more likely to persist in most environments, as well as under conditions of CE. We therefore suspect that increasing frequency and severity of various kinds of CE could likely result in insect communities with more "jack-of-all-trades, and master of none" species.

2.2 | Effects of TE on different insect life stages

Many insects go through distinct life stages before they develop into adults and various life stages may differ in vulnerability to TE. Moreover, exposure to TE in one life stage may affect later life stages (Bowler & Terblanche, 2008). Insect eggs are sessile, and their location is determined by the adult female. The microclimate of the oviposition site will determine egg incubation temperature, but also the risk of exposure to TE that may occur after oviposition (Potter et al., 2012). Thermal environment plays an important role in egg incubation (Atkinson, 1994). For instance, the temperature-size rule posits that eggs that are (temporarily) exposed to high temperatures produce smaller and (physically) weaker individuals (i.e., the temperature-size rule; Atkinson, 1994; Sibly & Atkinson, 1994). When insect eggs are exposed to TE (i.e., when TE are close to their thermal maxima), this commonly results in higher egg-larval mortality (Chen, Zhang et al., 2019; Rocha et al., 2017; Zhou et al., 2018), and reduced larval growth (Potter et al., 2011), which in turn can result in reduced adult biomass (Chen et al., 2014; Klockmann et al., 2017; Sniegula et al., 2017) and fecundity (Chen, Zhang et al., 2019; Zhou et al., 2018).

Exposure to TE during their larval stage can affect adult fitness parameters, such as body size and longevity (Bauerfeind & Fischer, 2014; Bowler & Terblanche, 2008). The effects of TE stress become especially apparent if exposure occurs in the later stages of larval development (Knapp & Nedvěd, 2013; Zhang et al., 2015). Depending on the insect species, exposure to TE during the pupal stage may lead to increased or decreased longevity of the adults, reduced fecundity, or increased mortality (Chen et al., 2018; Zheng et al., 2017). Although insect pupae, like eggs, are immobile, late-instar larvae will often find secluded space to pupate (e.g., hiding or burrowing into the soil). This behavior may provide some protection from TE in the pupal stages, but these protective behaviors may not suffice with increasing duration or severity of the TE. Exposure to TE during the adult stage can reduce fertility and fecundity directly following the event (Dickinson, 2018; Huang et al., 2007; Mironidis & Savopoulou-Soultani, 2010; Sales et al., 2018; Sentis et al., 2013; Zhang et al., 2013), although in some species TE may benefit future insect generations through adaptive conditioning (Adamo & Lovett, 2011). Adult exposure to TE can lower subsequent hatching rates and larval survival in the following generation (Cui et al., 2008). The effect size further depends on the duration and frequency of the TE event (Colinet et al., 2015; Gillespie et al., 2012; Zhang et al., 2013).

Modular life cycles may allow insects to deal with various forms of environmental stress (Potter et al., 2011; Zhang et al., 2015). For instance, brief periods of exposure to TE in the egg–larval stages increase insect sugar levels in subsequent life stages, which may be an adaptive mechanism to protect and stabilize proteins against heat-induced denaturation (Back et al., 1979; Chen, Zhang et al., 2019). Although many studies show that exposure of eggs to TE can negatively affect larval growth, phenotypic plasticity in advanced larval stages can overcome the negative impacts of prior exposure to TE (Potter et al., 2011). In addition, TE exposure during earlier life stages does not always affect fitness in the adults (Abarca et al., 2019; Chen, Zhang et al., 2019; Potter et al., 2011; Zhang et al., 2015) and reduced fertility and fecundity following TE exposure of adults may be transient and disappear after several days (in males), or after re-mating with unexposed males (in females; Dickinson, 2018; Sales et al., 2018). Given the short life cycles of most insects, under conditions of recurring or extended TE, many insects may not be able to recover even short periods of fertility loss. It is likely that the effects of TE are thus more profound for temperate univoltine insects with short life cycles and/or short reproductive periods. Furthermore, the effects of TE exposure are more difficult to overcome by individuals that are near adult eclosion, which occurs primarily in spring and summer in most insects.

