2022

# Insects as indicators of climate change: A literature review

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ENTO 888

Spring 2022

## Introduction

The International Panel on Climate Change (IPCC) has consistently predicted rising global temperatures since it began reporting in 1988. Researchers have noted that climate extremes have been identified beginning in the 1990s and are apparent in various climate indicators. The most recent IPCC reports show that the rate of warming has sped up considerably, and that global warming will increase from pre-industrial levels by 1.5 degrees Celsius in the next 30 years, and possibly by 2 degrees C if considerable mitigation efforts are not put in place (IPCC, 2021). By 2017 global temperatures had already increased by about 1 degree Celsius from pre-industrial levels. Since the 1970s CO2 emissions have increased by 90%, and the rate of surface temperature has doubled in the past 50 years (EPA, 2017).

Global warming does not just increase surface temperatures. Complex interactions due to a warmer earth will have an impact on most if not all earth systems. Impacts can and will include, for example, increased rainfall in some regions and longer drought periods in others, and more severe and extreme weather events. These changes will result in a loss of habitat and host plants for many insects, while also increasing the number and duration of pest outbreaks. "The appearance of novel climates poses an important challenge for scientists trying to predict the ecological and evolutionary responses of organisms to climate change" (Kingsolver et al, 2011, p. 719).

All insects are poikilothermic (cold blooded) organisms, and accordingly, warming impacts their development, physiology, movement, behavior and ecology (Vickery, 2008) and can also change the host plant (Kharouba et al., 2018) and thereby interactions between the two. Because insects are sensitive to temperature change, they are useful bioindicators of global warming (Colares et al, 2021). Due to the diversity and size of the Insecta class, research on the impacts of warming on arthropods has demonstrated complicated and nuanced outcomes.

This literature review will synthesize research that examined how insects respond to warming temperatures or other climate change indicators such as loss of sea ice, loss of habitat and reduction of host plants. The majority of the reviewed research was published in 2021, with the inclusion of older studies for historical context or discussions of insect physiology. A great deal of the research relies on modelling the IPCC's warming scenarios to make predictions about how varied species will respond. The reviewed literature not only shows how insects are impacted by climate change, but how these effects contribute to ecological system dynamics. Stated most simply, the presence or absence of an insect species can have a far-reaching effect on an ecosystem. This paper is organized by themes represented in the literature including impacts on species in different climates, evidence of plasticity through evolution, impacts on development and life cycles, impacts on pest and disease outbreaks, and plant-insect interactions. Recommendations for solutions and future research are presented at the conclusion of this paper.

## Changes in Biodiversity

In the last 25-30 years there has been a 75% decrease in insect biodiversity (species richness) in terrestrial ecosystems (Vickery, 2008). A recent meta-analysis showed that nearly half of insect species are declining and one-third are close to extinction (Sánchez-Bayo & Wyckhuys, 2019). In addition, there has been a 70% decline in flying insects over the past 30 years. Most declines began in the 1950s. Further, 70% of butterflies are declining in abundance, and since 1970 there been a loss of 10% of moth species per decade. Among bumblebees, worldwide declines and increases vary, but overall there is a downward trend and three species in the US have suffered from colony collapse (Wagner, 2019).

Research has shown that depending on the complex interactions described in the modeling of climate scenarios, some species of insects will benefit from warming, while others will decrease. What remains clear is that regardless of the scenario, biodiversity will be reduced. Thom et al. (2017) modeled 36 diverse climate scenarios and disturbances over 1,000 years to predict biodiversity among forest habitats. Changes in land cover, precipitation and temperature were modeled. They found that Carabidae, saproxylic (deadwood dependent) beetles and tree beetle species were predicted to decrease significantly, while other species responded positively to climate change. Diversity of Hymenoptera, Mollusca and Syrphidae were predicted to double. Frequent and severe climate disturbances were shown to be benefit biodiversity, while disturbance size had a negative impact. Biodiversity hot spots are currently found in low to mid elevation but shifted to higher elevations in predicted models. Increased precipitation increased ground vegetation and therefore Syrphidae. Further, greater numbers of oak and hornbean trees influenced diversity, although an increase of canopy cover was found to have negative effects.

