

15. Effects on distributions and biological invasions

Lucie Aulus-Giacosa*¹, Olivia K. Bates*¹, Aymeric Bonnamour*¹, Jelena Bujan*¹, Jérôme Gippet*¹, Gyda Fenn-Moltu*¹, Tristan Klafthenberger*¹, Cleo Bertelsmeier¹

¹ Department of Ecology and Evolution, University of Lausanne, 1015 Lausanne, Switzerland
Correspondence to: cleo.bertelsmeier@unil.ch

*equal contribution

Abstract

Large-scale range shifts towards higher latitudes change have occurred in many (but not all) studied species. Yet, spatial changes may be more complex. Because insects are small organisms, fine scale environmental heterogeneity (topography, habitats, land use and microclimate) may be more relevant to understand their response to climate change. In addition, insects differ in their ecophysiology and life history traits, preventing an overall forecast of insects' responses to climate change. Species range shifts are often not synchronized, creating new opportunities for interactions (facilitation or competition) within new communities. Moreover, climate change may affect the introduction probability, establishment likelihood and dispersal dynamics of introduced species. A variety of models have been developed to predict future insect distributions, ranging from simple species distribution models to more complex mechanistic models integrating species demography, dispersal and biotic interactions. Combining these predictions with experimental data will improve our understanding of species distributions under climate change.

Key words

Range shifts, niche, microclimates, ecophysiology, ecological traits, human-mediated dispersal, biotic interactions, species distribution models, range dynamics

1. Introduction

Since the early 20th century, the global surface temperature (land and ocean) has increased by approximately 1°C (Brönnimann 2018), and models predict continued warming of 2-6°C by 2100 (Christensen *et al.* 2007). Climate change during the past 50 years has mainly been caused by human activities (Intergovernmental Panel on Climate Change, Cooper *et al.* 2002 and temperatures are rising ten to 10,000 times faster than during the last deglaciation. Climate change also involves cascading effects such as rising sea level, and the increasing frequency of extreme weather events such as floods, storms, and droughts (Bale *et al.* 2002). Several metrics can be used to describe the multiple dimensions of climate change: the magnitude (difference in climate parameters and probability of extremes), the timing of climatic events (e.g., change in seasonality), and the availability (area of analogous climates and emergence of novel climates) or position (change in distance to analogous climate and climate change velocity) of climates (*for more detail see* Garcia *et al.* 2014). The combination of the several dimensions of climate change will not only affect species specific responses to climate change but also the pattern of population dynamics and global biodiversity of insects

(Kiritani 2013), thus providing local and regional opportunities for some species to maintain or expand their range while others will be threatened (Fig. 1).

