Chapter 11

Climate Change and Temporal and Spatial Mismatches in Insect Communities

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1. INTRODUCTION

As ectotherms, insect performance is heavily dependent on climate. Warming from climate change will alter insect development time, voltinism, foraging behaviour, emergence time and survivorship [1]. These changes, which alter population size and distribution, will affect the temporal and spatial dynamics of insect communities. Many insects provide important ecosystem services (e.g. pollination, decomposition, etc.) or affect human activities (e.g. via pest activity) and the effects of climate change could alter these services or exacerbate these effects. To date, geographic range shifts and early emergence are the best documented responses of insects to climate change, but some species have experienced population increases, changes in cyclical population dynamics and local extinctions or genetic and phenotypic changes that may be examples of rapid evolution. Further, more research is needed to understand how species-level changes affect interacting species. Overall, the sensitivity of insects to climatic factors makes them ideal for tracking and understanding the effects of climate change on biodiversity.

This chapter provides an overview of the effects of climate change on insects and their interactions with host plants and predators. We provide examples from the literature using herbivorous insects and their host plants and predators because herbivores are a large, well-studied group of insects that affect human activities and provide important ecosystem services. While the effects of increasing carbon dioxide levels are also important, particularly the resulting changes in host plant chemistry [2,3], the focus of this review is on the effects of warming and increased variability in precipitation associated with climate change. We also offer a novel analysis of northern range limit comparisons between North American butterflies and their host plant species to delineate the potential for spatial disassociations (i.e. differential range shifts between herbivorous insects and their host plants under climate change). Finally, we discuss potential impacts on future communities of insects and altered community effects on ecosystem services.

Life history traits such as resource specificity, geographic location, trophic level and dispersal ability are potentially good predictors of the magnitude and direction of the response of insect species to climate change. For example, habitat and/or resource specificity may limit the tolerance of specialists to changing conditions, potentially leaving habitats dominated by generalists. Warren et al. [4] found that butterflies with strong habitat specificity and limited mobility have reduced distributions and have fared worse under changing climatic conditions than generalists that share the same geographic range. Another study on beetles identified climate change response groups based on host plant specificity and distribution size, and the authors project that cosmopolitan species may be the most resilient to climate change while specialists will be faced with extinction if they do not move with their host plants [5]. Furthermore, Deutsch et al. [6] concluded that tropical species that have narrow thermal limits are more likely to be negatively affected by climate change. Yet Bale et al. [1] also highlight other vulnerable groups: insects that are cold-adapted, restricted to montane areas and also those in polar areas, where proportionally larger temperature increases are expected. In addition, Voigt et al. [7] report that species in higher trophic levels are sensitive to climatic change due to the combined indirect effects of climate change on lower trophic groups. When possible, we relate our article back to life history traits to allow for generalisations because insects as a taxonomic group are too diverse to be studied exhaustively. Our only hope for understanding insect responses to climate change is through generalisations from well-studied species to others.

Climate change can decouple interactions between insects and their resources and/or predators. Variable responses of these interacting species to climate change can lead to differential changes in the geographic ranges of species (herein ‘spatial mismatches’) as well as differential changes in the phenology, or timing, of species (‘temporal mismatches’). These mismatches could lead to places where and times when insect populations could greatly decline towards local extinction. In this review, we identify studies that demonstrate such mismatches, focusing, where possible, on those that have yielded negative effects on ecosystem services provided by insects.

2. DIRECT EFFECTS OF CLIMATE CHANGE ON INSECTS

The impact of climate change on insects is multifaceted. We begin by reviewing the direct effects of climate change on the temporal and spatial dynamics of insect populations. Thus far, enhanced individual and population growth in warmer temperatures have resulted in early emergence and changes in the location, through geographic range shifts, of insect species. A few studies also have linked climate change to genetic and phenotypic changes in insect populations, which we discuss here, but this response is not anticipated due to a number of constraints in evolution under human-caused, rapid climate change.