Much attention on thermal tolerance in insects has focused on upper lethal limits (critical thermal maximums, CT_{max}) when exposed to TE (Bowler & Terblanche, 2008; Klok et al., 2004; Lutterschmidt & Hutchison, 1997). At this point exposure to high temperatures for even a limited time can lead to a breakdown of metabolic functions in organisms leading to their precocious death. However, as discussed above, exposure of different insect stages or ages to TE may not necessarily lead to short-term mortality, but still result in significant costs on fitness and demographics through a reduction in fertility. This can intraspecifically affect males, females, or both sexes concomitantly (Janowitz & Fischer, 2011; Sales et al., 2018; Saxena et al., 1992; Zhang et al., 2013). Based on these findings, Walsh et al. (2019) have proposed "thermal fertility limits" (TF_{max}) as a framework for understanding the effects of heat exposure on reproduction. Importantly, TF_{max} may occur at lower temperatures than CT_{max}, and need to be factored into models of population persistence and outbreak–breakdown scenarios.

3 | EFFECTS OF TE ON TROPHIC INTERACTIONS

The effect size of TE on insects may vary with their position in the trophic food chain (Figure 1b). For instance, there is evidence that upper thermal limits vary among species in different levels of single, two, three-, or even four trophic-level interaction chains (Agosta et al., 2018). If this is a widespread phenomenon, then it suggests that food webs exposed to TE may be weakened because of a reduction in the strength of top-down or bottom-up processes (Brooks

& Hoberg, 2007; Dyer et al., 2013; Rosenblatt & Schmitz, 2016). In general, the sensitivity of species to high temperatures increases with trophic level (Voigt et al., 2003), which can be explained to some extent by resource availability and/ or quality incrementally affecting each trophic level above, and also due to greater metabolic demands of animals at the top of food chains. Differences in the responses of organisms within and across trophic levels and the ability of these organisms to adapt to warmer environments can result in a disruption of trophic relationships. For instance, warming has been shown to result in latitudinal range expansions and shifts in phenology (Parmesan, 2006). If species do not respond to warming in the same way, this may result in a temporal and or spatial mismatch in the abundance of species at different trophic levels (Parmesan, 2006; Thakur, 2020). More importantly, the occurrence of TE is more unpredictable and has an immediate impact on species, and directly or indirectly, on the species that they interact with, especially those that are more sensitive to these conditions. In some cases, however, insect responses to TE may only become evident after the event has ceased—so called "lagged" effects. To understand immediate and lagged effects of TE on insects, we discuss the importance of both shifts in plant-mediated (bottom-up) and enemy-mediated (top-down) trophic interactions.

3.1 | Effects of TE on plant–insect herbivore interactions

In the section on physiological effects of exposure to TE, we focused on direct effects of TE on insects. However, as approximately 50% of insect species are herbivorous, TE may indirectly impact on many insects through their food plant. Similar as for insects, responses to TE involve the synthesis of heat-shock proteins that help the plant to mitigate the negative impacts of TE exposure (Hasanuzzaman et al., 2013; Wahid et al., 2007). Extended exposure to high temperatures may inactivate enzymes in chloroplasts and mitochondria, blocking of protein synthesis and loss of membrane integrity, which in turn affect plant growth and result in the production of toxic compounds and reactive oxygen species (Wahid et al., 2007 and references within). These changes in plant physiology and chemistry, both primary and secondary (e.g., Bita & Gerats, 2013; Pincebourde et al., 2017; VanWallendael et al., 2019), are likely to change the quality and quantity of plants as food for insect herbivores (Bauerfeind & Fischer, 2013; Buse et al., 1998; DeLucia et al., 2012). For instance, several studies have shown that the induction of heat-shock processes in response to TE can result in a suppression of primary and secondary metabolism (Escobar-Bravo et al., 2017; Veteli et al., 2002) weakening the plant's defense against insect herbivores. Heat stress can also alter the emission of plant volatile organic compounds (Kask et al., 2016; Loreto & Schnitzler, 2010), which play an important role in mediating interactions between plants and associated insects (Bruce, 2015; Dicke & Baldwin, 2010). Plant hormones, in particular salicylate, ethylene, and jasmonic acid play a vital role

in mediating the plant's response to biotic stresses, such as attack by herbivores, and abiotic stresses, including exposure to TE (Balfagón et al., 2019; Bita & Gerats, 2013; Dar et al., 2015). Little is known about how hormonal control under conditions of TE affects plant–herbivore interactions.

