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Complex responses of global insect pests to climate warming

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Although it is well known that insects are sensitive to temperature, how they will be affected by ongoing global warming remains uncertain because these responses are multifaceted and ecologically complex. We reviewed the effects of climate warming on 31 globally important phytophagous (plant-eating) insect pests to determine whether general trends in their responses to warming were detectable. We included four response categories (range expansion, life history, population dynamics, and trophic interactions) in this assessment. For the majority of these species, we identified at least one response to warming that affects the severity of the threat they pose as pests. Among these insect species, 41% showed responses expected to lead to increased pest damage, whereas only 4% exhibited responses consistent with reduced effects; notably, most of these species (55%) demonstrated mixed responses. This means that the severity of a given insect pest may both increase and decrease with ongoing climate warming. Overall, our analysis indicated that anticipating the effects of climate warming on phytophagous insect pests is far from straightforward. Rather, efforts to mitigate the undesirable effects of warming on insect pests must include a better understanding of how individual species will respond, and the complex ecological mechanisms underlying their responses.

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Insect pests are major constraints on agricultural and forestry production (Oerke 2006; Pureswaran *et al.* 2018), and their impacts are likely to increase in importance as the global human demand for food (Godfray *et al.* 2010), fiber, bioenergy feedstocks, and other renewable products continues to grow (Figure 1). The consequences of infestations are sizeable: pest species – mainly insects – cause estimated losses of approximately 18% of total global annual crop production (Oerke 2006). Although there are no similar global estimates for forestry systems (Niquidet *et al.* 2016), forest pests such as the gypsy moth (*Lymantria dispar*) and mountain pine beetle (*Dendroctonus ponderosae*) are known to have serious ecological impacts. These include the displacement of native tree species, and widespread defoliation and mortality, thereby disrupting ecosystem functioning and reducing biodiversity (Fajvan and Wood 1996; Janes *et al.* 2014). In addition, managing insect pests is costly. For example, global efforts to manage the diamondback moth (*Plutella xylostella*) cost an estimated $4–5 billion annually (all dollar amounts are expressed in US dollars; Zalucki *et al.* 2012). Moreover, many agricultural and forest insect pests are invasive species that contribute to the estimated $76.9 billion annually required to manage and mitigate the impacts of biological invasions worldwide (Bradshaw *et al.* 2016).

Ongoing and anticipated challenges posed by phytophagous insect pests are likely to be exacerbated by projected global warming (IPCC 2013), which may promote pest population growth, increase outbreak frequencies, and facilitate the geographic expansion of many pest species, resulting in greater economic losses and reductions in food security (Sutherst *et al.* 2011; Andrew *et al.* 2013; Thackeray *et al.* 2016). However, insect pest severity may not be uniformly increased by warming temperatures, given the narrow environmental niche requirements, physiological tolerances of insects, and the variable effects of temperature on their phenology and life history. Because of these sensitivities, regional climate warming could

In a nutshell:

- Insect pests greatly affect the productivity and profitability of agricultural and forestry operations, and such impacts are expected to become more serious as the global climate warms
- The responses of 31 major global pest species to ongoing climate warming suggest that the damage they cause will increase for nearly half, but the majority exhibited mixed responses among possible categories (range expansion, life history, population dynamics, and trophic interactions) indicating that a single species can both increase and decrease in severity
- These mixed responses vary according to geographical region and biological traits
- The responses of insect pests to ongoing climate warming are not easily generalizable, and species must be assessed individually so their responses can be predicted more accurately