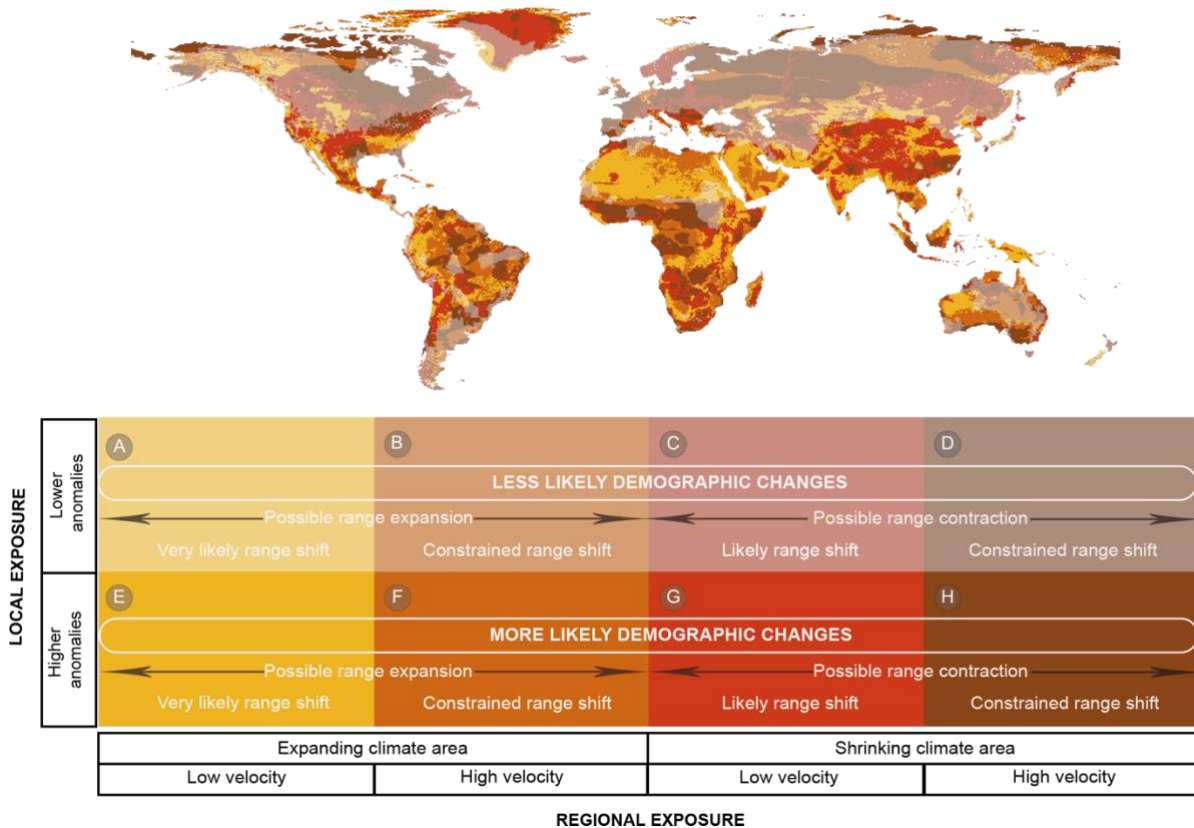


Figure 1. Spatial overlap of climate change metric and its effect on species range shift. The interplay of three metrics is displayed in this illustration adapted from Garcia et al. 2014 (see their paper for more details). Climatic metrics are displayed in black. One metric is at the local scale: the standardized local climate anomalies such as change in climate extremes and seasonality. The two other metrics are at the regional scale: change in area-baseline analogous climate and velocity of climate change. Consequences of the interplay of climate change metrics are displayed in white. Lower (A-B-C-D) and higher (E-F-G-H) local anomalies refer to values below and above the median, reflecting lower and higher chance of demographic changes. Expansion of analogous climatic area (A-B-E-F) is expected to increase the probability of species range expansion, whereas shrinking analogous climatic area may favor species range contraction (C-D-G-H). At low velocity changes (A-E-C-G), species may be able to track suitable climate over the region's topography and habitat structure, while this task may become more difficult at high velocity (B-F-D-H).

1.1. Niches and distributions

In order to understand how climate change will affect future species distributions, we will first discuss the determinants of historical species distributions and in particular the link between a species' climatic niche and its spatial distribution. All species have range limits beyond which they do not occur. It has been a central mystery in biogeography and evolutionary biology to understand what determines range limits (Bridle and Vines 2007). Across space, many environmental factors change including temperature, precipitation, solar radiation, wind speed or snow cover (Spence and Tingley 2020). Therefore, range limits might simply correspond to the most extreme conditions that a particular species can tolerate. This simple link between the species' biological requirements and its spatial distribution has been formalized in 1917 by Grinnell as the species' "niche" (Grinnell 1917). The environmental niche encompasses the range of conditions under which a species can thrive. As numerous different factors may be important for a species, the niche is generally viewed today as a space within

an n-dimensional hypervolume of environmental variables defining the full set of conditions enabling a species to survive and reproduce (Blonder *et al.* 2014).

However, it is only rarely true that a species' range limits correspond perfectly to its niche limits (Gaston 2009; Sexton *et al.* 2009). Transplant experiments have shown that there are often large areas with suitable environmental conditions that are not fully occupied (Hargreaves, Samis and Eckert 2014). To account for the frequent failure of species to establish under all suitable environments, Hutchinson has introduced the concept of the "realized niche", corresponding to the set of conditions where a species actually lives and not to where it could potentially live (i.e., its fundamental niche) (Hutchinson 1957). The constraints of realized niches can be summarised by the BAM (Biotic, Abiotic, Movement) model (Fig. 2) (Soberón and Peterson 2005). Species distributions are defined by biotic interactions (B), ecophysiological adaptations that determine the range of abiotic conditions they can tolerate (A) and the ability of the species to disperse and move (M) across geographic barriers such as mountain ranges or oceans. A species can survive where all three factors are met (Soberón and Peterson 2005). Most current research focusses on the realized niche (which is easy to infer from the species current distribution) and not the fundamental niche (which is hard to measure) (Fig. 2a).

Occasionally, a population may be found *outside* its fundamental niche. This may be because of source-sink dynamics at the metapopulation scale (Anderson *et al.* 2009; Watts *et al.* 2013) and this population would not be able to persist under unfavourable conditions without the constant arrival of immigrants. A population outside of its fundamental niche may also subsist after the environment has changed and go extinct with a certain time delay. Ongoing research is attempting to capture these types of complex time-delayed range dynamics (Lurgi *et al.* 2014; Zurell *et al.* 2016; Fordham *et al.* 2017)

1.2. Possible species responses to novel climates

The distinction between realized and fundamental niches becomes crucial for understanding species' responses to climate change. Following climate change, what does it mean for a species to experience abiotic conditions outside of the hypervolume of conditions previously experienced by the species? A large part of biodiversity might be confronted to novel climatic conditions in the future and there is currently no clear answer to that question (Bellard *et al.* 2012). If the "novel" climatic conditions are outside of the fundamental niche of a species, it will no longer be able to survive there. However, the novel climatic conditions may as well be outside the species' previous realized niche (Fig. 2, the intersection of B, A and M), but still within its fundamental niche (Fig. 2, the intersection between B and A). In that case, the species will be able to persist. Without knowing how much of its fundamental niche a species currently occupies, it is difficult to predict how it will fare under "novel" climatic conditions.

