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The effect of climate change on invasive crop pests across biomes

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Climate change has various and complex effects on crop pests worldwide. In this review, we detail the role of the main climatic parameters related to temperature and precipitation changes that might have direct or indirect impacts on pest species. Changes in these parameters are likely to favour or to limit pest species, depending on their ecological context. On a global scale, crop pests are expected to benefit from current and future climate change. However, substantial differences appear across biomes and species. Temperate regions are generally more likely to face an increase in pest attacks compared with tropical regions. Therefore, climate change effects should be studied in the context of local climate and local ecological interactions across biomes.

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Introduction

Human-induced climate change is now affecting all regions of the world [1] and has various impacts on most ecosystems, including the cultivated lands [2]. By affecting both plants and insects in various ways, climate change is predicted to be one of the major drivers of change in crop–pest interactions worldwide, along with agricultural intensification. While climate change can impact plant physiology in multiple ways, therefore, though changes in plant defences, directly or indirect impact insect herbivores or their predators [3], this review will focus on the direct link between climate change and insects, and not the interaction between insect herbivores and plant responses. Insects are ectothermic, tend to generally have a short life cycle, and are more mobile than plants. As a consequence, insect species can potentially react faster to climatic variations than plants [4,5]. In particular, insects are well known to be very sensitive to temperature. A warmer and changing climate is thus likely to stimulate plant consumption by pest species, in turn reducing crop yields in the future [6•]. However, climate change is a complex process that, in addition to the overall increase in mean temperature, can involve a wide variety of other climate parameters. Among other shifts, potentially disproportionate changes in extreme temperature and in annual, seasonal and extreme precipitation are likely to occur. In addition, changes are expected in a whole suite of climate-related parameters, which can act on one another and have different impacts on pest species. Furthermore, climate change affects the entire ecosystem in which a pest species lives, therefore affecting not only the herbivore insect pest, but also the host plants, the predators and parasitoids of the herbivores, and the interactions between all organisms [7,8••], therefore affecting species via top-down and bottom-up effects [9].

When averaged across the globe, climate change is characterised by an increase in mean global temperature, which is currently reaching 1.1°C average positive deviation compared with the preindustrial era [1]. However, higher latitudes and continental areas are warming faster than this average. Extreme events such as droughts, heavy precipitation and heat waves are also increasing in terms of both frequency and intensity in most regions of the world. According to all available scenarios, these climatic trends are predicted to amplify during the next decades, with important impacts on ecosystems, including cultivated ones. Climate change has already impacted insect pest species in many ways, including driving shifts in distribution poleward and towards higher elevations [10], causing shifts in spring phenology [5,11•], and increasing the number of annual generations by accelerating their development and lengthening their developmental season [12]. In several systems, climate change can favour the build-up of insect pest populations: for instance, milder temperatures compared with preindustrial times may enhance rates of winter survival, therefore favouring the overwintering of species, including invasive ones, in temperate regions [13]. On the other hand, climate change can also be detrimental to insect pests: for instance, heat waves may be a limiting factor for some species that are already living close to their thermal limits [14], and heavy precipitation may also inhibit flying or

Table 1

Summary table highlighting the principal findings of this review relating climate change effects on insect pest-crop interaction across major biomes (tropical versus temperate)

Climatic parameter	Region	Impact of climate change on pests
Mean temperature during the development season	Temperate, tropical	Mostly expanding [12,20,21]
Minimum temperature during winter	Temperate	Expanding [13,24]
Maximum temperature during summer	Temperate, tropical	Reducing [29,30]
Precipitation	Tropical	Mixed [15,33]
Extreme weather events	Temperate, tropical	Mixed

mating success [15]. In sum, all crop–insect–pest interactions rely on specific climatic parameters, with either positive or negative impacts for pest species and in turn for crops, depending on the context and magnitude of the changing climate parameters.

In this review, we present the multiple and complex impacts of climate change on crop pests in light of the most recent publications. Specifically, we highlight the impact of key climatic parameters, namely temperature and precipitation, on insect pests and pest–crop interactions. Because of space constraints, we only here briefly touch on the effect of climate change on higher trophic levels (e.g. predators and parasitoids), although we acknowledge that climate change, by impacting carnivore insects, can indirectly impact the herbivores in unexpected, and to date, still largely unexplored ways [16•,9]. Because climate change patterns differ depending on the local macro-climate and meso-climate [1], we also describe differences between temperate and tropical regions (Table 1). Finally, we discuss the results of the impact models used to predict trends in pest damage under future climates, and the ways to understand the impacts of climate change on the ecological interactions involving pest species in agricultural ecosystems.