## Indicator Species

Insects are ectotherms and as such are sensitive to temperature change. Butterflies, in particular, are good indicators of a changing climate. For example, the northern range of many European butterflies is associated with the 'June-July isotherm'. However, suitable habitats must be available when butterflies emerge. Specialist butterflies that require a specific or particular host (such as the Monarch that can only use milkweed as a host), may be most impacted by habitat loss. As early as the 1970s many butterfly species were sighted earlier than in years previous. Each year there are earlier, and an increasing number, of new species entering colder climates (Vickery, 2008). Climate change also affects the survival of food resources and host plants due to drought or flooding, impacting where females may lay their eggs. The Monarch is projected to lose it's over wintering habitat in the oyamel fir forests of Mexico (Hellman et al, 2016). Further, estimates have been made that 50-90% of insect species remain unidentified, making it difficult to accurately keep track of population changes and diversity. Butterflies have declined more rapidly than native bird and plant species. They can also act as an indicator of climate change for other taxa including dragonflies, bees, ants and hoverflies (Thomas, 2005).

Recent research has also noted a significant decline in moth populations. One study looked at patterns of change from 1970-2016 in Europe. While 31% of species decreased, 38% increased. In addition, 34% of species showed a significant decrease in abundance. In the Netherlands alone, 71% of large moths showed significant decreases. While warming climates benefit some moths, particularly those that live in temperate regions of the UK and US, habitat loss extends their range even further north, so species are prevented from benefiting from the warming temperatures. Because moths, like other Lepidoptera, are adapted to temperate climates and have short life cycles, their decline is a reliable indicator that warming has reached unmitigated levels. Like butterflies, their early emergence and flight indicates warmer temperatures. In the United Kingdom, 81% of moths have been observed flying earlier. In Europe, moths are important nighttime pollinators and their caterpillars are a major food source for nocturnal animals (Poyser, 2020).

Insects living in tropical mountain climates may have a narrower thermal limit and narrower elevation distribution than insects living at sea level. Colares et al (2021) identified five taxa of Coleoptera in a Brazilian rainforest mountain that are useful as bioindicators of global warming: Cerambycidae, Eumolpinae, Chrysomelidae, Lampyridae and Phengodidae because they are abundant and narrowly distributed. Temperature decreases by .5 degrees C at each 100 meter increase of elevation, meaning that these insect species will likely be found at higher elevations as temperatures warm. Further, predators over herbivores are more likely to succeed in increased temperatures.

Mayflies (Ephemeroptera) are an important indicator of water quality in freshwater systems, due to their sensitivity to stream flow changes, water temperature, and pollution among other variables. In one study, 83% of mayfly species studied in African streams decreased in response to increased water temperature (Ramulifho, et al, 2020). In another study, an analysis of aquatic insect biodiversity assessed in the Pawmpawm River in the eastern region of Ghana showed no significant difference in diversity over a 40-year period, although there were significant reductions in the volume of insects (Nnoli, et al., 2019). In particular there was a lower abundance of Simulium (black flies) and Centroptilum (mayflies). The rise in current flow reduces the ability of the Centroptilum to feed, while a river blindness control program along with deforestation affected the Simulium. Low evenness was also demonstrated because a few mayfly genera, such as Baetis and Cloeon, are more dominant in fast flowing rivers.

A dataset of 42 freshwater species showed that an increase in temperature of 1.88 degrees C resulted in a reduction of abundance by 81% and increase in adult emergence by 15 days (Baranov et al, 2020). Data prior to 1990 showed there was an increase in richness of species, diversity and evenness of abundance of species with an increase in temperature. However, the second half of the dataset commencing in 1990 demonstrated drier conditions. These conditions changed sedimentation and therefore habitat structures. As other research has shown, scientists predict that generalists are more likely to survive. Climate change may initially increase diversity, but then may eventually lead to a declining trend in richness of species.

## Distributional Shifts of Insects Due to Climate Change

Because insects are sensitive to temperature change, an increase or decrease in temperature by a certain threshold can reduce or extend larval development and adult emergence. Insects native to diverse environments such as polar, temperate and tropical climates have different thermal limits. Due to these diverse tolerances, distributional shifts in species will continue to be seen as the planet warms.