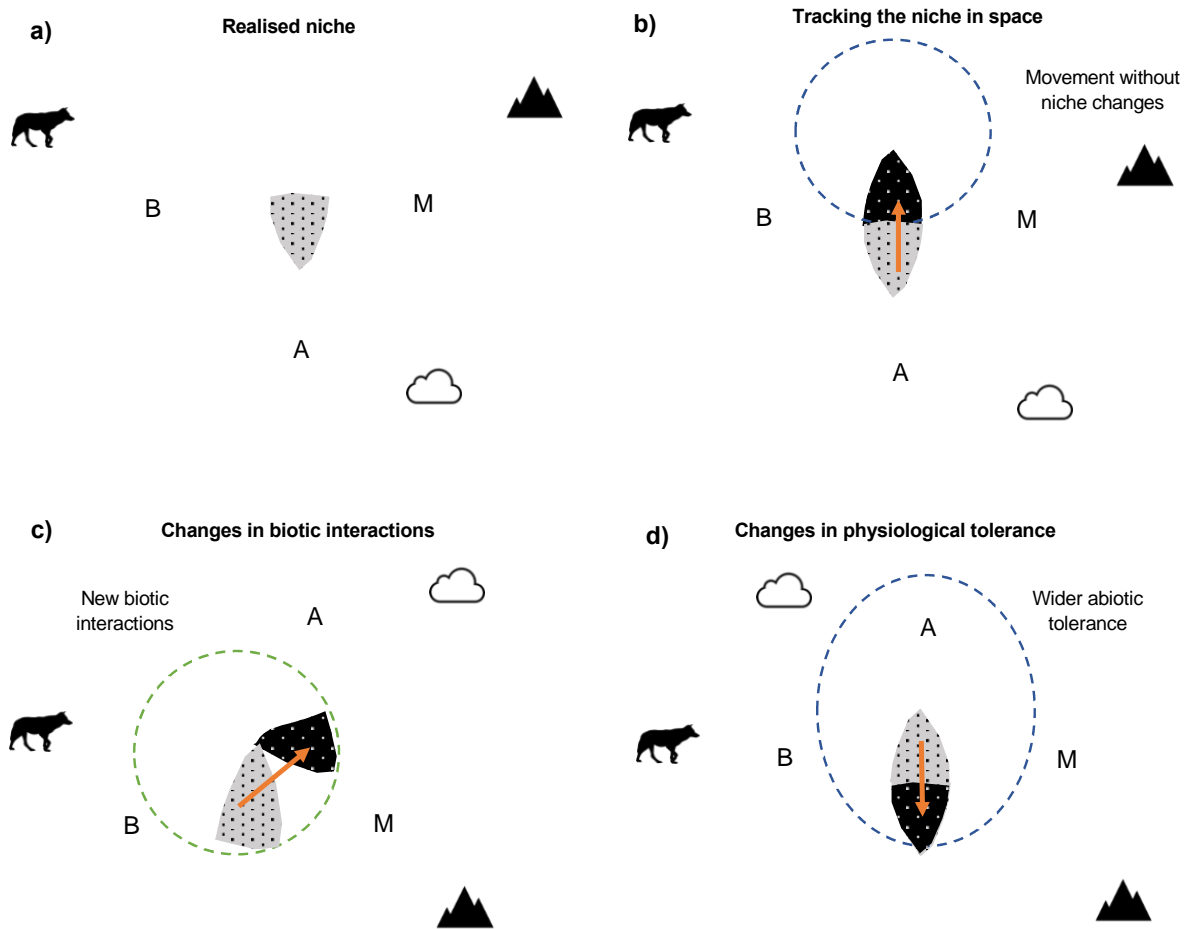


Figure 2. a) The ‘BAM diagram’ is a simplified framework for understanding species distributions. Three sets of factors determine where a species occurs: the abiotic niche (A) and biotic interactions (B), and the possibility to access the area (through species ‘movement’ (M)). The realized niche corresponds to the area where the three factors intersect (light grey area). Areas at the intersection of A and B are areas that correspond to the species’ fundamental niche (biotic and abiotic) but are currently not colonized due to geographic constraints. b) Following climate change, the location where the abiotic requirements (A) are met may shift and the species could survive by tracking its niche in space through movement, resulting in range shifts (to the black area). c) Climate-change induced range shifts may require modifications in species interactions. D) Species may persist at their current location when the conditions have become unsuitable (black area) by changing their physiological requirements through adaptive evolution or acclimation. Adapted from (Peterson 2011; Bates and Bertelsmeier 2021)

If a species is exposed to a climate outside of the range of conditions that it can tolerate, there are three possible ways to respond to avoid extinction (Bellard *et al.* 2012).

First, a species may change its spatial distribution to remain in equilibrium with suitable climatic conditions (through movement – M, Fig. 2b). This may occur at large spatial scales, in the form of range shifts to higher latitudes or elevations. But it can also happen at a local scale, within habitats presenting heterogeneous microclimatic conditions. Especially small-sized and mobile organisms may be able to select more favourable microclimatic conditions, buffering against unfavourable macroclimatic changes (Suggitt *et al.* 2011; Montejo-Kovacevich *et al.* 2020; Pincebourde and Woods 2020). Elevational range shifts are predicted to be more likely than latitudinal range shifts (Colwell *et al.* 2008) as elevational temperature gradients are steeper. Elevational range shifts are also a complex interplay between land-use constraints

and topography (Elsen, Monahan and Merenlender 2020). Here, species at the highest altitudes are the most vulnerable to climate changes (Urbani, Alessandro and Biondi 2017), because they cannot move further up in elevation (Colares *et al.* 2021). On the other hand, species living at high latitudes might be more robust to climate change than tropical species because they evolved under large daily and seasonal variations in temperature.