Impacts of temperature

Temperature plays a key role in insect development. The correlation follows an asymmetric curve ranging from a cold lethal threshold to a hot one, with an optimum temperature in between [17]. Therefore, mean temperature during the development season is a major determinant of population dynamics for many pest species, although with a high degree of context dependency [18]. In contrast, the minimum and maximum temperature extremes determine the potential geographical range and species distribution, in addition to influencing population dynamics.

Mean temperature during the development season

An increase in mean temperature leads to accelerated insect consumption, development, and movement, fecundity, survival, generation time, population size, and geographic range distribution, and these effects depend on the species' ecology, feeding mode and degree of specialization [19]. For example, polyvoltine pest species (i.e. those capable of producing more than one generation per year) are likely to produce additional generations during warmer years [20,21], and thus, producing multiple attacks per season. A second major impact on insect pests occurs when mean annual temperatures are close to the species' thermal optimum. In this case, the growth rate increases, which leads to greater food consumption [22]. Finally, an increase in mean temperature above the thermal optimum is expected to reduce pest populations and, if not detrimental to the plants, enhance crop yield [23].

Minimum diapause temperature

Resistance to low temperature during diapause differs among species. In temperate regions, minimum winter temperature is a key factor determining the potential extent of the population range and the population dynamics of less resistant pest species [24,25]. An increase in minimum temperature can thus lead to an expansion in terms of latitude and/or elevation [13]. Colder winters may delay and reduce the outbreaks of some pest species. For example, a negative impact of cold winter days (Tmin $<-5°C$) on spotted wing drosophila (*Drosophila suzukii*) outbreaks was observed in north-western America [26]. Likewise, Gu *et al.* [27] identified late-spring cold events (Tmin $<10°C$), which also tend to increase in light of the current inflated climate variability [28], as a limiting factor for the cotton bollworm (*Helicoverpa armigera*) in north-western China. Increasing winter and spring minimum temperatures thus usually favours pest outbreaks, particularly in temperate regions.

Maximum summer temperature

As insects have upper lethal temperature thresholds, the increase in frequency and intensity of heat waves is likely to increase the mortality of sensitive pest species [29,30]. Higher maximum temperatures may also limit adult dispersion. Still, the lethal impact of high temperatures strongly depends on the life stage of the insects, and on their phenotypic plasticity [31]. In a laboratory experiment using green peach aphids (*Myzus persicae*), nymphs and reproductive adults were more severely impacted than late-reproductive adults [32]. Along these lines, another major challenge is to predict the impact of heat pulses across trophic levels [33,34]. For instance, the growth and developmental responses differed significantly between diamondback moth (*Plutella xylostella*) and its specialist endoparasitoid *Diadegma semiclausum* when exposed to daily heat pulses [33]. The parasitoid was more sensitive than its host, suggesting that extreme temperature fluctuations may disrupt host–parasitoid synchrony, and ultimately have cascading effects on host plants. On the other hand, heat waves might likely affect host plant nutritional quality and defences, therefore affect insect pests through bottom-up effects, but these effects need to be studied more thoroughly across a range of systems [35].

Impacts of precipitation

Compared with temperature, the overall impact of precipitation changes on pest species and on their host crop plants is much more difficult to assess, mostly due to a more limited number of studies, particularly in temperate regions. Impacts of extreme events, such as heavy precipitations or droughts, on insects have been observed in tropical regions. In southern China, heavy precipitation during the preflood season has been observed to be a limiting factor for the eastward summer migration of the white-backed planthopper (*Sogatella furcifera*) [33]. On the other hand, very dry seasons can indirectly impact insect herbivores by limiting the availability of food during their development period. For instance, it has been postulated that cotton infestation by the cotton bollworm (*Helicoverpa armigera*) in northern Benin depends on the extent of heterogeneity of host plants (cotton, corn, tomato, sorghum) in the landscape, which in turn depends on the variability in drought and flooding patterns [15]. Similarly, changes in rainfall patterns could induce changes in coffee berry ripening time, and in turn negatively impact the development period of the coffee berry borer (*Hypothenemus hampei*). The present magnitude of precipitation changes in temperate regions (e.g. extreme summer droughts along the US west coast and very humid summers in Central Europe) thus likely impacts crop plants and their insect pests, but further assessments and the occurrence of similar events over time and across species are necessary to explain the processes in detail. For instance, drought might affect sap-feeding insects, such as whiteflies or spider-mites, differently than it would affect lepidopteran stemborers, but such comparative studies are to our knowledge largely lacking.