### *Distribution of Pollinators*

Pollination services are essential to food production to support human life. Up to 8 % of crop production relies on pollination (Suzuki-Ohno et al, 2020). Although research on pollinators has largely focused on honey bees, wild bees can pollinate in temperate and subarctic climates. Recently, these species have declined due to changes in land cover and flower availability. Using citizen science data collected in Japan, Suzuki-Ohno et al modeled range shifts of six bumblebee species. Estimated rising global temperatures results in a shortened range of five of the species, and expansion of one species -*B. ardens*- for which higher temperatures are suitable. However, when modeling changes in land coverage, the ranges increased for five species and was reduced for *B. diversus*. In addition, up to a certain threshold, an increase in forests provide habitats for bumblebees as they populate the forest edges to visit foraging sites. Excessive growth in forests, though, will reduce the forest edges and adjacent grasslands where bees forage.

Consequently, range shifts and expansions poleward will result in the colonization of new habitats. Butterfly oviposition sites that had expanded in range due to climate change among *Lycaena dispar* were studied by Martin et al (2020). Establishment of oviposition sites are a key indicator of new populations. An ecological niche factor analysis showed that in forest microhabitats newly populated habitat edges had lower ambient temperature than at core. Edge populations do not have a narrow range of habitat, and ovipositing females at the edge demonstrated generalism and laid eggs in a diverse range of habitats, as supported by other studies. The authors showed that "the thermal time window for active female behavior was reduced in edge populations, which could significantly decrease the time budget for oviposition and decrease the threshold of acceptance during microhabitat" (p. 2342). Reduced time budgets reduce choosiness of egg laying location, and in turn will reduce maternal fitness among offspring. Thus, increased time stress may select for those individuals who are less choosy and fast deciding –in turn reducing good or appropriate hosts.

Range shifts as they relate to host plants are also important indicators of insect migration. Using data from multiple sources (museums, biological surveys, and citizen science data) Wilson et al (2020) were able to predict the rapid range shift of the giant swallowtail butterfly (*Papilio cresphontes*) which is a specialist of common prickly ash, southern prickly ash, and common hop tree. The swallowtail's range expansion north has been increasing since 1959 (the earliest data available) with more rapid increases since 2000. The range of swallowtail distribution largely matches that of the host range, although host ranges were more complex in distribution. A similar northward shift of *Z. americanum* occurred nearly 145 years ago, likely due to a drought, which impacted plant and nectar distributions.

### ***Thermal Limits and Distributions***

Thermal performance curves explain how temperature affects an animal's fitness and physiological functions including movement, development and reproduction. As noted above, climate change will result in range shifts although the behavior and physiological responses of insects from various climates and ecosystems (tropical, temperate, aquatic, and Arctic, for example) drive the complex interactions between environment and insect.

Although it is expected that temperate insects may be driven poleward as their thermal limits are exceeded due to warming temperatures, insects in tropical climates may experience a greater change in fitness due to the difference in optimal temperatures for development and survival. There is a smaller window for thermal safety as they will be pushed beyond their thermal maximum (Johansson et al., 2020). Alternately, insects in temperate regions will benefit from climate change as current temperatures are below their thermal maximum. An examination of global eco-physiological datasets across latitudes, including thermal tolerance and temperature thresholds for development, show that insects cannot develop below an established minimum temperature. Insects at higher latitudes (colder temperatures) are only active during warmer months and enter diapause in cold months. Diapause is triggered by exposure to light rather than temperature. These insects are expected to evolve to enter diapause when mean temperatures falls to the lower development temperature threshold. Thus, insects in temperate, higher latitudes possess greater warming tolerance and thermal safety. However, there is surprisingly little difference in warming tolerance between temperate and tropical species, indicating that temperate and tropical species are both at risk for reduced fitness due to narrower thermal safety margins. Overtime warming temperatures will result in an impact in reduced tropical species (biodiversity) and increased temperate species.

## Insects as Indicators in Polar climates

The Polar Regions provide climate change researchers with important information as climate warming is occurring to a greater degree in winter than in warmer months, particularly in higher latitudes. A warmer winter lengthens the growing season, induces snow melt earlier, and more pathogens are present. Since snow acts as insulator, lack of snow cover makes it difficult for insects to overwinter. Extreme temperatures also leave trees and shrubs susceptible to insect pest infestations (Box et al, 2021). Other climate changes include weakening of the jet stream which increases winter weather extremes, such as allowing arctic air to travel further south. Thus, in addition to temperatures being warmer overall there will also be more extreme periods of cold weather. Extreme cold causes injury, tissue damage, apoptosis, overall low fitness and death or delayed death among both animals and plants (Marshall et al, 2020). Further, responses to evolution may occur *in situ*. Successful species will be cold hardy, which occurs through phenotypic plasticity. Since insects often consume less or no food during the winter, expending additional energy can be fatal.