Second, a species may subsist through trait changes altering its biotic interactions (B) (Fig. 2c) or abiotic requirements (A) (Fig. 2d) that limit its range, either via plastic changes (such as acclimation) or via adaptive evolution (see section 5). It is a hotly debated question to what extent species will be able to evolve in response to novel climates. Indeed, the time scale at which current changes are happening appears too short for many long-lived organisms to adapt.

A final possibility (where B, A and M remain stable) for the species is to change the timing of life-cycle events to match the new conditions, for example by changing phenology (flowering, reproduction) or diurnal rhythms (shifting activity patterns to cooler hours of the day). Most of these species' responses are expected to occur in the future as the climate will dramatically change over the next few decades. Much research effort has concentrated on predicting species distribution. To achieve that, increasingly complex statistical tools and methods to work with large-scale data sets are being developed. However, empirical observations and tests of species responses *in situ* are comparatively rare, as they rely on long term datasets which are difficult to collate (except for some taxonomic groups such as butterflies, see section 2).

To observe species responses to novel climates, one possibility is to use introduced species as model system (Moran and Alexander 2014). These are species that have been moved outside of their native area and frequently encounter novel conditions (Mack *et al.* 2000). Studying introduced species allows addressing questions about the expected frequency of niche shifts, the importance of life-history and ecophysiological traits in enabling such shifts and the role of biotic interactions. It may also allow testing for adaptive evolution potentially underlying these shifts using common garden experiments or reciprocal transplantation (Bertelsmeier and Keller 2018). Moreover, introduced species are among the greatest threats to biodiversity besides climate change (Bellard, Bernery and Leclerc 2021). Introduced species are thought to be successful at expanding geographically because they are assumed to be rather highly competitive generalist species with high adaptability (van Kleunen, Weber and Fischer 2010; Weis 2010). Multiple drivers of global change including the globalization of trade, habitat loss and land-use change may increase the risks of biological invasions in the future (Gippet *et al.* 2019; Bertelsmeier 2021). Throughout this chapter, we will therefore consider effects of climate change on distribution of native and introduced species.

1.3. Current and future distributions of insects

Knowledge of species distributions arise from observational records across the world. Despite representing the largest group of animals on Earth with more than 1 million described species, insects are in fact the group of animals with the greatest gaps in knowledge of taxonomy (Linnean shortfall) and distribution (Wallacean shortfall) (Diniz-Filho, de Marco and Hawkins 2010). While more than 70% of all animals are insects (Lobo 2016), insects represent only 10% of species occurrences in the widely used Global Biodiversity Information Facility database

(GABI). However, insects are a particularly interesting group to study the impact of climate change on biodiversity. As ectotherms, insects depend on the thermal conditions of their environment for activities such as flight, reproduction, and foraging (Cox and Dolder 1995; Régnière *et al.* 2012; Kenna, Pawar and Gill 2021). Thus, climate change is expected to greatly impact insects' spatial distribution. Understanding how insect distributions will respond to contemporary climate change is urgent in light of recent population declines (Vogel 2017; Didham *et al.* 2020).

The number of studies on impacts of climate change on spatial distributions of insects has nearly doubled between 2000 and 2010 (Halsch *et al.* 2021). Here, we consider how studies on insects' distributions and climate change are gaining interest while summarizing the available literature on Web of Science by performing a qualitative metadata analysis of 4195 articles from 1990 until present (Fig. 3a). The literature search was performed on Web of Science in December 2021 using the topic search terms (title, abstract, authors, keywords): (insects* OR PROTURA* OR COLLEMBOLA* OR DIPLURA* OR MICROCORYPHIA* OR THYSANURA* OR EPHEMEROPTERA* OR ODONATA* OR ORTHOPTERA* OR PHASMOTODEA* OR GRYLLOBLATTODEA* OR MANTOPHASMATODEA* OR DERMAPTERA* OR PLECOPTERA* OR EMBIIDINA* OR ZORAPTERA* OR ISOPTERA* OR MANTODEA* OR BLATTODEA* OR HEMIPTERA* OR THYSANOPTERA* OR PSOCOPTERA* OR PHTHIRAPTERA* OR COLEOPTERA* OR NEUROPTERA* OR HYMENOPTERA* OR TRICHOPTERA* OR LEPIDOPTERA* OR SIPHONAPTERA* OR MECOPTERA* OR STREPSIPTERA* OR DIPTERA*) AND ((climate OR weather) AND change*) AND (range*OR migration* OR distribution*), which identified 4615 studies. To be included in our metadata-analysis, we performed several filters. We removed 166 articles and book belonging to categories recording less than 20 articles. We restricted the language to English (43 additional articles were removed). We removed books and duplicated articles using the Cadima website¹ which led to 93 additional disregarded articles. Finally, we removed conference papers and journal reviews (118 articles), yielding 4195 articles. To study detailed information on taxonomy and geographical study range, we randomly selected 210 articles for which title and abstract were specifically referring to insects, range shifts and climate change among the filtered 4195 articles. Using these 210 articles we extracted information on species name, species order, geographical scale of study and continent of the study.