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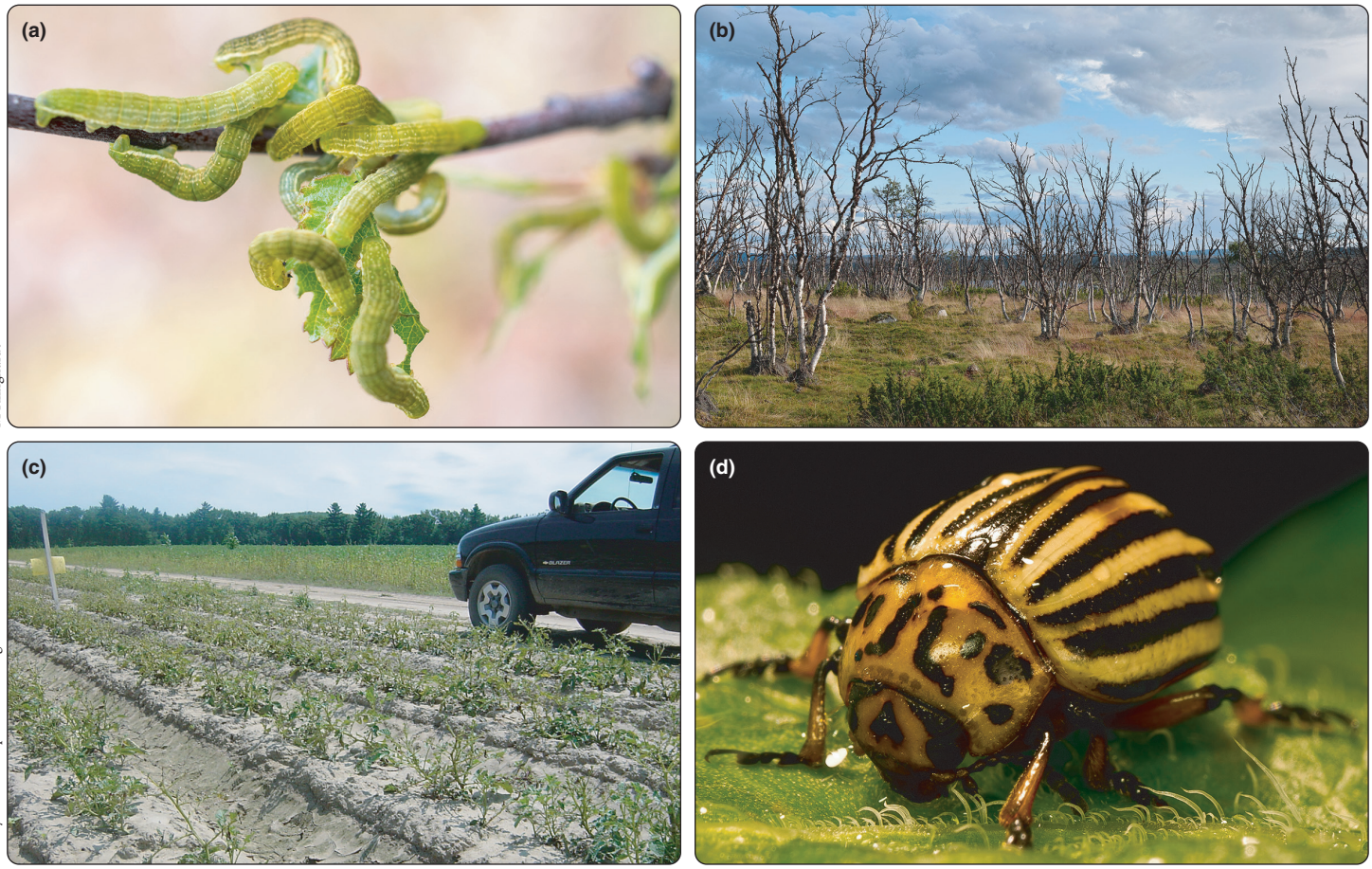

Figure 1. Examples of insect pests and the damage they cause. (a) Feeding by larvae of the autumn moth (*Epirrita autumnata*) can lead to mass mortality of (b) mountain birch (*Betula pubescens czerepanovii*). (c and d) Damage to potato plants due to feeding by Colorado potato beetle (*Leptinotarsa decemlineata*) (c) larvae (photo by ©A Alyokhin, used with permission) and (d) adults.

in fact lead to local population declines or extinctions (Taylor and Hastings 2005; Thackeray *et al.* 2016). This uncertainty about pest responses to rising temperatures needs to be addressed in order to develop effective pest management strategies. Policies based on a universally anticipated, generic increase in pest severity will be misguided; rather, a more detailed understanding of insect pests' responses to climate warming is essential to inform effective allocation of public and private resources for pest management efforts in the future. Unfortunately, information about how most insect pests will respond to increased temperatures is scarce (Sutherst *et al.* 2011; Bebber *et al.* 2013; Urban *et al.* 2016).

Climate warming and insect pest biology

Attempts to predict the effects of increased temperatures on insect pests typically rely on observational studies of population responses to spatial and temporal variations in climate, mechanistic studies of insect responses to varying abiotic conditions (often in controlled laboratory environments; Parmesan 2007; Bonebrake *et al.* 2014; Pureswaran *et al.* 2018), climate modeling projections (Bellard *et al.* 2016), or some combination of these approaches (Sutherst *et al.* 2011). However, several sources of complexity in pests' responses to warming can limit the reliability of these analyses. For example, one common assumption of pest-response research is that climatic limiting factors, such as temperature or water availability, are constant across a species' geographic range (Grayson and Johnson 2018). As a result, studies often ignore intraspecific differences, a well-known source of variability in pest responses to climate change (Moran and Alexander 2014; Pureswaran *et al.* 2018). Also, pest ranges generally span multiple environments that often include various types of managed landscapes (Tscharntke *et al.* 2012), forming complex dynamic matrices of pest–ecosystem interactions (Bebber *et al.* 2013; Karp *et al.* 2018). Finally, analyses tend to consider a single response (eg range expansion) as opposed to the full range of a pest's potential responses to warming temperatures (Bebber *et al.* 2013). These responses can be divided into at least four categories (Urban *et al.* 2016): changes in geographic range (Pecl *et al.* 2017), life-history traits (Robinet and Roques 2010), population dynamics (Cammell and Knight 1992; Logan *et al.* 2003), and trophic interactions (DeLucia *et al.* 2012) (Figure 2), any of which can influence the amount of economic damage caused by pests. Trophic interactions encompass pest–host shifts, changes in host-plant–pest interactions, and pest–enemy

interactions (eg through the effects of warming on natural predators and parasites).