2.1. Temporal Changes

Insect life cycles depend on climatic variables such as degree days, minimum winter temperatures, average maximum summer temperatures, total precipitation and aridity. Generally, higher temperatures result in faster development, increased number of generations and increased overwinter survivorship [1]. As a result of enhanced and accelerated growth, climate change has been linked to phenological advances in many insects [8,9]. Gordo and Sanz [10] found earlier spring emergence in honey bee *Apis mellifera* (L.) and small white *Pieris rapae* (L.) populations in the Iberian Peninsula over the past 50 a. Several other studies of butterflies have documented early emergence [11–14], and it also has been observed in aphids [15,16] and in members of Heteroptera [17]. Decreased generation time due to warming has been observed in the mountain pine beetle (*Dendroctonus ponderosae*), leading to increases in the abundance of this pest species [18]. In some cases, the direct effect of increased temperature on insect development leads to simple population increases (e.g., *D. ponderosae*). In other cases, however, it can change synchrony of herbivores, host plants and predators, producing more complex community effects.

2.2. Spatial Changes

Increased overwinter survivorship, growth rates and generations have led to range shifts in many insect species. Many insects, including some pest species (e.g. the pine processionary moth (*Thaumetopoea pityocampa*)), have shifted their distributions poleward and to higher elevations to track recent climatic changes [19–27]. Still others have been unable to track the changing climate, and some have experienced range contractions or local extinctions [18,28–30]. These results and others have helped to establish a simple paradigm for the responses of species to climate change: populations will contract and go extinct in the equatorial portion of the range and poleward populations will expand and colonise new locations as the climate warms.

The ability of a species to shift its distribution is determined largely by its ability to disperse into newly suitable areas and the availability of suitable resources, that is breeding habitat and host plants, in those sites [4,31]. Thomas et al. [22] examined four insect species that recently expanded their ranges northward and found that two butterfly species increased the range of habitat types that they historically used while newly established populations of two bush cricket species had more longer-winged individuals than their source populations, suggesting that only the best dispersers were able to reach new habitat. Similarly, Warren et al. [4] have argued that climate change will leave habitats dominated by mobile generalists. Later, we discuss how limitations in resource use may lead to spatial mismatches between herbivorous insects and their host plants.

2.3. Genetic and Phenotypic Changes

Climate change has altered the selection pressures on insect populations, and some insects have responded via genetic and phenotypic change. Several groups have found that *Drosophila* populations are tracking climate change through genetic changes, for example, with genotypes characteristic of equatorial latitudes increasing in frequency with warming over the past few decades [32–34]. Rodríguez-Trelles and Rodríguez [35] found a decrease in diversity of a chromosome polymorphism in *Drosophila*, and they argue that this alteration correlates with climatic change. Rank and Dahlhoff [36] found allele frequency shifts in an enzyme related to heat stress in the leaf beetle (*Chrysomela aeneicollis*) that they linked to climatic changes occurring in the Sierra Nevada during the 1990s.

Phenotypic changes in insects also have been linked to recent climate change. For example, Bradshaw and Holzapfel [37] found that northern populations of the pitcher plant mosquito (*Wyeomyia smithii*) have shifted their critical diapause photoperiod towards that of their southern counterparts over the past 24 a. de Jong and Brakefield [38] found changes in melanism clines in the two-spot ladybird (*Adalia bipunctata*) that they also linked to recent climatic change. Such rapid evolutionary response under climate change, however, may be rare since high genetic diversity is required for adaptation to occur and co-variation among traits can slow the process [39,40]. Gienapp et al. [41] also caution that other studies claiming evidence of microevolution under climate change fail to separate genetic change from phenotypic plasticity.

Now that we have examined the direct effects of climate change on insect populations, we will explore the indirect effects of climate change. These indirect mechanisms of change can lead to spatial and temporal mismatches between insects and their food or predators. These mismatches ultimately affect the ecosystem services that we gain or lose due to insects.