The number of published papers on the topic has multiplied by ten during the past decade compared to the 90's. However, it can also be noted that these studies are taxonomically (Fig. 3b) and geographically restricted (Fig. 3c), with most studies considering Lepidoptera in Europe.

This chapter will focus on possible and observed spatial changes, at large scales (section 2) and small scales (section 3) and discuss the role of natural and human-mediated dispersal (section 4), species traits (section 5) and biotic interactions (section 6) in enabling range shifts. We will also review novel modelling techniques (section 7) that are attempting to characterize the fundamental niche and dispersal processes more mechanistically.

¹ <https://www.cadima.info/index.php>

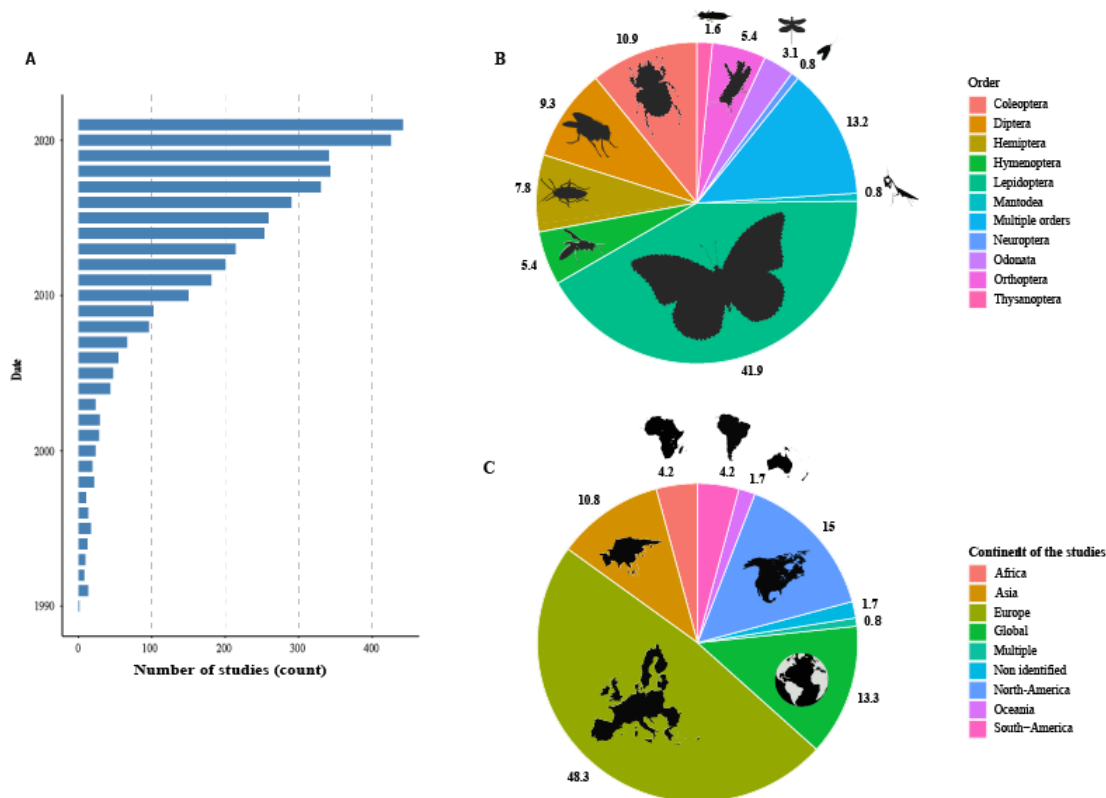


Figure 3. Trends in studies on insects' distribution responses to climate change from 1990 until present. a) General trends in publications over time (4195 studies), b) insect orders studied. Lepidoptera were 2.4 times overrepresented compared to the total number of species described (~160 000 species, 17% of described insects, while Coleoptera (~400 000 species, 40% of described insects) were 4 times underrepresented, c). Study locations. Most studies on insects' distribution responses to climate change were done in Europe (48.3%), followed by North-America (15%).

2. Large-scale range shifts of insects

2.1. Latitudinal range shifts

Large-scale patterns in climate and biodiversity on Earth are strongly linked to latitude, with an increase in biological diversity from the poles to the equator (for details see Willig, Kaufman and Stevens 2003). Latitudinal range shifts are the most frequently observed type of range dynamics in relation to climate change (Lenoir and Svenning 2015). Yet, range shift may involve more than one geographical limit at the same time, including for example southern and northern limits (Fig. 4). Depending on how the different limits are changing, the original range size may increase or decrease. Changes in range size depend on the differential change between leading and trailing range limits (Fig. 4).