Heat-induced changes in plant morphology and physiology may persist over time and may also affect future plant–insect interactions. The impact of TE on plant productivity is often species specific, but is usually negative in the short term (Dreesen et al., 2012). Over time, plants may overcome the short-term negative effects on productivity via compensatory growth (Dreesen et al., 2012; Hoover et al., 2014). Heat has the most detrimental effects on plant productivity when multiple stressors are combined (e.g., heat and drought), which is frequently the case during exposure to TE (De Boeck et al., 2016). Furthermore, the negative effects of TE on plant productivity and physiology become more pronounced when TE events reoccur at short intervals (Dreesen et al., 2014). Little is known about the extent and direction of plant physiological responses to TE over longer time periods, but it has been shown that other CE, such as droughts, can leave lasting legacy effects on insect resistance in forests (Rouault et al., 2006). Moreover, differences between plants and herbivores in their ability to recover from exposure to TE may have enduring repercussions (Piessens et al., 2009), that could eventually result in insect outbreak or breakdown scenarios as discussed in segment four.

3.2 | Effects of TE on insect herbivore–natural enemy interactions

Most studies of insect responses to CE have been on a single trophic level, with focus on insect herbivores. Less attention has been paid to TE responses of natural enemies (parasitoids and predators) of insect herbivores and on how these in turn affect the biology and ecology of insect herbivores (but see Stoks et al., 2017). Many parasitoids have limited host ranges and may be more sensitive to heat than plants and their herbivore hosts. This is because they are affected both directly and indirectly through the effects of high temperature on the insect host and the host plant (Agosta et al., 2018; Hance et al., 2007; van Baaren et al., 2010). Previous studies have shown that TE may deleteriously affect the behavior and performance of parasitoids in terms of survival, development, flight and host-finding efficiency, and oviposition behavior (Agosta et al., 2018; Chen, Gols, et al., 2019; Flores-Mejia et al., 2016; Jerbi-Elayed et al., 2015). TE exposure has also been shown to affect predator–prey interactions by modifying consumption rate, growth, and behavior, potentially leading to differences in voltinism and phenology, predator population size, and dispersal (Damien & Tougeron, 2019; Jamieson et al., 2012; Sentis et al., 2017).

Few studies have investigated the effect of TE involving three trophic levels, let alone four. Gillespie et al. (2012) manipulated the frequency and amplitude of TE and investigated their effects on a system consisting of pepper plants, aphids (*Myzus persicae*) and two

parasitoid species (*Aphidius matricariae* and *Aphelinus abdominalis*). They found that daily, compared to weekly, exposure to temperatures of 32°C or 40°C both reduced population growth of the aphids and the formation of winged morphs, and extended the development time of both parasitoid species. Interestingly, the direct negative effects of high temperature on the plants (reduced growth and increased osmolarity) were overruled when aphids were feeding on them. The two parasitoid species were differentially affected by heat exposure regimes in terms of parasitism success (Gillespie et al., 2012). Schreven et al. (2017) found that the effects of exposure to daily heat pulses during the entire immature phase of both parasitized and unparasitized host caterpillars depended on the amplitude of the heat pulse (+5°C or +10°C) with the parasitized caterpillars being positively affected by a heat pulse of 5°C (higher body mass, faster development), but negatively by a heat pulse of 10°C. They also found that the host *Plutella xylostella* was less sensitive to temperature variability than its parasitoid, *Diadegma semiclausum* (Schreven et al., 2017). In two other studies, in which TE were simulated to mimic heatwave conditions, the survival of hyperparastoids in the fourth trophic level was significantly lower at the highest temperature (Chen, Donner, et al., 2019; Chen, Gols, et al., 2019). Development time of both the primary parasitoids and their hyperparasitoids was also reduced at the highest temperature, but faster development of the primary parasitoid reduced the window for parasitism by the hyperparasitoids and lowered their reproductive success. In addition, the extent to which the hyperparasitoid was affected by high temperature depended on differences in life-history traits, such as fecundity, egg production, longevity, and host-feeding behavior (Chen, Donner, et al., 2019; Chen, Gols, et al., 2019). Similarly, Hall et al., 2019 found that TE affected larval survival of primary parasitoids of *Cardiaspina* psyllids more strongly than survival of their herbivore host. These results suggest that the impact of TE may also be positive (e.g., faster development) when the amplitude of the TE is relatively low and the event is incidental. However, when these events are more extreme or occur more frequently, their net effect is more likely to be negative with higher trophic level insects suffering more than lower trophic level insects (Figure 1b).