Climate change will also impact phenology, resulting in earlier springs and later autumns, and the availability of the host plant at larval or adult feeding stages (Marshall et al, 2020). Further, diapause, as noted previously, is usually induced by photoperiod as well as winter temperature. Some species do have a chilling requirement prior to resuming development– entering diapause too early can cause energy drain.  In addition, there has been an increase in tundra biomass and greening, increased rainfall due to rising water temperature, and therefore an increase in ‘freshening’ of ocean water (reduced salinity), in particular. However, reduction of snow will extend the growing season, and increase vegetation and CO2 uptake, but it will also increase respiration so the net carbon balance may not be impacted (Box et al, 2019).

Geographically isolated regions of the Arctic, such as the Svalbard archipelago, will likely see the greatest climate shifts (Anisimov et al, 2007; Coulson et al, 2002). Species of insects from the south will potentially migrate to these Arctic areas. However, given the distance from Europe and North America, as well as ice barriers and atmospheric circulation, survival will be impeded. The diamondback moth *Plutella xylostella* was examined as a possible indicator species of insects that disperse via air (including Diptera, Hymenoptera, Hemiptera and others) because these moths have been found to survive in the Arctic. As noted, earlier development, in part, is triggered by photoperiod cues. Climate warming will not alter photoperiodism; however, warming periods can provide a ‘synoptic window’ in which cold weather adapted species may migrate to Arctic regions (Coulson et al, 2002). What these migrations mean for survival of these species, if they do not establish colonies in these regions, remains to be determined. It is possible that species who migrate northward, and then cannot establish habitats, overwinter and survive, may be at risk.

The Arctic aphid has also been indicated as a model insect to detect changes in temperature. The effect of temperature on the aphid’s distribution and abundance has also been studied. The Arctic aphid proliferates 2-3 generations per year and has a more restricted range than its host plant. It requires a certain number of days above zero degrees during the summer for successful development. From the 1970s to 1990s temperature was warm enough to allow for development of usually two generations. However, modeling predicted that an increase in summer temperature of 2 degrees C resulted in a third generation indicating that a proliferation of what are considered agricultural pests may be observed as temperatures warm, even in the Arctic (Hodkinson & Bird, 1998).

Conversely, Antarctica's fauna only includes two native species of invertebrates, chironomid midges (the winged *Parochlus steinenii* Gerke and the brachypterous *Belgica antarctica* Jacobs), and two established invasive species with currently restricted ranges, *Eretmoptera murphyi* (Diptera: Chironomidae) and *Trichocera maculipennis* (Diptera: Trichoceridae). If predicted models of climate change are correct, then freshwater will be impacted and *P. steineni* will be at risk as it does not tolerate freezing. *P. steineni* is not currently found on the mainland but could extend its range if ice retreats by about 4%. If there is a lack of competition or predators, these insects could rapidly inhabit the continent.

Distributional shifts will be predicted by indicator species. At the poles, previously temperate dwelling insects will be found, while tropical insects may migrate to temperate regions. Further, there may be a proliferation of some species in previously unpopulated regions due to intolerance to temperature extremes.

## Insects in Forest Habitats

The proliferation of insect pests in forest habitats has already had a significant impact on the forest industry. Research has shown that warming will only increase the range and degree of pest infestation in forests. Hof and Svahlin (2016) modeled the distribution of 30 insect pests (Coleopteran and Lepidopteran) in boreal forests in Sweden. They predicted increased ranges and new locations of infestations and larger infestations, which will result in more damage. In addition when trees are heat stressed, they are more susceptible to pest infection and damage. In addition, the duration of outbreaks will persist due to warming, even in higher latitudes as natural diapause periods may be shortened (Pureswaran et al, 2015).