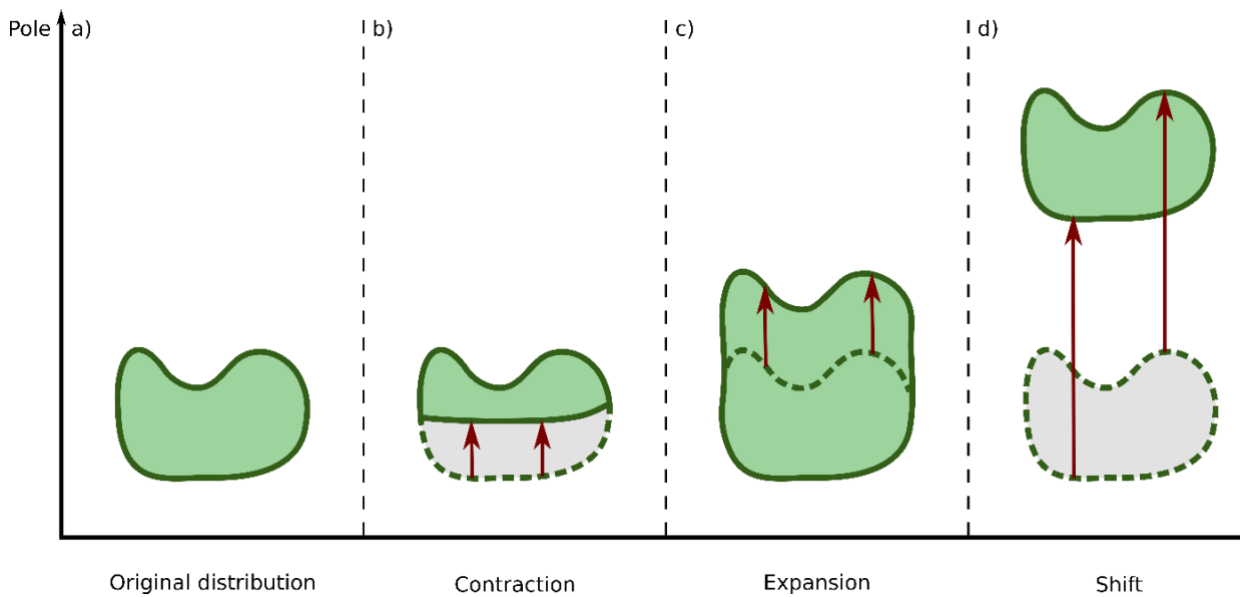


Figure 4. The main types of distribution changes and their consequences on range size. a) the original distribution area, b) a poleward contraction, c) an expansion of the original distribution, d) a complete poleward shift of the original distribution with an equal shift of both lower and upper limit. This figure is not intended to be exhaustive. More complex spatial changes can occur resulting in differences between the lower and upper limits of the original range distribution, impacting the original range size. Fragmentation or changes in abundance can also occur (for more details see Lenoir and Svenning 2015a; Yang et al. 2021).

2.2. Empirical observations of latitudinal range shifts

Latitudinal range shifts have been reported in many different taxa (Fig. 5). Studies generally indicate a trend of poleward range shifts in insects as expected (Parmesan *et al.* 1999; Warren *et al.* 2001; Parmesan, Yohe and Andrus 2003; Hickling *et al.* 2006; Lowe *et al.* 2011; Mason *et al.* 2015; Poniatowski *et al.* 2020). To study latitudinal range shifts due to climate change, historical occurrence data collected at either the northern or southern range limit, but seldom both, are compared to current occurrence data and correlated with past climate change. Therefore, few studies on range shifts can conclude on the impact of climate change on total range size.

The first major large-scale study of latitudinal range shifts focused on 35 non-migratory European butterflies (Parmesan *et al.* 1999). Within one century, 63% of species moved poleward (with shifts ranging from 35 to 240 km), while 34% maintained their original distribution and 3% shifted southward. Many subsequent studies have focused on Lepidopteran species in Europe and North America (Lenoir and Svenning 2015) because historical data is more easily available (Andrew *et al.* 2013). But southern hemisphere insects for which there are far fewer data and studies, seem to show a similar pattern. For example, 3 Coleoptera and 5 Lepidoptera species in South Africa showed a poleward range shift over the last two decades (Perissinoto, Pringle and Giliomee 2011), with an extension of the southern limit (ranging from 90 to 830 kilometers). Two distinct meta-analyses confirmed a general trend of a poleward range shift (Parmesan, Yohe and Andrus 2003; Chen *et al.* 2011). The first meta-analysis found an average poleward shift of 6.1 km per decade (Parmesan, Yohe and Andrus 2003), while the second study found an even higher median rate of 16.9 kilometers per decade with a higher rate in places that experience higher warming levels (Chen *et al.* 2011). Both studies included only multi-species studies to limit the impact of publication biases towards reports of shifting compared to non-shifting species. However, average range shifts may not be relevant at a finer taxonomic scale because species may differ

greatly in terms of physiology and dispersal ability. Here, we calculated the mean median response for vertebrates, non-insect invertebrates, and insects based on data from Chen et al. (2011) (Fig. 5). Compared to the average range shift of 16.9 km across all taxa reported by the Chen et al. (2011), vertebrates respond on average slower (7.6 km per decade), non-insect invertebrates faster (22.9 km per decade), and insects even faster (26.8 km per decade) (Fig. 5). Perhaps insects show larger range shifts in response to climate because as ectotherms they are more sensitive to external temperature changes (Sheldon, Yang and Tewksbury 2011). Higher temperatures increase development and survival rates in insects in temperate areas, enhancing establishment likelihood at higher latitudes (Stange and Ayres 2010).