The net effect of TE on species interactions depends on the relative response of individual species at each trophic level (de Sassi & Tylianakis, 2012). In a field experiment with artificial heating, it was shown that herbivore biomass increased more than that of the plants, whereas biomass of parasitoids did not change in response to higher temperatures. The net effect of heat exposure was a community that was increasingly dominated by herbivores (de Sassi & Tylianakis, 2012). TE may also restructure food webs or even disrupt their integrity. Barton and Ives (2014) showed in a system consisting of corn, aphids, predators, and aphid-tending ants that raising the temperature by 5°C above the ambient temperature led to a reduction in aphid abundance, despite their faster population growth rate. This was attributed to the ants being less abundant and less aggressive toward aphid predators at elevated temperatures. In another study, experimental warming modified interactions among herbivorous grasshoppers, predatory "sit and wait" spiders, and "active

hunting" spiders. In response to high temperatures, the spider species and grasshopper species shifted their location in the vegetation. Consequently, the "active hunting" spiders became alternative prey to the "sit and wait" spiders, which in turn reduced predation rates on the grasshoppers (Barton & Schmitz, 2009). While this study only exposed organisms to moderate warming, future studies examining the effects of TE on multitrophic interactions may find even more dramatic effects on processes like intraguild predation.

In parasitoids, of which many exhibit narrow host ranges, the response to TE exposure can be more "finely-tuned" than in predators because a large part of the parasitoid life cycle is intimately associated with that of the host. This is especially true in koinobiont endoparasitoids, where the parasitoid larvae develop in a host that continues feeding and growing during much of the interaction (Harvey, 2005). Female parasitoids of the same and different species often lay eggs in the same individual host, a phenomenon referred to as "intrinsic competition" (Harvey et al., 2013). TE events have been shown to modify the outcome of intrinsic competition (Chen, Donner, et al., 2019; Gillespie et al., 2012). Aphids harbor facultative bacterial endosymbionts of which some play a role in immunity against parasitism. Exposure to high temperatures can compromise this immunity, resulting in a switch from resistance against parasitism to high susceptibility (Bensadia et al., 2006). Both changes in intrinsic competition and host susceptibility can influence the dynamics and structure of host–parasitoid multitrophic interactions. Moreover, the restructuring of food webs caused by exposure to TE will leave a lasting legacy effect on plant–insect communities.

4 | EFFECTS ON TE ON INSECT COMMUNITIES

Individual- and population-level responses of insects to TE are likely to propagate into insect community responses (Gillespie et al., 2012; González-Tokman et al., 2020; Huey et al., 2012; Ma et al., 2015). In general, such community-level responses are manifested via changes in insect community diversity and/or biomass. On the other hand, the characteristics of insect communities, such as the diversity of thermal specialists in an insect assemblage, the availability of resources, and the enemy pressure, could determine how population-level responses of various insects unfold during TE (González-Tokman et al., 2020; Urban et al., 2016). Thus, a combined approach of population- and community-level responses and their interaction can significantly advance our understanding of insect community responses and recovery during and after TE events. Toward this end, we discuss how population-level responses to TE may affect insect community biomass and insect diversity, and how community context of insects may determine the population-level response of various insect species living in a particular community.

TE are most likely to asymmetrically affect different insect species living within the same community in an environment (Colinet et al., 2015; Musolin & Saulich, 2012). This can be attributed to physiological diversity of insects even when they live in similar

environments (Chown & Terblanche, 2006; Sinclair et al., 2012). The extent of asymmetric insect responses to TE may depend on variation in population-level responses of species. For instance, three co-occurring aphid species differed in their demographic responses with their developmental rates varying much more than their lifespan when exposed to TE (Ma et al., 2015). Greater asymmetry in key demographic responses of co-occurring insects can cause shifts in insect community features, such as a reduction in insect evenness (Ma et al., 2015; Nooten et al., 2014). Demographic variables, such as the intrinsic rate of population growth, often closely correlate with thermal safety margins or thermal performance curves (Huey & Berrigan, 2001; Sinclair et al., 2016). Using species-specific demographic responses and their thermal tolerance together can help understanding symmetric versus asymmetric insect responses to TE events. For instance, when thermal safety margins of insect species are low, increases in temperature substantially reduce the intrinsic rate of population growth (Deutsch et al., 2008; Kingsolver et al., 2013). In such cases, we could expect a more symmetrical response among insect species within a community when exposed to TE events with a possibility of local population extinction of several insect species. While the evenness of such insect communities may show nominal changes due to symmetrical responses, they may still become species-poor insect communities.