One of the most damaging pest species of boreal forests in Europe is *Ips typographus* (Christiansen & Bakke, 1988; Tudoran et al, 2016). It can cause substantial damage to spruce stands and has had a large impact on the forestry sector. Other researchers have shown that damage-causing insects (largely beetles) in Sweden since 1850 include *I. typographus, Neodiprion sertifer, Tortrix viridana, Hericium abietis* and *Tomicus piniperda*, most of which infest conifer host trees. These preferences reflect the abundances of tree types in Sweden and Norway (Tudoran et al, 2016).

Mountain pine beetles, as well as other tree beetles, do not have effective predators and therefore, low winter temperatures generally cause mortality. Increased warming, however, has increased larval survival and therefore the beetle population. Adults are cold adapted, but larvae cannot survive temperatures below a certain threshold. Due to warming, pine beetles have destroyed North American pine forests on a large scale. Where cold snaps would control the outbreaks of beetles, damage was periodically limited to sporadic 'epiphytotics' (epidemics among plants). Ecosystem services have been impacted by pine beetle infestation and has health effects on human populations due to increased runoff, water turbidity, fires, and an increase in water and respiratory diseases. Forests also act as a carbon sink, thus their destruction creates additional warming opportunities (Embrey et al, 2012).

Contrary to other studies, some simulations have shown that climate change can provide a mitigated environment among fragmented forests. Plant-herbivore insect networks provide a window into the impacts of reduced diversity in these forests. Climate change has and will continue to reduce biodiversity among plants. However, Bahner et al (2017) showed that the increase in forest edges allows some adaptable plant species that are light adapted, and thermostolerant, to robustly survive the forest edge. In other words, forest management has resulted in less diverse inner forests and generalists have adapted to this narrow availability of host plants.

It is possible to predict thermal limits for larger animals and insects with current climate models that give very broad ranges of temperature extremes (Pincebourde & Woods, 2020). However, microclimates for smaller insects have demonstrated more variability. Forest understory buffers thermal extremes, providing a microclimate that may be protected to some degree from warming. Accordingly, insects can adapt to temperature although the variability of microclimates on a finer scale are hard to predict. Presently, warming predictions are fairly broad. Plant surfaces are warmer than the understory and ants have shown more adaptability to thermal limits than those in the understory and select for generalist species. Further, transpiration rates differ by almost 10 degrees C for herbivore species. These variations should be kept in mind when considering interactions in micro-climates.

## Host-plant interactions

Changes in synchrony and phenology will cause disruptions in host- plant interactions. Insects do not respond to climate change in a linear fashion. Development is hastened by warming temperatures but increased temperatures can also cause diapause to last longer. Further, climate change does not just indicate warming surface, air and ocean temperatures. It causes complex interactions that can have diverse impacts on ecosystem depending on geography.

High temperatures change the physiological traits of plants and causes heat stress which can reduce resistance to disease. High CO2 can inhibit photosynthesis and growth. Increased watering can mitigate some negative effects, although increased watering can impact food quantity by ‘interrupting leaf increments’. Thus, specialist herbivores will likely be most threatened by warming temperatures (Park et al, 2020).

Indirect effects for plant-herbivore interactions as a result of elevated CO2 were studied among *Pieris napi* (green-veined white butterfly), whose host plant is *Sinapis alba* (Kuczyk et al, 2021). While ovipositing females preferred plants with higher levels of glucosinolate glucosinalbin (GG), and climate change models have shown that higher temperatures cause higher concentrations of GG, drought stress reduced the levels of concentration. Even though GG likely acts as an oviposition and feeding stimulus, as females and larvae prefer these plants, performance (number of eggs deposited, body size, shorter development time, growth rates, mass, and activity) of the butterfly was more positively impacted by plants grown at typical (control group) temperatures. Thus, the plant-host chemistry was impacted by climate change, and herbivores did not select plants most beneficial to their survival and performance. Shorter development time is favorable as risk of death prior to maturation favors future generations.

The impacts of climate change and increased CO2 also has indirect effects on insects. For example, even if increased CO2 will not impact insects directly, it will have an impact on plant chemistry. Some insects increase feeding rates to compensate for lower nitrogen content. Additionally, increased temperatures will directly affect chewing herbivores. Lepidopterans may engage in greater feeding of low-quality food to meet nutrient requirements, causing greater damage to ecosystems. Aphids will increase in population abundance due to increases in CO2. Further, reduced plant fitness will decrease resistance to disease and pests. Increased CO2 will impact phytohormones used as secondary defense metabolites. Increased temperatures will also increase fungal pathogens (Trebicki et al., 2017).