To assess the current state of empirical evidence showing pest responses to climate warming across these four categories, we reviewed the primary literature for data on 31 globally important insect pest species (WebPanel 1). Species were selected to include both agricultural and forestry pests, and to represent various feeding guilds (WebFigures 1 and 2), presence in various biomes, and extensive geographic ranges (Figure 3). Only species that have been well studied over a long period were chosen for our analysis. We also focused on responses attributed to warming, as temperature is perhaps the most widely measured and well-documented abiotic variable. We did not consider pest responses to changes in other climate variables (such as solar radiation, precipitation, soil moisture, humidity, or interactions among abiotic variables), even though these may also be influenced by a warming climate (Pincebourde and Casas 2019).

Using Web of Science searches and pest management databases, we selected three types of studies: those that compared climate trends and empirically determined trends in relevant aspects of the chosen pests (eg range, abundance, economic/ecological damage); those that tracked population-dependent differences in relevant traits (eg voltinism [number of broods or generations in a year]) of the pests across time; and those that modeled attributes of the pests, including a substantial historical data component. On the basis of these criteria, we identified 105 studies reporting pest insect responses to climate warming (WebTable 1). Although our criteria for selecting species may have resulted in geographic and taxonomic biases, these were somewhat offset by the availability of high-quality datasets for the chosen species (WebPanel 2). Comprehensive data are critical for an integrated assessment of all four of the major response categories noted above for each species. Given the need for information on biological mechanisms relating to past and present climate warming for single organisms (Urban *et al.* 2016), we include four potential categories of mechanism (range expansion, life history, population dynamics, and trophic interactions) for the selected species so that the data can be used for further predictive modeling.

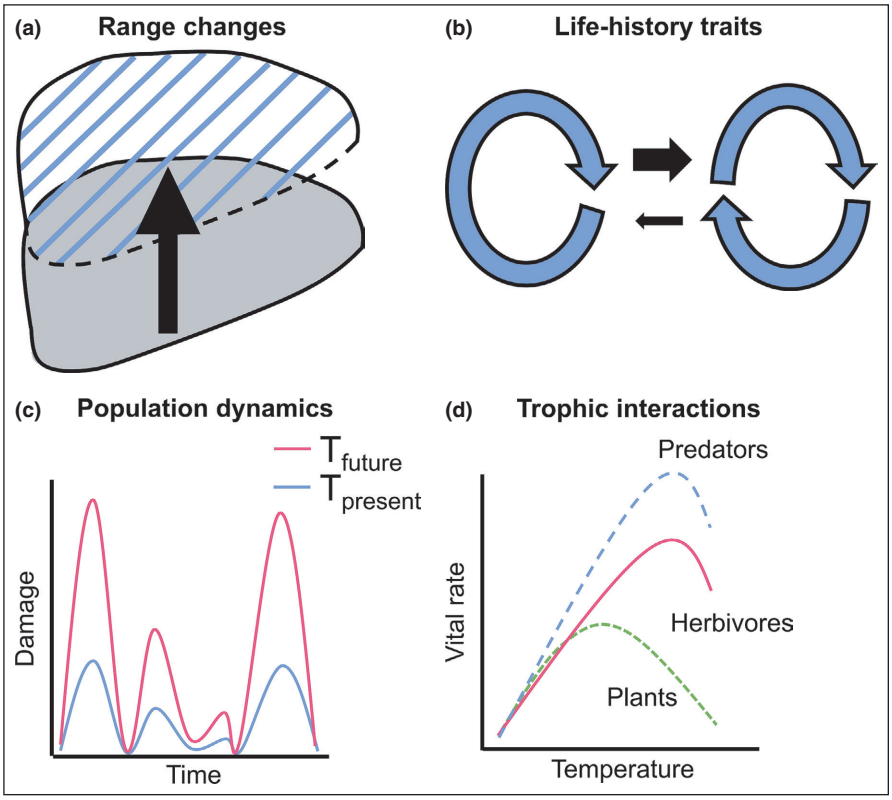

Figure 2. Four major categories of responses to climate warming. (a) Range changes include range expansions or shifts (latitudinal or altitudinal). (b) Life-history changes primarily consist of alterations to biological timing events or the number of annual generations. (c) Population dynamics reflect population size, and damage is expected to increase whenever temperature limits performance, but if threshold temperatures are reached, control and related feedback mechanisms may be triggered. $T_{present}$ reflects current temperature fluctuations over a time period (eg a year or a day), whereas T_{future} reflects future temperatures over the same period. (d) Trophic interactions reflect temperature responses of organisms and trophic groups (plants = dashed green line, herbivores = solid red line, predators = dashed blue line). Because vital rates (ie rates of important life-history traits, such as growth, dispersal, and reproduction) may vary, climate warming could strongly affect trophic relationships. Reproduced with permission from Berggren *et al.* (2009).

Mixed responses to climate warming among insect pests

Of the 31 insect pest species selected for assessment, 29 (94%) were reported to be responding to contemporary climate warming (WebTable 1), with 28 (90%) exhibiting multiple responses (Figure 4a). Of the 29 species showing some response, 26 (90%), 18 (62%), 16 (55%), and four (14%) exhibited changes in geographic range, population dynamics, life history (traits related to phenology and voltinism), and trophic interactions, respectively. While increased pest severity is likely to be a common result among almost all of these species (eg via range expansion, increased abundances), 59% (17/29) of these species also exhibited responses that were likely to reduce pest damage (eg range contraction, reduced physiological performance) (Figure 4b). Reductions in pest impacts were often found to occur in conjunction with other responses likely to increase their effects (WebTables 1 and 2). The most common severity-reducing responses were decreased pest population densities (13/29) and range contractions (6/29) (Figure 4, c and d).