The close association of symmetrical or asymmetrical population-level responses of insects with community-level changes during TE events can be extended to explain how variation in insect responses affects insect competitive dynamics. As discussed above, changes in resource availability and predation pressure during TE are crucial for our understanding of insect responses. If resources are not limiting (Müller et al., 2015) and predation effects are weaker at higher temperatures (Thakur et al., 2018), we could then make predictions at the insect community level from their population or demographic responses that are related to thermal safety margins. When TE make resources more limiting (Piessens et al., 2009), and higher temperatures enhance demographic rates (Brown et al., 2004), insects that are able to survive with lower resource consumption will have a competitive advantage over others that lack this ability (Ohlberger, 2013). Moreover, insects expressing higher phenotypic plasticity, for example, through reduction in body size, can also lower resource consumption in warm and resource-limiting environments (Gardner et al., 2011; Ohlberger, 2013; Sheridan & Bickford, 2011; Thakur et al., 2017). However, whether insects are able to offset metabolic demands under TE is less understood than under gradual and moderate warming. In environments with increased predation in response to higher temperatures (Thakur et al., 2017; Vucuc-Pestic et al., 2011), insects also need to modify various strategies (e.g., behavioral traits) to be able to simultaneously escape from predation and still be better at acquiring resources and mating partners than their competitors. An important question that remains to be addressed is to what extent insect species differ in their ability to modify physiological and behavioral responses during exposure to TE that are also likely to affect resource availability and predation risk? The answer

to this question may require a more in-depth examination of the ecology of plant–insect communities.

Community characteristics of insects are often determined by the habitat in which they live. Heterogeneous habitats, in terms of resource availability, often harbor a greater functional diversity of insects, which could relate to a greater diversity in physiological traits among the community members (Hunter, 2002; Lassau & Hochuli, 2004; Lassau et al., 2005). A number of studies have reported that heterogeneous habitats are able to buffer the negative effects of TE on insect communities characteristics such as insect diversity (Loboda et al., 2018; Papanikolaou et al., 2017; Pincebourde & Suppo, 2016). Habitat heterogeneity provides insects with a multitude of microhabitats they can use to buffer against abiotic stress of TE events (Kleckova et al., 2014; Scheffers et al., 2014; Thakur et al., 2020). Some of these (micro)habitats (e.g., unexposed soils, deadwood, caves) are very well-buffered in temperature conditions (Mammola et al., 2019) and consequently, are often occupied by organisms that are strongly adapted to these buffered conditions. In fact, several studies have also shown that variation in thermal physiology of insects correlates with spatial heterogeneity of their habitats (Baudier et al., 2015; Bonebrake & Deutsch, 2012). For instance, maximum critical temperatures in nine army ant species were much lower for those species living belowground than those living on soil surface (Baudier et al., 2015). Conserving habitat heterogeneity, such as buffered micro- and macrohabitats, will conserve physiological diversity within insect communities, which is important not only for protecting insects during TE events, but also a key predictor of how insect communities may respond to severe thermal stress.

The ability of insects to modify trait expression in overcoming thermal stress may be compromised even more in homogenous habitats. Increasing homogeneity of habitats across the biosphere has dramatically reduced the physiological diversity of insects (Murphy et al., 2016; Wagner, 2020). A few insect species exhibiting high thermal tolerance may still be able to survive under the dire conditions of TE even in homogenous habitats (Kingsolver et al., 2013; Macgregor et al., 2019). Periodic outbreaks of thermally resilient insects under TE may ultimately reduce insect diversity and community resilience. We discuss in the next section how such periodic outbreaks of thermally resilient insects will likely increase in frequency with increasing TE events but will also increase the frequency of outbreak–breakdown type of dynamics in insect communities.