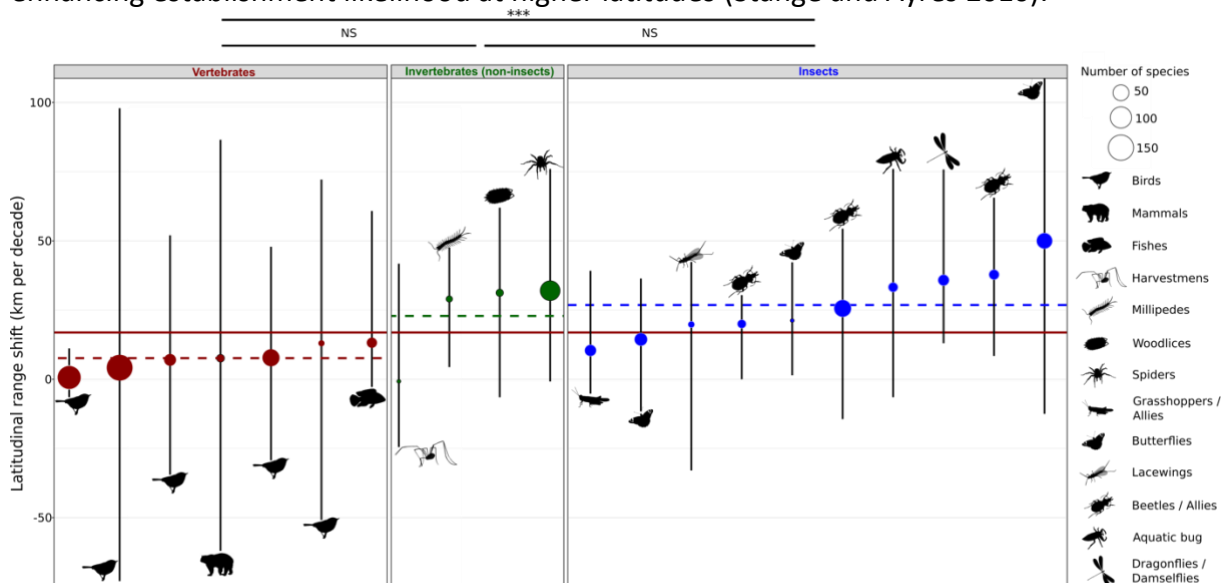


Figure 5. Latitudinal shift per decade for three main groups, based on data available from a previous meta-analysis (Chen *et al.* 2011). Each circle represents the median latitudinal shift per decade for a taxonomic group in a specific study region as described in the meta-analysis. The error bars represent the 90th and 10th percentile. Note that the last point on the right has a 90th percentile equal to 268.75. The size of each circle is proportional to the number of species studied. The red solid line represents the median latitudinal shift across all species, reported by the authors. The dotted lines represent the mean median latitudinal shift per decade for the three main taxonomic groups. For each pair of main groups, a Man-Whitney test was calculated. The mean median latitudinal range shift (dotted lines) of vertebrates and insects is different (p -value < 0.001).

2.3. Limitations of studies on large-scale range shifts

Large-scale range shift studies suffer from several limitations. First, there is a geographical bias towards the northern hemisphere (Lenoir and Svenning 2015). In particular, studies in tropical areas have focused on elevation rather than latitudinal range shifts (Thomas 2010; Lenoir and Svenning 2015). Although, the climate is expected to change more slowly in tropical than in temperate areas (Loarie *et al.* 2009), limiting the necessity for a latitudinal shift. However, tropical insect species live closer to their thermal tolerance limits than temperate species (Khaliq *et al.* 2014), increasing potential impacts on insects (Deutsch *et al.* 2008) and their need to shift poleward. To gain a better understanding of range shifts in insects, it would be interesting to study their link with variation in thermal tolerance and the complex geography of climate change.

Second, scientists focus mainly on the north-south gradient with five times as many studies on latitudinal range shift as on longitudinal range shift (Lenoir and Svenning 2015). However, focusing on a unidirectional distribution shift neglects the complex interactions between temperature and precipitation (Vanderwal *et al.* 2012). For example, it is commonly

accepted that continentality (distance from the sea) can have a significant impact on temperature and precipitation (Makarieva, Gorshkov and Li 2009; Brunt 1924). Consequently, large-scale range shift studies should include both latitude and longitude to capture the complexity of climate change.

Finally, research on large-scale range shifts focuses mainly on one distribution limit (Lenoir and Svenning 2015). However, changes in a single distribution limit (without considering changes in total range size) are a poor proxy of the real species' response to climate change and can lead to a misleading estimate of a species' local extinction risk (McCain and Garfinkel 2021).