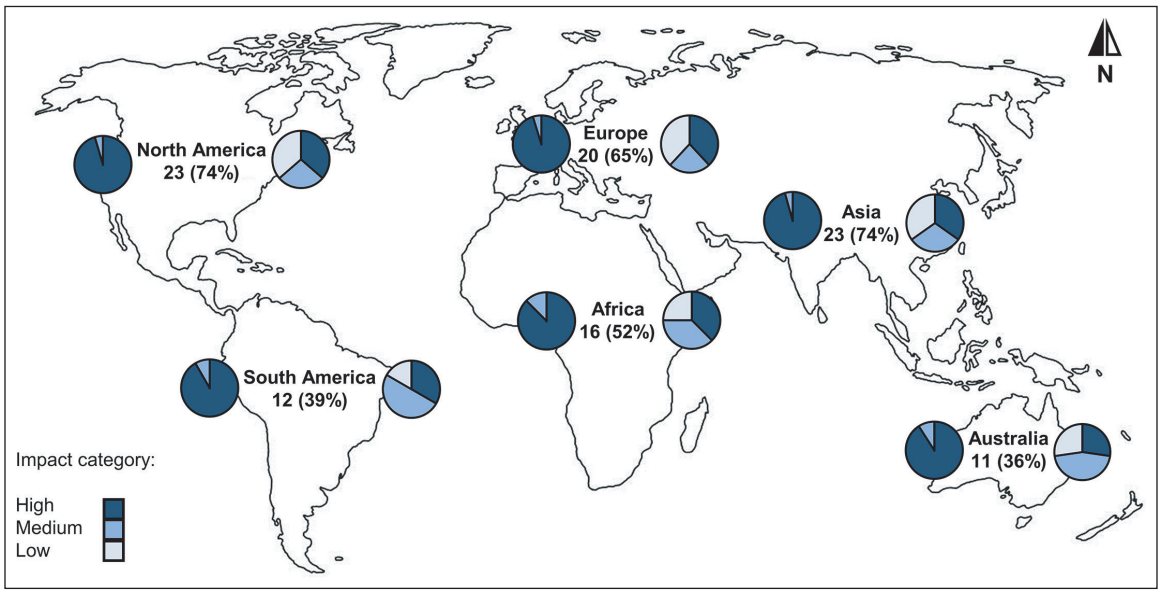

Figure 3. Distribution of the 31 insect pests used in the current study occurring on each continent (with the percentage of all those included) according to the Centre for Agriculture and Bioscience International. Note that many species occur on multiple continents. Pie charts flanking continental maps show the distribution of socioeconomic impacts (left pie chart) and ecological impacts (right pie chart) caused by these species. Dark blue represents high impacts, intermediate blue represents medium impacts, and light blue represents low impacts.

Fifty-nine percent (17/29) of the pest species with reported sensitivity to warming temperatures were found to vary in their responses in different parts of their ranges. For example, the Colorado potato beetle (*Leptinotarsa decemlineata*) has expanded northward in Europe in recent decades, while its population density has increased in core European areas (WebTable 1). The winter moth (*Operophtera brumata*) has also moved to higher latitudes and toward higher altitude inland continental areas at the northern European edge of its range, while its trophic interactions have changed in the boreal–tundra ecotone, where outbreaks have spread from its main host (mountain birch [*Betula pubescens czerepanovii*]) to alternative hosts (dwarf birch [*Betula nana*] and willow [*Salix* spp]) beyond the Arctic–alpine tree-line (WebTable 1). Several insect pest species also exhibited contrasting responses in different parts of their ranges. For instance, thermal tracking has been observed in several temperature-sensitive species, with responses varying across their range (4/17). In the US, for example, the eastern spruce budworm (*Choristoneura fumiferana*; WebTable 1) has shifted northward, while its range has retracted or abundance declined at lower latitudes; also in the US, a northward range expansion has been observed for the hemlock woolly adelgid (*Adelges tsugae*), while the economic damage it causes is decreasing in the southern part of its range due to poor heat tolerance among young nymphs in the summer (WebTable 1).

Responses of phytophagous pests of annual and perennial crops

Insect pests of annual (mainly agricultural pests) and perennial (mainly forest pests) crops exhibited similar response patterns to climate warming, albeit with some subtle differences. Contrary to expectations based on differences in feeding or host ecology and evolutionary constraints, the amount of pest damage to annual crops was lower than to perennial crops (eg trees). To assess the potential impact of agricultural and forest pest responses to climate warming, we categorized species according to their historical and current socioeconomic and ecological impacts, and the current effects of rising temperatures on those impacts. Overall socioeconomic and ecological impacts have reportedly increased across the geographic ranges of species that have shown a response to climate warming (Andrew *et al.* 2013; Bebber *et al.* 2013). More importantly, while all the perennial crop pests considered in this study already have major ecological impacts, 85% (17/20) of annual crop pests currently have relatively low ecological impacts beyond the cropping systems they infest. Nonetheless, rising temperatures may be causing increases in the ecological impact of some annual crop pests. For instance, the southern green stink bug (*Nezara viridula*) and spotted stem borer (*Chilo partellus*) are displacing native bugs and borers, respectively, as their ranges expand (WebTable 1). Similarly, recent expansion in the European range of the western corn rootworm (*Diabrotica virgifera virgifera*) could potentially cause extensive ecological damage because this species is a vector of the maize chlorotic mottle virus, which can spread to several natural hosts (WebTable 1). One potential explanation for the increase in ecological impact of pests on annual crops is that reductions in phenological constraints associated with climate warming (mediated, for instance, by the expansion of a host plant's growth season, or shorter and milder winters; Bale and Hayward 2010)