5 | INSECT OUTBREAKS AND BREAKDOWNS UNDER TE

Ecological responses are described as extreme when they are also rare, which implies that some response thresholds should be reached or exceeded during an extreme event with subsequent alteration in ecosystem functions (Smith, 2011). From the perspective of insects, we hereby propose insect outbreaks and breakdowns as two extreme responses to TE (Figures 1c and 2 for example species). Insect
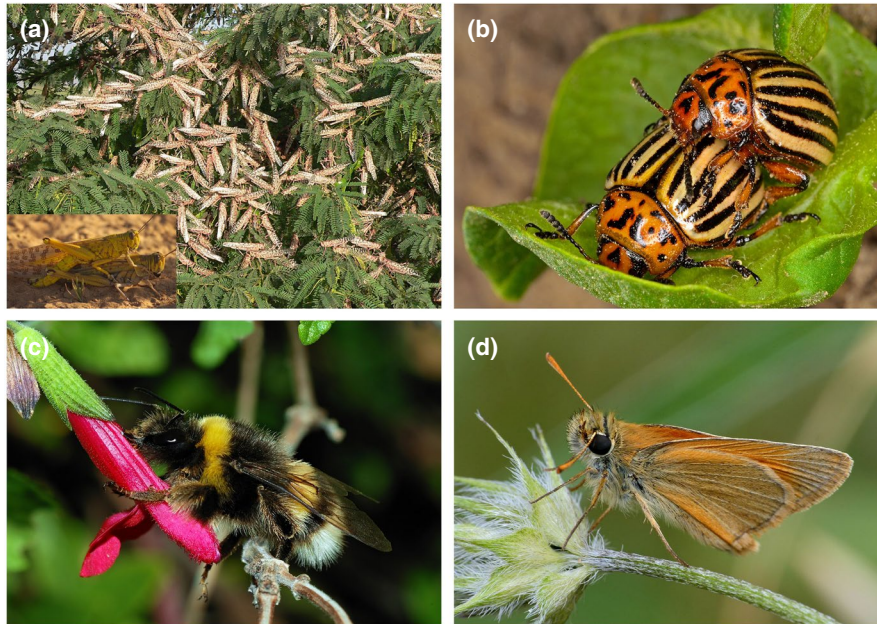
FIGURE 2 Across the biosphere, insects are responding, both positively and negatively, to temperature extremes (TE). (a) Outbreaks of the desert locust, *Schistocerca gregaria*, in eastern Africa, are driven by a combination of high temperatures and extreme precipitation events. These outbreaks are leading to significant crop losses in several countries. (b) The Colorado potato beetle, *Leptinotarsa decemlineata*, originates from warm regions of the southwestern United States and Mexico. Climate warming has enabled the species to invade many temperate regions globally where it is a major pest of potato crops. It thrives when exposed to high temperatures. (c) In many temperate biomes, bumblebee (*Bombus* sp., depicted *Bombus terrestris*) species are declining rapidly. Although several anthropogenic stresses are driving these declines, exposure to TE during heatwaves has recently been shown to be a major factor. (d) Many butterflies (Lepidoptera), including species that were once numerous, are declining rapidly in North America and Eurasia. Grassland-dependent species, such as the small skipper, *Thymelicus sylvestris*, respond poorly to heat stress, owing to the negative effects of TE on host plant quality and abundance. Copyright information: *Schistocerca gregaria* swarm: ©ChriKo, 2014, Wikimedia Commons License CC-BY-SA-4.0; *Schistocerca gregaria* pair: ©Adam Matan, 2013, Wikimedia Commons License CC-BY-SA-3.0; *Leptinotarsa decemlineata*: ©Tavo Romann, 2013, Wikimedia Commons License CC-BY-SA-4.0; *Bombus terrestris*: © Alvesgaspar. 2007, Wikimedia Commons License CC-BY-SA-3.0; *Thymelicus sylvestris*: ©Bernard DuPont, 2014, Wikimedia Commons License CC-BY-SA-2.0

outbreaks are defined as an exponential increase in insect population at a given spatio-temporal scale with severe negative effects on their resources (e.g., food and shelter). Insect breakdowns are defined as population crashes leading to local extinctions of insect populations. Both extreme scenarios of insect population responses can have far-reaching negative consequences on biodiversity and ecosystem functioning. Moreover, insect outbreaks owing to TE are transient states of populations, which are most certainly going to crash over time resulting into outbreak–breakdown cycles (Figure 2). These two extreme scenarios are driven by insect physiology, trophic interactions, community context, and ultimately thermal (mal)adaptations as discussed in detail earlier. We first discuss the current understanding of climate change-induced insect outbreaks and breakdowns, and then elaborate on how TE can enhance the outbreak–breakdown cycle in insects (Figure 1c).