3. HOST PLANT-MEDIATED EFFECTS ON INSECTS

The persistence of herbivorous insects depends highly on interactions with plants. Host plants impact herbivore populations directly through phenological and nutritional conditions [42–46]. For example, Nzekwu and Akingbohungre [47] showed that utilisation of different types of host plants has significant effects on insect development. Previous studies on butterflies also have shown that larvae need long-lasting host plants with the proper phenology to be able to withstand environmental changes [48]. Any variation in resources may influence the dynamics and abundances of herbivores [49]. Mismatches between herbivorous insects and their food plants are caused by differential responses in the two groups; for example, earlier emergence and range shifts in insects can occur at a faster rate than those of plants. These mismatches can lead to declines in insect populations. For those species that affect processes such as pollination, this could lead to a reduction in ecosystem services.

3.1. Temporal Mismatches Between Insects and Their Host Plants

The indirect effects of climate change on insects are largely occurring because of altered host plant phenologies and quality [50–53]. Reduced host plant quality results in increased mortality because insect larvae compensate for the decrease in nutritional value by increasing consumption and development time, which in turn increases their exposure to predators and other environmental stresses [2,54]. In addition, species that feed on ephemeral resources are more likely to be sensitive (e.g. increased population variability) to asynchronies with host plants [55]. For example, insects whose eggs hatch before bud burst in their host plants will likely starve while those that require young foliage that hatch late will be forced to eat leaves that are more heavily defended [56].

Experiments have shown that temperature increases are altering insect development proportionately more than that of their host plants [57,58]. In fact, asynchrony has already occurred between the winter moth (*Operophtera brumata*) and its host plant, pedunculate oak (*Quercus robur*) because *O. brumata* egg hatch has advanced more so than bud burst in *Q. robur* [59]. In this particular case, however, the authors speculate that high levels of genetic variation in *O. brumata* may allow rapid adjustment to phenology of *Q. robur* over time. Such information about the plasticity of species is lacking for most taxa; therefore, it is difficult to predict if this will be a general response (see Visser [60] for a discussion of adaptation to climate change).

Insects that provide important pollination services, for example, butterflies, are particularly vulnerable to temporal mismatches with their food resources. On average, butterfly species are advancing faster than herbs [61]. For example, in Britain, the migratory red admiral butterfly (*Vanessa atalanta*) has advanced its return flight over the past couple of decades, but its host plant, stinging nettle (*Urtica dioica*), has not advanced its flowering time, creating a mismatch in phenology [62]. In another study, McLaughlin et al. [28] linked increased variability in precipitation associated with climate change to extinctions in two populations of the Bay checkerspot butterfly (*Euphydryas editha bayensis*). This variability caused extinctions by accelerating plant senescence relative to larval development [28,48]. Simulations by Memmott et al. [63] concluded that 17–50% of pollinators, including insects, will suffer a disassociation with their food, and, as with other cases, small diet breadth was a greater risk factor for asynchrony with food. Later, we will discuss how other species that negatively affect human activities are benefiting from temporal mismatches with predators.

3.2. Spatial Mismatches Between Insects and Their Host Plants

In many insect systems, the dispersal ability of the insect is greater than its host plant. Such differential dispersal capacity of specialist herbivores, if they are to remain host plant-limited, could cause range contractions. Many insects have the ability to move long distances. For example, some butterflies in Europe have shifted their distributions northward 240 km in the past 30 a [19]. Recent shifts are not as well documented for plants, but post-glacial range expansions with past climate change were up to 100 km over 100 a with a median of only 20–40 km per century [64]. This is not surprising since plants, especially large trees, typically have long generation times and lower recruitment than insects [65]. These differences between plants and insects are further complicated by habitat fragmentation, which may be especially restrictive for plant migrations because of their limited dispersal ability [66–68].

To illustrate the potential impact of spatial mismatches under climate change, we analysed the relationship of specialist butterflies reaching a northern geographic limit in the United States with that of their primary host plants. A total of 74 butterfly species from 15 subfamilies have both a northern range boundary within the United States and utilise a single host species. Of these, 59 species have county-level distribution records for both butterfly and host plant.