Mutualism is another example of how complex interaction impact insects in nonlinear ways. The southern green stink bug relies on a specific gut bacterium for development and survival. Simulated warming showed that the elevated temperature suppressed the bacterium symbiont thereby significantly reducing adult emergence and survival (Kikuchi et al, 2016).

Species that previously did not interact such as sessile (immobile) plants and mobile insects, may begin to overlap due to warming, changing the composition of a community (Rasmann et al., 2014). Although, these changes may be mediated by plant mechanisms. Rasmann et al. used gradients in elevation to model how plant defense and herbivorous insects interact as habitats migrate. Herbivory decreases as elevation increases, but due to abiotic stresses, plants also develop mechanisms to resist herbivores such as leaf toughness and flavonoids. Further, viruses can induce changes in host plant behaviors. They often manifest physical color changes that affect vectors such as aphids and whiteflies.

## Insect Adaptations to Climate Warming

Warming temperatures and increased CO2 will have direct physiological impacts on insects particularly as it relates to development and reproduction. Insects living in colder climates are larger than those living in hotter climates, although smaller insects will be produced in increased temperatures because developmental rates are hastened and shorten the life span. Metabolic rates will increase, reducing body size and lipid reserves, and increasing protein due to hydric stress (Scheider et al, 2020). Fecundity will increase but larval survival will decrease due to reduced fitness of the host. In addition, lipids and protein levels will decrease and increase respectively when insects are exposed to high temperatures –which also leads to increased metabolic rates. However, CO2 and high temperatures may mitigate each other.

While climate change is expected to have an impact on many organisms' ability to survive, some insects have demonstrated the ability to develop adaptations to warming temperatures and increased CO2. These adaptations include morphology (color), biochemistry (heat shock proteins), interactions with new host plants, life history (maximum growth rate, voltinism, and interactions with prey, predators, mutualist and competitors). Insect groups that are mostly likely to evolve rapidly include those living within a large population, and those possessing neutral variation for relevant traits and heritability of key traits. Traits that constrain the ability to adapt include unequal trait linkage, biochemical or physiological limits, life history trade-offs, and gene flow from adjacent populations (Garnas, 2018). Traits that climate change will likely select for include thermal and drought tolerance, modified thermal limit for growth and voltinism, low temperature tolerance, dispersal traits such as wing size and flight behavior, reduced melanization for lighter colors, adaptive phenology, particularly for temperature, and photoperiod thresholds, extended diapause, generalism, and resistance to pesticides. Interactions with symbiont communities will also be predictive of survival. For example, the loss of antagonistic microbes will predict the success of invasive species.

As noted previously, butterflies are an important indicator species due to their susceptibility to temperature change. For example, *Colias* larvae have demonstrated adaptability to local climates for feeding and development, but adult adaptations manifest in melanin of the wings and thickness of the thoracic setae (Kingsolver et al, 2011). Larvae are cryptically colored, in that color is not related to thermoregulation, and will thermoregulate only in extreme temperatures. At dangerously high temperatures, adults will change their flight position to be parallel to the sun and reduce exposure. Semi-aquatic insects, whose juvenile and egg stages are spent in water, will have more thermally stable environments due to the high specific heat (ability to heat and release heat) of water. Other Lepidoptera exhibit similarly complex adaptions and reactions to climate variability at different life stages. Thermal extremes can not only impact survival but also life history traits, which will affect population dynamics. Insects can buffer thermal extremes through thermal regulation, plasticity, tradeoffs, or adaptations. However, there may be fitness related costs for individual and population dynamics in terms of development, reproduction, fitness, phenology synchronization (Ma et al, 2021).

Some insect species have demonstrated thermal melanism as a reversible color change, called seasonal polyphenism. In effect, darker colors protect in cold climates, and a warmer climate should select for lighter colored organisms, as light is reflected from lighter colors (Clusella-Trullas & Nielsen, 2020). However, climate change has and will resulted in complex interactions that may confound the true cause of color change. For example, pollution, vegetation change, and pathogen resistance, as well as coloration changes related to warning, sex and social interactions can drive color. Thermal melanism can be both an indicator of climate change but also an adaptation that supports survival beyond thermoregulation as locomotion can be improved. While melanism is impacted by a complex set of environmental and inherited genes, some insects such as lady bird beetles, butterflies, and flies are often good models of how color changes are impacted by climate factors.