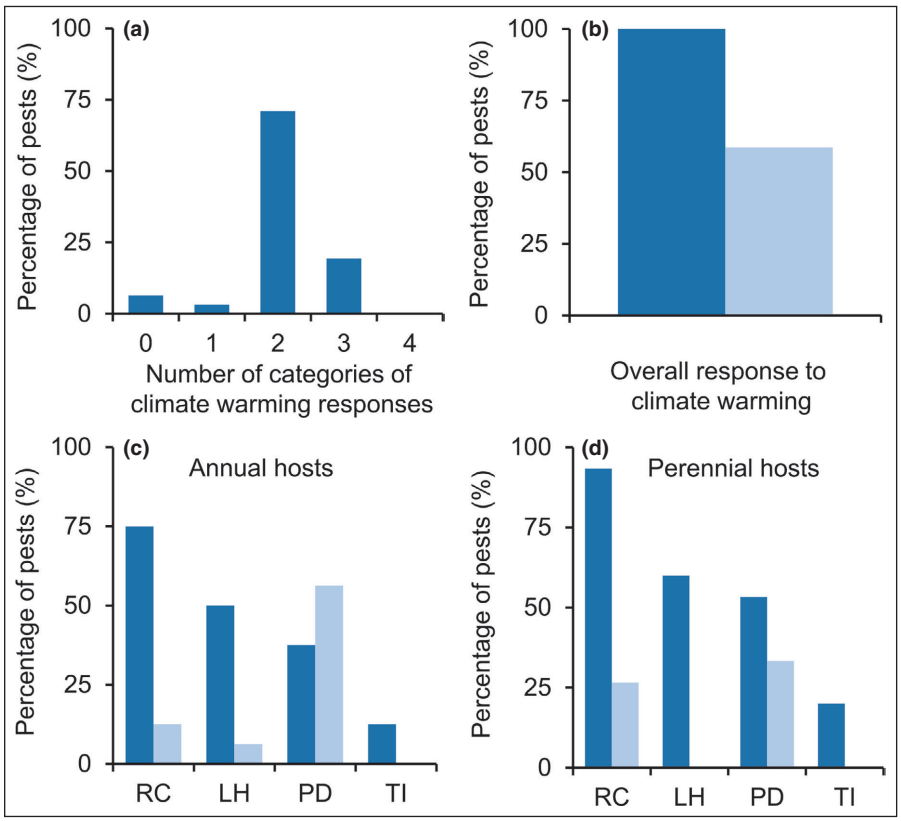

Figure 4. Responses to climate warming of 31 insect pests with high socioeconomic and/or ecological impacts. (a) The number of species in which 0–4 traits responded to ongoing climate warming. Columns in (b–d) show percentages of the 31 insect pest species displaying severity-increasing (dark blue) and severity-decreasing (light blue) responses to climate warming in the four traits investigated here. RC: range changes; LH: life-history traits; PD: population dynamics; TI: trophic interactions. Percentages (b–d) are based on data only for the 29 species that exhibited at least one response (a).

could increase interactions between pests in annual agricultural habitats and surrounding ecosystems (Singer and Parmesan 2010; Cohen *et al.* 2018), thereby increasing the ecological impacts of these pests. Indeed, even small phenological mismatches could have large knock-on effects for ecosystem function and predator–prey interactions (Thackeray *et al.* 2016; Cohen *et al.* 2018).

In addition to the fact that latitudinal differences in pest distributions might modulate climate-warming effects, several other mechanisms could be involved in the disparity between effects in annual and perennial systems. More so than forest pests, agricultural pests are generally associated with fragmented habitats (Bianchi *et al.* 2006) and may therefore have higher local extinction risks due to Allee effects (ie low population densities that make it difficult for individuals to find mates) or to localized high temperatures as the climate warms (Taylor and Hastings 2005). Moreover, while increasing temperatures can disrupt biological control by natural enemies in either annual or perennial systems (Eigenbrode *et al.* 2015), introduced classical biological control agents in annual systems may have lower genetic diversity than native predators, and therefore lower adaptive capacity to respond to environmental changes (Thrall *et al.* 2010). Direct effects of climate warming on important life-history traits (eg growth, dispersal, and reproduction) and phenology of pests have been detected in both annual and perennial systems. Because pests often persist through part of the season in a resting or dormant stage, especially at high latitudes and/or altitudes (Bale and Hayward 2010), climate warming can contribute to phenological mismatches between hosts and the emergence of key life stages (Singer and Parmesan 2010; Thackeray *et al.* 2016; Pureswaran *et al.* 2018), as is the case for *O brumata* (WebTable 1). However, pests in annual and perennial systems might differ in their general susceptibility to phenological mismatching, with pests in annual systems possibly more sensitive to phenological host limitation, especially compared to bark beetles and root feeders. Furthermore, host specialists may show differing sensitivities to phenological mismatching in a particular direction (eg low sensitivity to earlier host availability, but high sensitivity to later host availability). Taken together, while some differences appear to depend on whether the system is annual or perennial, pests in both systems display enormous variability in how climate warming influences their ecological and associated socioeconomic impacts.