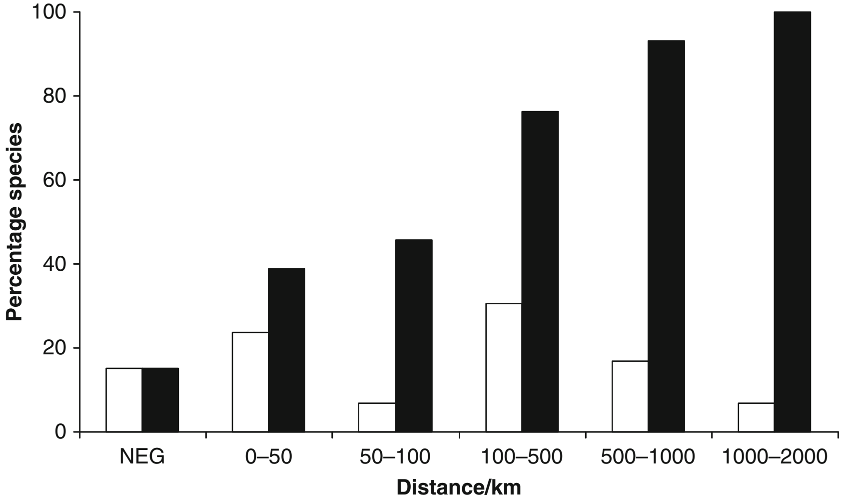

FIGURE 1 Categorisation of spatial distances between the northern-most geographic distributions of host-specific butterflies and their larval host plant in North America. Distances based on county-level centroid locations of observational butterfly and vegetation records (ET SpatialTechniques, ArcGIS, Version 9.0) [71]. White bars are totals within each category and black bars represent the additive totals across categories.

Geographic centroids were calculated (ET SpatialTechniques, ArcGIS, Version 9.0, ESRI) for the northern-most county within each species' range [69] and that of its host plant [70]. Spatial discontinuity distances were calculated by subtracting the centroid latitude of the host plant from that of the butterfly species (Fig. 1).

Of the 59 specialist species assessed, 46% show a northern-most geographic range distribution within 100 km, 76% within 500 km, 93% within 1000 km and 7% extend more than 1000 km beyond the range edge of their host (Fig. 1). Of these, ten species (17%) reach their current range limit in the same location as their host. Furthermore, nine species (15%) show distributions extending beyond their current food plant range margin (negative values in Fig. 1). This is likely a result of sampling error arising from the scale of the observational data used, broad longitudinal distributions leading to multiple northern range fronts, inaccurate assessments of range boundaries due to occasional migrants into sink habitats or undocumented range extensions of species.

Spatial differences between butterfly and host range margins will determine how far butterfly ranges can expand under climate change, assuming relatively static host plant margins and consistent host preference for specialist herbivores. Where the geographic distance between the boundary of the butterfly and its host is small, there may be a small distance available for butterfly range expansion. Given the extent of range change seen in European butterflies (upwards of 240 km over 30 a) [19], we would estimate that up to 59% of specialist butterflies in North America will reach the range limit of their host by 2050, assuming no change in host plant distribution and unlimited dispersal. For example, the Florida Leafwing, *Anaea floridalis*, which occurs less than 100 km from the edge of its host distribution, will approach host boundaries in just over a decade, as will other insect species. Up to 4% of the total butterfly fauna of North America could experience contracting geographic ranges where limiting food resource distributions interact with future climate warming to prevent adequate climate tracking. Simple risk assessments such as this procedure of comparing insect versus host plant poleward distribution boundaries can help identify species of greatest risk under climate change.

Now that we have explored how climate change can cause temporal and spatial mismatches between herbivorous insects and their food, we turn to examine how climate change can decouple interactions between insects and their predators, potentially leading to increases in and movement of species that diminish habitats, that is via outbreaks.