Longer term climate warming has already been suggested as a key factor driving insect outbreaks and breakdowns in temperate regions. For instance, winter is a major biological control agent, and as winters get warmer, they enable vulnerable insect stages in diapause—especially eggs and larvae—to survive in habitats where they were once killed by extreme or extended cold (Fleming & Candau, 1998; Jepsen et al., 2008; Klapwijk et al., 2012; Kurz et al., 2008; Neuvonen et al., 1999). Increased winter survival and warmer temperatures allow insect populations to build up much more rapidly in spring, leading to an increased number of generations per year and summer outbreaks. On the other hand, some insect species that undergo winter diapause may be negatively impacted by higher temperatures in winter, for instance because of faster depletion of resources under warmer winter conditions (Sinclair, 2015; Williams et al., 2012). Moreover, winter warming can also disrupt insect life cycles if these are tightly coordinated with their food plants and/or natural enemies, leading to a disruption in trophic interactions (Johnson et al., 2010; Klapwijk & Lewis, 2009; Renner & Zohner, 2018). However, thus far, little attention has been paid to outbreak and/or breakdown scenarios under TE events disrupting typical seasonal phenomena such as diapause.

Climate warming and TE, in combination with human forest and landscape management practices (e.g., simplification and/or in monocultures), are driving breakouts of several notorious insect pests. For instance, climate anomalies associated with warming such as TE and drought and practices that create warm microclimates are triggering outbreaks of bark beetles (Curculionidae: Scolytinae) in Europe and the United States (Bentz et al., 2010; Marini et al., 2017; Raffa et al., 2008). Outbreaks are occurring

due to changes in resource dynamics and temperature-mediated increases in beetle generations (Økland & Berryman, 2004). Similarly, oak and pine processionary moths have recently expanded their European distributions northward as a result of warming and both species thrive under TE conditions (Godefroid et al., 2020; Netherer & Schopf, 2010; Robinet & Roques, 2010). The oak processionary moth favors warm microclimates, especially in late winter and early spring and has clearly benefitted from the practice of growing oak trees in strips along roads where thermoregulation is optimized. Moreover, natural enemies such as the ground beetle *Calasoma sycophanta* and specialized dipertan and hymenopteran parasitoids have not apparently tracked the northward expansion of the oak processionary moth (De Boer & Harvey, 2020).

TE can directly (via exposure) or indirectly (via variable effects on several species in trophic chains) affect the ecology and evolution of insects. Non-linear effects of TE among different species in food webs can generate trophic cascades that have implications for community structure and function (Renner & Zohner, 2018). Heat- and drought-induced mortality of plants are becoming evident in many biomes, and this in turn will have cascading effects up the food chain, potentially decimating the food supply for herbivorous insects. This will also negatively affect higher trophic levels, such as predators and parasitoids. Moreover, the vast majority of insect herbivores have largely specialized diets (Loxdale et al., 2011) and as such depend on a narrow range of suitable food plants found in their habitat. This means that they cannot switch diet when their food plant is depleted during TE-mediated outbreaks. Being well-adapted to one or only a few plants may enable specialist herbivores to breakout during TE, but after exhausting their food supply they are also more prone to breakdowns than generalists which can switch to alternative food plants. A potential outbreak may also occur when TE more negatively affect higher trophic level natural enemies than their herbivore prey or hosts (Agosta et al., 2018; Figure 2). In this scenario, herbivores are better adapted to TE, whereas excessive exposure to heat decimates number of their natural enemies. This enables the herbivores to explode numerically, outbreaking as result of enemy release (Keane & Crawley, 2002).