While wildfires are predicted to increase due to drought, some insects possess adaptations to, or can even benefit from, wildfires. For example, prairie mole crickets benefit from improved acoustics in their burrow for signaling to mates, while forest beetles benefit from colonizing new, better quality habitats (Koltz & Murphy, 2018). Although high ground temperatures from severe fires can kill ground nesting insects, less severe fires can hasten development. Fires can also temporarily offer relief from specialist predators. Insect responses to fires can have lasting impacts on ecosystem functioning, as insects are key herbivores and pollinators –fire response is dependent on biomass recovery and habitat structure. For example, a fire can open space for flowering plants to 'thrive', attracting pollinators, particularly generalist bees. Additionally, frequent exposure to low impact fires can increase resin production in trees, which protects against bark beetles. Some insects have adapted to fire by developing the ability to detect fire or smoke via antennae (i.e., *cerambycid* beetles [longhorn beetles]), or other behaviors such as climbing trees and burrowing in soil.

Polyphenism is found in all living things and can result the production of new tissue or organs, among other changes. Insects have demonstrated phenotypic plasticity that can be triggered by environmental cues (epigenetics). However, climate change can impact the environmental stimuli that triggers polyphenism (Richard et al., 2019). For example, warming can modify chemicals released by predators which induce dispersal polyphenism in aphids. Temperature can also influence the density and quality of resources, which can trigger polyphenic changes. Warming can decrease plant quality causing aphids to produce more winged offspring. Temperature also influences plant and insect development due to the impact on phenology of host plants, leading pests of host plants to develop earlier and thus increasing density and triggering the presence of dispersal traits among other insects. Similarly, reduced plant/food quality can impact thermal plasticity and responses to thermal stress (Gautier et al, 2019).

Thermal limit sensitivity can vary among life stages (Kingsolver & Buckley, 2020). Insects in temperate or higher latitudes overwinter in a dormant state at a particular life stage, while tropical and subtropical insects are dormant during the dry season. Climate change will impact phenology and may cause a mismatch between development/emergence and when resources are available and when natural enemies are present. For species that only produce one generation a year, it is easier to predict the relationship between development and seasonal changes. For multivoltine species (more than one generation a year are produced), the relationship is less clear. Plasticity during diapause can be an important evolutionary response to warming temperatures and is an important component of survival. Insects can also undergo hardening and acclimation (Sgro et al, 2016). In addition, genetic variations can be due to responses to stress.

## Increase in Agricultural Pest Outbreaks

Due to increased range shifts, adult emergence and survivability, agricultural pest outbreaks are expected to become more prevalent. Aphids cause significant damage to crops worldwide. Aphids benefit from elevated CO2 levels compared to other herbivore insects. Research has shown though that some plants have developed increased R-gene resistance to aphids due to elevated CO2 (Johnson and Zust, 2018). Modelling heat stress events on small insects including aphids, Zhu et al (2019) found that sporadic, short, extreme heat events act as a buffer to longer heatwaves and can impact the fecundity of these pests. These are important considerations on whether global warming will indeed reduce the efficacy and damage done by these pests.

Schneider et al, (2020) simulated climate change using the model predictions for the year 2100 to assess an economically important Mexican bean weevil that attacks the common bean. Higher temps and CO2 improved development from egg to adult, and reduced fat storage and increased protein content but not body size. Fecundity and larval survival were lower than predicted via thermal tolerance, however.

Climate change can also negatively affect soil ecology bacterial composition that is beneficial for disease resistance, drought and heat stress (Shahzad et al, 2020). Conversely, increased CO2 will also affect stem and leaf growth, bringing about denser canopies that can promote fungal growth. Further, an increase in pest insects will impact crops and food insecurity. Increases in pests will also result in increased pesticide use, particularly in the American Midwest region.