4. PREDATOR-MEDIATED EFFECTS ON INSECT POPULATIONS

Few studies have considered the influence of climate change on higher trophic levels (i.e. predators, parasitoids and pathogens) and its subsequent effects on insect herbivore populations. Climate change is expected to affect the relationship between predators and their prey by independently altering the dynamics of each trophic group [71]. In addition, higher trophic levels have been found to be more sensitive to climate change, likely due to the combined effects of climate change on lower trophic levels [7] and greater sensitivity to abiotic stress among higher trophic levels [72–74]. Changes in top trophic levels can cause trophic cascades. The loss of predators, therefore, can disrupt interactions between lower trophic levels including herbivores and primary producers [75,76].

Predators, particularly parasitoids, play an important role in controlling insect populations [77–82]. In some cases, they have been found to cause cyclical dynamics of herbivorous insects ([82,83]; but see Refs. [80,84] for exceptions). Recent studies of forest insects have linked population outbreaks to climate change as a result of phenological changes in insect life histories [85–87]. The role of higher trophic levels in causing insect outbreaks under climate change, however, has only started to be addressed [88]. We review the current observations and evidence to date of climate change causing temporal and spatial mismatches in predator–prey relationships and its subsequent effects on herbivore outbreaks.

4.1. Temporal Mismatches Between Insects and Their Predators

Herbivore development often changes rapidly and dramatically in response to changing climatic conditions, and this leads to large temporal variation in their populations. Parasitoids also may be affected by both climate variation and its effect on host dynamics. For example, a study by Stireman et al. [88] used data from multi-year inventories of caterpillars reared from natural ecosystems to relate parasitism frequency to interannual climate variability. They found that parasitism frequency was negatively related to variability in precipitation. This suggests that there will be increased outbreaks of herbivores occurring under climate change as a result of increased climate variability causing mismatches in parasitoid–herbivore interactions.

Temporal mismatches could occur if predators and their insect herbivores respond differentially to changes in climate. Hosts and parasitoids may have different thermal preferences or different capacities to survive extreme temperatures and differential responses to climate could disrupt synchronisation [89]. For example, there is evidence that parasitoids often have lower temperature tolerances than their hosts [90, and references therein]. Models predict that increasing phenological asynchrony between predators and prey due to differential responses to climate can cause destabilisation of their population dynamics and extinction of the system [91,92].

Few studies, however, have empirically shown differential responses of predators and prey to changes in climate. Van Nouhuys and Lei [93] found that the light-coloured parasitoid *Cotesia melitaearum*, which is restricted to shaded habitats, develops slowly, while the dark-coloured larvae of its butterfly host, *Melitaea cinxia*, seeks out warm microhabitats where the sun increases body temperature, allowing individuals to develop faster. In cool but sunny springs, therefore, parasitoids emerged after most of their larval hosts had already pupated. In warmer springs, the synchrony between host and parasitoid was maintained and parasitism rate was high. In this study, the authors detected no effect of synchrony on local host population size, but disruption of synchrony is likely important for overall host metapopulation dynamics.

There is evidence of increasing sensitivity to climatic variation and other forms of abiotic stress in higher trophic levels [7,73,74,94]. This could be due to combined effects of climate variation on lower trophic levels [7]. Menge and Sutherland's [72] theory of community regulation predicts that higher trophic levels are more sensitive to abiotic stress as organisms in high trophic levels are likely to be larger and more mobile, enabling them to disperse from suboptimal areas. Species in higher trophic levels have been found to have slower recovery rates after catastrophic events [95,96], for example. In addition, Spiller and Schoener [94] found reductions in predators after two hurricanes in 1999 and 2001 on ten small Caribbean islands that likely explained observed increases in herbivory. Preisser and Strong [74] also observed mass mortality of lupine, *Lupinus arboreus*, off of the coast of California after 2 years of below average precipitation that was associated with El Niño events. Lupine die-offs were due to an outbreak of a root herbivore, *Hepialus californicus*. *H. californicus* populations are regulated by the nematode *Heterorhabditis marelatus* [97], which is dependent on soil moisture for movement. In their study, Preisser and Strong experimentally increased soil moisture content to levels of wet El Niño years (above average precipitation levels) and found that increases in moisture levels directly affected the predatory nematode but not lupine or the ghost moth. Increases in the predator suppressed *H. californicus,* indirectly protecting lupines. Climate change is expected to increase such extreme events [98].