Impact of temperature and precipitation on migratory pest species

Several insect pest species' geographic distribution is tropical, but climate change can drive to expand their ranges in poleward waves during the favourable season, or to migrate en masse to temporary locations where they can do enormous damage, such as the migratory locusts [36]. Climate change is likely to have a major impact on these migrations, and both temperature and precipitation can be critical parameters driving the impact of migratory pests on crop plants [37]. Meynard *et al.* [38] highlight the role of change in precipitation patterns on desert locust outbreak in East Africa. While droughts and desertification are expected to reduce the outbreaks, the predicted increase in extreme events, including rainfalls, is likely to produce massive outbreaks reaching unusual places. This phenomenon was observed in 2018 after two tropical storms in the Arabian Peninsula. In China, Zeng *et al.* [39] related the increase in temperature with an expansion of the migration range of the noctuid *Agrotis ipsilon*. This is associated with an advancement of the phenology of the species, and with an expansion of the potential overwintering areas, as a response of the increase in winter temperature.

Impact models

While strong context dependency remains, some generalities about climate-change-mediated impacts on insect pests can be modelled. Based on climatic models, Deutsch *et al.* [40••] predicted a global increase in crop pest damage to wheat, rice and maize production of 10–25% per degree of global warming. Such losses will likely concern every biome, but temperate regions are expected to be more affected than tropical ones. This is also true for the presence of insect pests at a given site. Indeed, according to Yan *et al.* [41••], the mean probability of invasive pest presence should increase at the global scale under future climate conditions. Specifically, an increase in insect pest species richness is predicted to occur mainly in areas with a current mean temperature below 21°C, and in areas with current annual precipitation below 1100 mm. However, responses to climate change differ strongly among pest species and among regions [42•,43]. The damage created by a single pest species may simultaneously increase in some regions and decrease in others [21].

Conclusions

The impacts of climate change on crop insect pest species are multiple and complex. They depend mainly on temperature, with specific impacts of both mean and extreme temperatures, but they likely also depend on other climatic factors such as heavy precipitation or drought. While consequences can be both positive and negative for pest species, most climate change scenarios tend to favour pest proliferation worldwide [40••]. This is particularly valid in temperate regions, where the cold season currently remains a limiting factor for pest development. Further, invasive species are predicted to proliferate and expand more easily in temperate than in tropical regions [44]. Overall, the increasing impact of climate change on insect pests is expected to extend into the future, especially as mean global temperature is predicted to increase during the next decades according to all available climatic scenarios [1].

The impact of climate change on crop pest damage at different scales of organisation of life, from biomes to local agroecosystems, remains difficult to model, as it involves complex ecological relationships between plants, insect herbivores and their natural enemies [16•]. From a top-down view, the effects of higher temperatures and more severe droughts are likely to reduce the pressure parasitoids impose on pests [45]. Further, phenological mismatches can occur between pest species and their host plants or predators, although their impacts remain difficult to evaluate [46••,47]. This phenomenon threatens specialist predators more than polyphagous ones [48•], and could have an impact on the effectiveness of biological pest control. From a bottom-up perspective, severe droughts, for instance, are likely to increase plant vulnerability, leading to more damage in the case of a pest attack [49], thus potentially synergistically exacerbating the negative impact of insect pests on crop yield.

Based on our review of recent literature, we recommend that future models of pest damage consider: (1) the multiple dimensions of climate change, (2) the direct impacts of climate change on different crop species, (3) the direct impact of climate change on various pest species, (4) the impacts of climate change on higher trophic levels, (5) the broader farming context, (6) the core determinants of ecological resilience, and (7) the combined effect of all these impacts. While such a complex task might seem overwhelming at first, agroecosystems can in fact be broken down into their constituting parts more easily than natural ecosystems [43,50,51], and in this sense they could actually be used as case studies for modelling the impacts of climate change across entire biomes. Such novel modelling approach will be important in term of selecting novel plant varieties that will be more resistant to the interactive effect of climate variables' change and insect responses to these changes [52].

Conflict of interest statement

Nothing declared.

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- • of special interest
- •• of outstanding interest

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