Some insects can provide a solution to sustainable agriculture. Ants have a social organization that allows them to often act as a super organism (Benckiser, 2009). Ants can convert low nitrogen and high carbon, organic material by storing the nitrogen temporarily in the cuticle and by maintaining the nest carbon/nitrogen ratio. Ants also act as biological control by using antibiotics to keep other invaders at bay. While ants may provide a solution to carbon mitigation, caveats include the difficult in controlling a large enough colony to not induce detrimental effects.

## Insect-Borne Diseases

After decades of decline in vector-borne diseases in the United States, rates of infection are increasing at a rapid rate. Pathogens transmitted though arthropod bites including mosquitoes, ticks and fleas increased from 27,388 cases in 2004 to over 96,000 cases in 2016 (Halabi, 2020). As climate change is increasing the development rate, adult emergence and distribution ranges of insect vectors, disease incidences are only expected to increase.

Research has described the increase of Leishmaniases, which is transmitted by sandflies that are hosted by a variety of mammals in tropical climates (Kholoud et al, 2018). Further, increases in minimum temperatures creates endemic conditions because larvae are able to survive winters, when previously they did not. Therefore, prevalence of sandflies will increase because natural interruptions to development, such as seasonal cold bouts, will occur less frequently. It is important to note that socioeconomic factors and cultural practices can mitigate some of the incidences of insect vector outbreaks.

In another example of rising infections, Chagas disease is caused by the bite of the parasite, *Trypanosoma cruzi,* which is transmitted by *Mepraia gajardoi* and *Mepraia spinolai.* These triatomine are endemic vector species. These species are found in various climes of Chile. Climate modeling has shown that the distribution of these species will likely increase. Chagas disease has afflicted 6-8 million people and caused 12,000 deaths per year (Garrido et al., 2019). However, humid environments may cause rainfall to propagate the growth of fungi, which decrease the fitness of the species.

One of the most important vectors of disease are mosquitoes. *Aedes Egypti* has long been known to transmit malaria, chikungunya viruses, disease, Zika, West Nile and Dengue fever among other viruses. Each year 700,000 people die from malaria and dengue fever. These diseases are prevalent in tropical regions, but as global temperatures rise, it is reasonable to predict that the prevalence of mosquito and other insect vectors of diseases will increase and thus so will the incidence of these diseases in humans. Simulations of IPCC predictions, modeling temperature and CO2 changes for Brazil for the year 2100, on *Aedes Egypti* did not show an impact on larval survival; however, warmer temperatures increased adult emergence (shorter larval periods) resulting in a greater proliferation of the mosquitoes (Piovezan-Borges et al, 2020).

While the increase in vector borne diseases are mostly driven by globalization, climate change is expected to move the ranges of pests to higher latitudes or altitudes. In Europe, an increase in the tiger mosquitoes has caused an increase in dengue fever and ticks have increased Lyme and tick-borne encephalitis (Semenza & Suk, 2018).

## Conclusions

The predictions made in reviews of the ecological effects of climate published over 15 years ago still bear out in the most recent literature. The present paper confirms Parmesan's (2006) review of over 200 studies. These findings note that the following is expected to be observed: the range shifts of insects to higher latitudes, changes in plant and insect interactions, varied responses to warming, adaptations of species to new habitats in the new ranges, and new food resources. The findings are not linear, however. While range shifts are expected to go poleward, insects have also been observed to have varied thermal tolerances and have demonstrated plasticity that can impact favorable adaptations. Climate change will also impact phenology, and accordingly insect and plant interactions may shift. More research is needed to better predict how environmental factors resulting from climate change (warming and increased CO2) will be mitigated by epigenetics, plasticity and physical adaptations.

As noted above, the complex dynamic between plants and insects due to specific heat, transpiration and the presence of an understory, in addition to the great temperature difference between plant surface, ambient temperature, and ground temperature requires examination of how climate change will impact these microclimates and ecosystems. While climate change will favor generalists, distributions are more complicated to predict as insects may not migrate until their thermal limit is reached. For tropical insects, that limit may be reached more quickly. Climate change can increase swarming days and development of beetles is based on 'accumulated degree days' where a particular threshold needs to be met. Climate change will increase the range or shift the range to cooler temps, and new habitats will be established. While negative impacts such as range shifts and extinctions are expected to occur, complex ecological interactions may or may not be mitigated by climate change. Warming may reduce certain pests, but also that reduction may remove a food source for predators.

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