4.2. Spatial Mismatches Between Insects and Their Predators

Species are shifting their ranges in response to climate change, but as discussed above for the movement of herbivores and their plants, insect herbivores and their predators can shift at different rates. Predators that rely on close associations with their hosts such as parasites and parasitoids are expected to be especially affected by changes in the spatial distribution of their hosts. Colonising hosts could lack parasites or parasitoids and/or hosts that are infected could be less fit and therefore less successful in establishing in new locales [99]. In addition, native predators in newly colonised areas could switch from native hosts; however, some native predators may need to evolve phenological, behavioural or ecological specialisations before they can affect the colonising species. Predator species complexes, therefore, may be less rich with lower attack rates than those in the native range [100–102]. Reductions in parasitoids or other predators at the edges of expanding ranges of herbivorous insects could give expanding species an advantage (e.g. increases in population size) through release from predator control.

Only one study to date has investigated differential rates of spread of insect herbivores and their parasitoids under climate change. Menéndez et al. [103] found that the Brown Argus butterfly (*Aricia agestis*), a species that has shifted its range northward due to climate warming, experienced lower mortality from parasitoids in newly colonised areas. Other studies of invasive insects that have been introduced into new areas or of insects that have expanded their ranges as a result of their host plants being introduced also have found lower parasitoid rates in newly colonised areas [100,104]. Reductions in enemies of invasive species in their invaded ranges have been documented for a number of other plant and animal species as well (e.g. [105,106]).

Menéndez et al. [103] found no difference in parasitoid richness in the expanded and native ranges of *A. agestis*; they did, however, find a difference in parasitoid species composition. The majority of species attacking *A. agestis* in its newly colonised range were generalists that were already present in that area attacking *Polyommatus icarus,* a native butterfly. Other studies have found that specialist parasitoids were lost when insect hosts expanded their ranges and that the majority of species attacking hosts in their invaded range were generalists that switched from alternative native hosts [100,104,107].

Specialist parasitoids that follow hosts are likely to be more efficient predators than generalist parasitoids that have switched from native hosts. Although more generalist parasitoids attacked *A. agestis* in its expanded range, the most abundant parasitoid was one that is believed not to have been present historically and therefore is likely a specialist that expanded its range with *A. agestis* [103]. Other studies of invading hosts have found similar results- that the most abundant predator in the invaded range are specialist predators that followed from the native range [106].

Generalist species in the expanded range could be less effective predators on new hosts that have undergone a range expansion. For example, while parasitoid species richness was similar in the native and expanded range of *A. agestis*, attack rates were lower for *A. agestis* compared to the native host *P. icarus* [103]. Similar results were found for a recent invasion of the variegated leafhopper (*Erythroneura variabilis*) into California's San Joaquin Valley. *E. variabilis* experienced lower attack rates from a shared parasitoid than the native grape leafhopper, *E. elegantula* [108]. Therefore, there is evidence that native parasitoids are slow to shift to new hosts because they are locally adapted to native hosts.

Over time, assemblages of predators and hosts in the invaded range would be expected to become similar to assemblages in the native range as enemies catch up to expanded host distributions. Most studies have found an increase in predator richness over time in the hosts' invaded or expanded range, however, resulting in different species composition than in the hosts' native range. Schonrogge et al. [104] found that for several cynipid wasps that were expanding their ranges, parasitoid assemblages in the introduced range were determined more by the parasitoid assemblages attacking existing cynipid species than by the parasitoids in their previous ranges.