Past, present, and future temperature stress

Some researchers have argued that ongoing climate warming will have a negative impact on insect pests due to reduced thermal suitability and increasing frequency of high temperature extremes, leading to reductions in the populations of these species (Terblanche *et al.* 2016). To examine this idea among our 31 focal insect pest species, we searched for correlations between optimum temperatures of developing life stages (T_{opt}) and ambient air temperatures (T_{amb}) in the habitats in which the insects developed (WebTable 3; Figure 5a). Relating T_{amb} during the growing season in past, present, and projected climates to T_{opt} revealed large variability in how pests are expected to benefit from climate warming due to regional complexity. In general, warming temperatures are expected to be beneficial for growth and development, and indeed, in all but two species, we found that T_{amb} moved toward T_{opt} when comparing past, current, near future, and future climates (Figure 5b). This conclusion was also supported by a regression analysis taking into account potential confounding effects caused by species

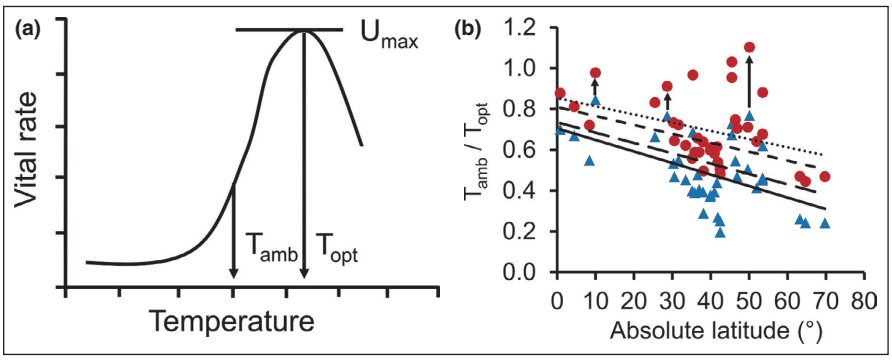

Figure 5. Thermal sensitivity of the 31 insect pests included in our analysis. Published optimum temperatures of the species (T_{opt}), the temperature at which performance is maximized (U_{max}), and mean ambient temperature (T_{amb}) of the region during the growing season were used as inputs. (a) Schematic thermal performance curve. Arrows reflect the temperatures at which the optimal vital rate and a lower vital rate are achieved. (b) T_{amb}/T_{opt} is plotted against latitude for the four periods investigated (historical: blue triangles and solid line; present: coarse dashed line; near future: fine dashed line; future: red circles and dotted line). All regressions were statistically significant (historical: $P < 0.001$, present: $P = 0.001$, near future: $P = 0.007$, future: $P = 0.011$). The three vertical arrows show example shifts in T_{amb}/T_{opt}.

relatedness (WebTable 4; Figure 5b). In addition, our analysis suggested that there is greater disparity between T_{amb} and T_{opt} among pests at higher latitudes, indicating greater capacity to benefit from climate warming among these species, unlike low-latitude pests that live in habitats where temperatures are already close to T_{opt}. Low-latitude species also potentially risk greater exposure to heat stress as a result of warming (Sunday *et al.* 2014), as indicated by the results of a recent analysis of the upper thermal tolerances of 15 dipteran pests (Terblanche *et al.* 2016).

Further examination of patterns – in more species; on other thermal traits, especially upper thermal limits; on fertility or fecundity; on feeding (damage) rates; and in several life-stages (Sinclair *et al.* 2016) – will be required to confirm whether pests truly are as thermally constrained as suggested by the present data. Agricultural pests accounted for only 4% of the ~380 species included in the database of upper thermal limits compiled by Hoffmann *et al.* (2013), highlighting a potential information gap in the current literature. While the pests included in our analysis represent a wide geographic distribution (Figure 3), the studies that focused on T_{opt} mainly reflected populations sampled at locations in the Northern Hemisphere (Figure 6). This geographic bias in existing datasets represents a problem common to other large-scale analyses of climate warming responses, such as phenological (Cohen *et al.* 2018) and insect metabolic or development rate–temperature databases (Irlich *et al.* 2009), highlighting the need for more research in underrepresented parts of the world. This is especially pertinent given that several of these regions (eg Asia, South America, Oceania) are major agricultural areas, and feature high human population densities and/or rapid population growth. Finally, given that ambient air temperatures are typically reported in global temperature databases, there is also a risk of underestimating microclimatic variability, and the extent to which insects can exploit this variability to buffer their body temperature in response to stressful ambient temperatures (Sunday *et al.* 2014; Pincebourde and Casas 2019).