Herbivore outbreaks are potentially transient because of two critical thresholds that may ultimately result in breakdowns down the road: in the first, the insect herbivore loses its natural enemies (that are more susceptible to TE) and then overexploits its food plant; this leads to a "boom-bust"-type breakdown of the trophic chain. Second, by decimating its food plant, it not only dooms itself but other species that may utilize or depend on that plant for food or shelter. The latter results into "breakdown cascades" with severe detrimental effects on ecosystem functioning. Moreover, if herbivores are more susceptible to TE than their natural enemies, then a collapse in abundance of the herbivore will clearly decimate numbers of its more specialized natural enemies by association, especially parasitoids and hyperparasitoids that depend on it. If the natural enemies are able to switch to attacking alternate species of herbivores, this can have a knock-on effect, that is, increased predation on the new prey, negatively affecting its abundance, leading to another breakdown. As discussed earlier, it is also important to recognize that insects have upper thermal limits for survival that may be higher than for fertility (Walsh et al., 2019). Thus, outbreaking species may suffer reproductive failure when exposed to temperatures below those which are lethal, leading to breakdowns that may be earlier than anticipated. Bearing these factors in mind, observed seasonal fluctuations in insect populations may dramatically change over the short term in response to single and/or sequential TE events (Figure 1c). Seasonal fluctuations of populations within ecological communities are crucial for the temporal partitioning of resources and hence are a key factor in understanding species coexistence (Chesson, 2000). Insect outbreak–breakdown cycles will hamper resource partitioning owing to temporally disproportional resource consumption. We therefore expect greater losses of insect biodiversity and insect-associated functions as TE enhance the probability of outbreak–breakdown type of population dynamics.

6 | CONCLUSIONS AND FUTURE DIRECTIONS

Temperature-related CE pose a great threat to biodiversity across all levels of organization. TE may amplify the effects of other anthropogenic stresses, such as habitat loss and fragmentation, pollution, agricultural intensification, and invasive species that are known to be driving declines of biodiversity, including insects, across much of the biosphere (Sánchez-Bayo & Wyckhuys, 2019). It is important to emphasize that CE do not necessarily occur independently but may overlap temporally, occur sequentially or in several rapid cycles over the course of days or weeks. For example, when insects are exposed to heat and drought, followed by heavy rainfall (signifying the passage of a cold front), they are physiologically subjected to significant abiotic shifts over a short period of time. Moreover, conditions may be considerably cooler before and after heat waves, or else build up over several days before TE occur. We argue that insect responses to fluctuating temperatures and to multiple simultaneous or sequential abiotic stressors associated with climate change should therefore be the focus of future research.

As we have discussed, asymmetrical responses of insects to TE may result in outbreaks and breakdowns. The mechanistic processes conducive to these conditions are still, however, little-known. Answering questions such as which (physiological) traits of insect species are important for outbreak potential, and how shifts in TE-induced trophic interactions result in outbreaks and/or breakdowns may provide insights for our understanding of underlying mechanisms. It is also important to investigate the indirect effects of outbreaks and/or breakdowns on genetic diversity, species diversity and ecosystem functioning and to study their implications for natural and agricultural ecosystems. Furthermore, we need to compare the effects of TE in tropical and temperate insects and how these affect breakout and breakdown cycles.

More attention needs to be paid to bridging the effects of TE from individuals to populations, and then scaling this up further to the level of food webs, communities, and ecosystem-level processes. Studying population dynamics in a multitrophic framework under TE conditions may help to understand how these can affect vital ecosystem functions that insects perform like pollination, nutrient cycling and pest control, and as food for vertebrates and in turn how these effects translate into the health (resilience and resistance) of ecosystems. Furthermore, although we know that exposure to TE can generate short-term physiological legacies in insects, our understanding of longer term (intergenerational or interannual) effects of exposure to TE at the population or species level is still unclear. It is important to measure the response of plants and their associated insects over several years following exposure to a record-breaking heat wave or drought, and to compare this in habitats that experienced variable exposure to these conditions. As we have discussed, the fingerprint of TE caused by anthropogenic climate change on insects can be quite significant. We therefore call for long-term and more integrative research among entomologists, climate change biologists, and conservation experts not only to improve our understanding of the ecology and evolution of insects in a world with increasing extreme events, but also to find pragmatic solutions to protect already dwindling insects from further breakdowns at multiple scales (Harvey et al., 2020).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTION

J.A.H., R.H. and M.P.T. conceived the initial ideas. J.A.H., R.H., R.G., and M.P.T. developed and wrote the manuscript.

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