No study to date has linked reduced predation after a host range shift to increases in populations of species that have undergone an expansion. Experimental manipulation of predators of species undergoing range expansions in different portions of their ranges is needed to link reductions in parasitoids in expanding ranges to changes in population dynamics. The invasion biology literature provides frameworks to test a reduction in enemies to host release in expanded ranges [99,109,110]. However, no tests to date have been conducted for insects expanding their range in response to climate change. Since many insects are important pests, we now discuss how climate change could favour native and non-native pests that impact important human activities and ecosystem services, including loss of forests and reduction in carbon sequestration.

5. CLIMATE CHANGE AND INSECT PESTS

Traits that enable a species to respond favourably to climate change are those very traits that pest species (native and non-native) often possess. For example, pests often have wide diet breadth, are multi-voltine, have rapid growth rates, are highly mobile and/or are phenotypically plastic [111–113]. Since many pest species have these traits, they are likely to respond favourably to climate change, perhaps more so than those that are specialised and/or rare.

Chown et al. [114], for example, found that invasive springtails were more phenotypically plastic in their ability to cope with desiccation under warming conditions compared to indigenous springtails.

Insect pests affect many human activities and ecosystem services. Many insect species are already damaging, and some may become more so under climate change. Insect pests are the most important agents of disturbance in North American forests, affecting areas almost 50 times larger than fire [18,115,116] with an estimated average annual economic cost of 2.1 billion dollars in the United States [117]. Many insect pests are non-native; up to 40% of major insect pest species in North America are invasive [118] with 62% of 29 major insect forestry pests being non-native [117]. Insect pests, both native and non-native, not only have economic impacts, but also have significant ecological impacts. For example, the invasive balsam woolly adelgid (*Adelges piceae*) has caused extensive death in relict stands of Fraser fir (*Abies fraseri*) and threatens other native species that depend on *A. fraseri* [119].

Many pest species have expanded their ranges as a result of climate change. The pine processionary moth (*T. pityocampa*), a pest of *Pinus* spp. and other conifers in southern Europe, has shifted 87 km north and to higher altitudes as a result of increased winter survival due to increased winter temperatures in the region over the last 30 a [26]. The mountain pine beetle (*D. ponderosae*) has also moved northward and to higher elevations in western Canada due to increased summer and winter temperatures and reduced precipitation [120]. In addition to expanding their ranges, these and other pests also are outbreaking more frequently and for longer durations [85–87]. Although causes of insect outbreaks are complex, observed increases in outbreak severity have been linked to both the direct effect of climate change on insect physiology and indirect effects through changes in their host plants (e.g., if their host plants are more drought stressed) and predators (e.g. [85–88,121–123]).

Finally, the effect of climate change on forest insect pests can affect the current balance of forest budgets. Widespread tree mortality due to *D. ponderosae* causes forests to have low primary productivity and increased carbon emissions as a result of tree decay. Over the next 20 a, it is predicted that pine forests in British Columbia, Canada will become net carbon sources rather than net carbon sinks mediated by increases in the severity of *D. ponderosae* outbreaks from recent climate change [86,87,124].

6. CONCLUSION

In this review, we demonstrate that the direction and magnitude of the effects of climate change on insect species are multifaceted. Changes are occurring both spatially and temporally, and these changes result directly from changing climate and indirectly through interactions with species in lower (i.e. plants) and upper (i.e. predators) trophic levels. In addition, trophic cascades can occur such that changes in interactions between herbivores and their host plants affect higher trophic levels, and changes between predators and herbivorous prey can affect primary producers.

Further, species traits such as dispersal ability, trophic level and degree of specialisation are potentially good predictors of the effects of climate change. Our prediction is that future communities will be dominated by mobile generalists, species with fast generation times, those that have high dispersal capabilities or those that have been dispersed around the globe by humans. Many of these species are already pests, and new species could become pests on new host plants or in new locations under climate change. These opportunists may affect important human activities, such as forestry and agriculture, with extensions into the role of forests as carbon sinks. Insects that provide important ecosystems services such as pollination or biological control could not fare as well.

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