Evolutionary responses to climate warming

Insect pests may evolve rapidly in response to current climate warming (Parmesan 2006; Hoffmann 2017; Diamond 2018), and seemingly sound projections of insect pest responses to increasing temperatures (Andrew *et al.* 2013) may be unreliable if evolutionary responses are not considered (Merilä and Hendry 2013). Indeed, rapid evolutionary effects have influenced – or could further influence – projections for several of the 31 species we considered (WebPanel 1). In parts of Europe, for example, disruption of phenological synchrony between *O brumata* and oak (*Quercus* spp) due to increasing temperatures appears to have been restored by a hereditary change in egg hatching dates (van Asch *et al.* 2013). In addition, range expansions among several forest pests that were induced by climate warming have been followed by rapid adaptation to new climate conditions (Janes *et al.* 2014). In the case of some pest species (eg *D ponderosae*), colonization of new areas has resulted in shifts to novel host tree species with negligible levels of innate resistance to the insects (Janes *et al.* 2014). In contrast, the similarity of crops grown across large areas might promote co-evolution between agricultural pests and their host plants (Wan and Yang 2016). Links between biological invasions or range expansion events, climate warming, and evolutionary processes have received recent attention (Parmesan 2007; Moran and Alexander 2014; Diamond 2018), but there is still a pressing need for further research in this field. The effects of management practices and evolution have typically been considered in isolation, especially in climate-change contexts (Thrall *et al.* 2010; Urban *et al.* 2016).

Conclusions

The 31 widely distributed pest insects included in our analysis exhibited multiple and contrasting responses to climate warming, a key component of ongoing anthropogenic climate change (IPCC 2013). By providing an up-to-date database of the biological responses to climate warming shown by these pest species (WebPanels 1 and 2; WebTables 5 and 6), we offer standardized information that can be explored further by other researchers. Although

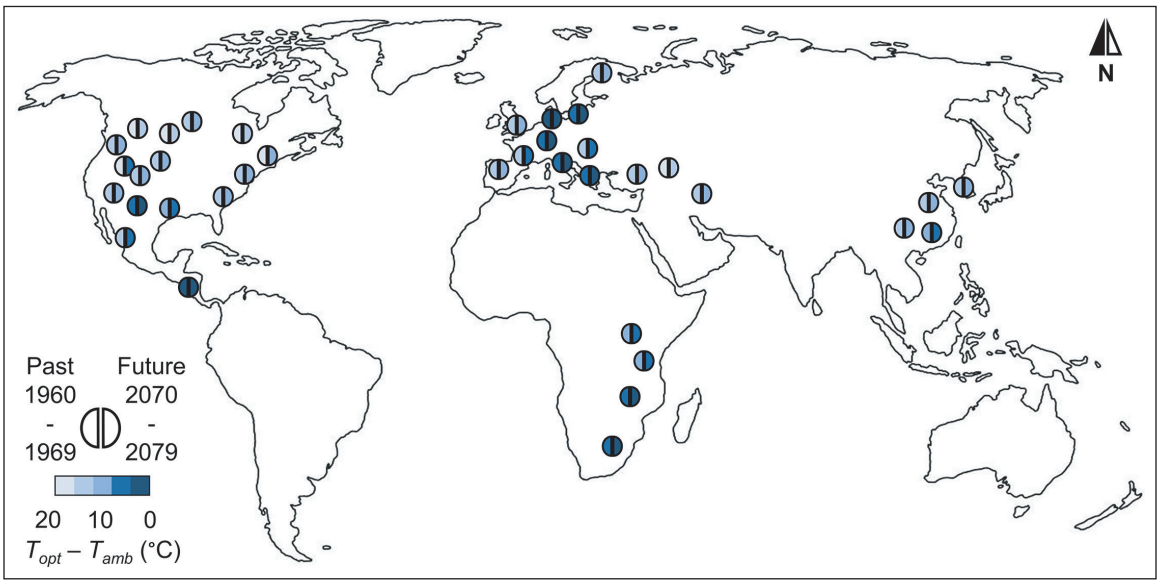

Figure 6. The number of degrees (°C) by which T_{amb} differs from T_{opt} in past (left half of circle) and future (right half of the circle) climates for populations of the pest species included in our analysis. Darker colors represent closer matches between T_{amb} and T_{opt}.

our analyses cannot be considered comprehensive and free of taxonomic, geographic, and study intensity biases (Bellard *et al.* 2013), we nevertheless observed several patterns that allow us to draw some general conclusions.

Determining the net change in pest severity in response to climate warming is difficult, because most of the species considered here have shown multiple, spatially variable responses (Hill *et al.* 2016). There is also strong evidence of mixed directionality of responses, for which we provide possible explanations based on general mechanisms. This set of complex but predictable outcomes and regional heterogeneity of responses is challenging when it comes to choosing management approaches, but cannot be ignored as it agrees with the emerging consensus from similar studies (Sutherst *et al.* 2011; Andrew *et al.* 2013).

We urge caution when drawing broad conclusions from single-trait analyses, given that individual pest species' traits often displayed mixed responses to increasing temperatures. The lack of information about interactions among different traits in each pest species may lead to incomplete or inaccurate conclusions. To compensate, more in-depth studies of several biological mechanisms in a few representative species are needed. For example, a recent meta-analysis demonstrated that models integrating biological mechanisms from multiple traits greatly improved predictions of climate-change impacts on global biodiversity (Urban *et al.* 2016).

Mounting evidence suggests that pests and their host plants are responding to climate change not only ecologically (eg by range expansion or voltinism shifts) but also through rapid evolution and local adaptation (Chown *et al.* 2010; Hoffmann 2017; Diamond 2018). Consideration of both ecological responses and the potential for evolution may enable the formulation of more robust strategies for pest management (as recently demonstrated in disease vector control programs; Bouyer *et al.* 2015). Indeed, evolutionary approaches may be generally underexploited in pest management strategies (Thrall *et al.* 2010). It would be useful in this context to identify species with increased capacity to evolve traits relevant to climate warming (Chown *et al.* 2010) and to determine whether these traits are fixed or exhibit plasticity (Sgró *et al.* 2015).

Combining data from large-scale experiments (eg mesocosms) and computer modeling may improve estimates of climate-warming effects (Sutherst *et al.* 2011; Diamond 2018). Experiments should be designed to measure the effects of changing climatic conditions on factors that have been shown, through modeling, to most strongly influence pest population growth, performance, and injury to their host plants (eg increased feeding of the Japanese beetle [*Popillia japonica*] on soybean [*Glycine max*] grown under enriched carbon dioxide; DeLucia *et al.* 2008). Observations suggesting that responses to climate change differ among trophic levels, translating into shifts in the relative importance of bottom-up and top-down population processes, must be examined in greater depth, as even relatively small changes could result in large effects when multiple interactions are affected simultaneously (Kollberg *et al.* 2015).

Standardized experiments enable high-throughput investigations of pests and facilitate the development of watchlists or approaches to prioritizing pests (eg the UK Plant Health Risk Register; Baker *et al.* 2014) for further research. However, because the current data suggest large regional variability in pest responses to warming temperatures, national or regional databases may be poor sources of information about invasions into other regions unless efforts are coordinated or standardized, as was shown in a recent study of the orange wheat blossom midge (*Sitodiplosis mosellana*; Wu *et al.* 2019). Unfortunately, however,

there are very few existing datasets that represent standardized, long-term monitoring of the traits investigated here; indeed, for several of the species included in our analysis, response predictions are weak at best (WebTable 5).

As T_{amb} is generally increasing toward T_{opt} for growth and development in these species, and potentially reducing thermal constraints on population dynamics, pest severity is generally expected to increase under future climate scenarios (Deutsch *et al.* 2008). However, the relative benefits of rising ambient temperatures is negligible for many of the studied pests (Figure 6). Indeed, because T_{amb} is already close to T_{opt} for low-latitude species, T_{amb} for these species may surpass T_{opt} with climate warming, and pest severity may therefore be reduced under future climates (Sunday *et al.* 2014; Terblanche *et al.* 2016). A recent analysis of potential future changes in crop damage caused by pests used a single generic model of insect physiological responses to warming, and projected increasing damage of key staple crops by insect pests (Deutsch *et al.* 2018); in addition, the authors predicted a greater proportional increase in crop damage at higher latitudes. Although this broad projection agrees with our results in general, our findings are illuminating in that the data used in our analysis represent specific pest species in specific locations. Moreover, our results indicate that responses have been variable among pests and that, contrary to expectations, warming is not projected to cause ambient temperatures to exceed optimal temperatures more often at lower latitudes; indeed, the two instances in which ambient temperatures exceed optimal temperatures (ie $T_{amb}/T_{opt} > 1$) in our analysis are located in the mid-latitudes, near 50°N and 50°S.

Analyses such as ours, which use T_{opt} and mean air temperatures, have several limitations. First, temperature data that have been averaged across months and/or years fail to capture extreme weather events, which can push insects beyond their lower and upper critical thermal limits. This can drive dramatic population turnover events (eg local extinctions, invasions, shifts in voltinism; Boggs 2016). Second, mean air temperatures do not reflect microclimatic variability and are likely not indicative of behavioral opportunities for thermoregulation. Pincebourde and Casas (2019) demonstrated that various species of insect herbivores induce different plant responses that impact the leaf microenvironment; capturing the full spectrum of microclimatic responses such as this one in pest population dynamic models will be challenging. Linking macro- to microclimatic conditions, while also highly difficult, cannot be ignored, and future studies must include estimates of microclimate operative temperatures and insect body temperatures if our understanding of warming responses across species is to be improved (Storlie *et al.* 2014; Woods *et al.* 2015; Sinclair *et al.* 2016). Ideally, these studies should be coupled with laboratory evaluations of thermal performance conducted under fluctuating temperatures and based on local conditions, where climate warming is estimated as an offset from natural fluctuations, generally leading to a larger daily temperature change. Research should also include assessments of the impacts of both daily and seasonal thermal variability. Most studies primarily focus on summer-related responses (ie growth, reproduction, migration) and often omit winter biology completely (Williams *et al.* 2014), which is surprising given that more dramatic changes are expected to occur during winter than summer in many regions (IPCC 2013).

Finally, the patterns of regional variability and complexity described for the 31 insect pest species we investigated are likely to apply to non-pest insects and non-insect species as well, and it is therefore critical that the generality of the responses observed in this analysis are examined across diverse taxa in future studies (Bebber *et al.* 2013; Thackeray *et al.* 2016; Diamond 2018).

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Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2160/suppinfo

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