3. Fine-scale range shifts of insects

Biotic and abiotic conditions such as air and ground temperature, precipitation, soil moisture and vegetation type can strongly vary across short distances because of fine-scale environmental heterogeneity linked to topography, habitats, land use and microclimates. These fine-scale environmental variations might affect species response to climate change, especially small organisms like insects (Pincebourde and Woods 2020). They can either exacerbate the risks of local extinction associated with climate change (Raven and Wagner 2021) or, on the opposite, act as microrefugia (by buffering the effects of climate change; (Suggitt *et al.* 2018) or help species track their niche locally (McCain and Garfinkel 2021) (Fig. 6).

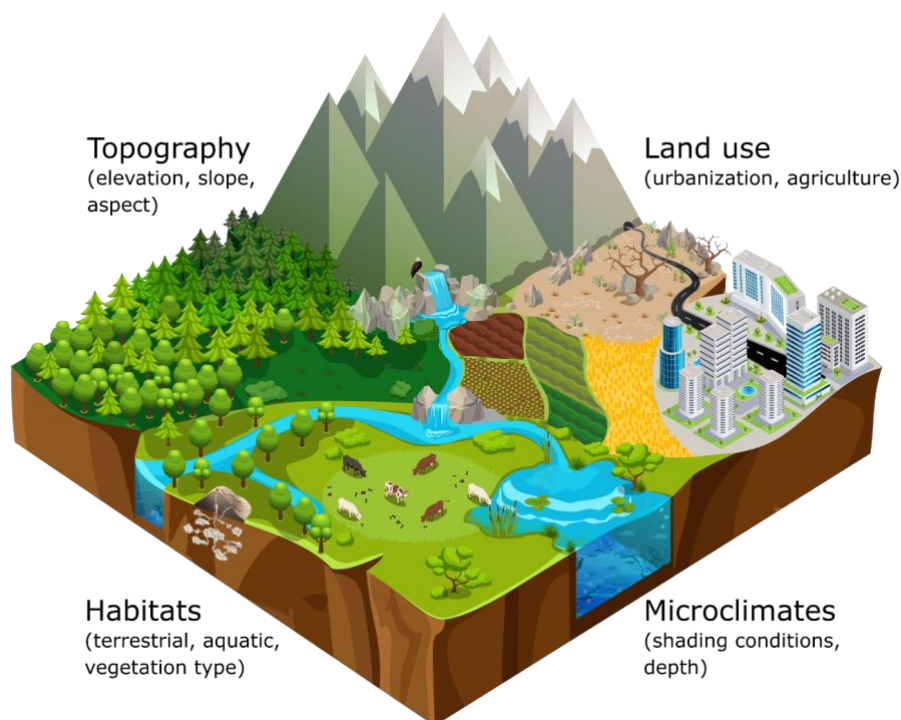


Figure 6. Landscapes are heterogenous. They vary in topography, comprise different types of habitats, and are subject to diverse anthropogenic modifications such as agriculture, urbanization, and pollutions. Therefore, within landscapes, environmental conditions can greatly vary over short distances and modulate the effects of climate change on insects' distribution (Artwork: P. Gippet-Vinard, based on vector images from www.freepik.com (authors: macrovector, pch.vector, uplyak, vectorpocket, vectorpouch, freepik and all-free-download.com)).

3.1. Topography

Changes in elevational ranges are the most studied fine-scale range shifts associated with climate change (McCain and Garfinkel 2021). It is expected that insect species shift, or at least contract, their range upward as climate warms (see McCain and Garfinkel 2021 for a detailed review) and multiple studies have already confirmed this trend over the last decades (Chen *et al.* 2009; Dolson *et al.* 2021; Halsch *et al.* 2021). However, upward shifts might not be a general pattern as many species do not show any elevational shift and some even shift unexpectedly downward (Halsch *et al.* 2021; McCain and Garfinkel 2021). For example, among 102 moth species sampled along an elevation gradient in Borneo, only 57% moved uphill over 42 years, with an average elevation increase of approximately 100 m (Chen *et al.* 2009).

In addition to elevation, slope and aspect (i.e., the compass direction that a terrain faces) can also affect insects' spatial distribution (Vessby and Wiktelius 2003; Bennie *et al.* 2008; Buse *et al.* 2015) as they strongly impact air and ground temperature by creating variations in solar radiation or wind regimes ((Liu and Luo 2011; Ebel 2012; Oorthuis *et al.* 2021) as well as soil properties (by affecting water movement, nutrient content) (Oorthuis *et al.* 2021). North-exposed slopes can be up to 10°C colder than adjacent South-exposed slopes (Rita *et al.* 2021) and could thus offer opportunities for horizontal spatial shifts that might have equivalent outcomes than vertical (elevational) shifts. However, the influence of slope and aspect on insects' response to climate change remains mostly unexplored so far (but see (Suggitt *et al.* 2018).

3.2. Habitats and land use

Depending on the habitat they occupy, species might not experience climate change in the same way or at the same pace (Uhler *et al.* 2021). Therefore, insects' response to climate change (including latitudinal and elevational shifts and contractions) might vary across habitats (Guo, Lenoir and Bonebrake 2018; Stralberg *et al.* 2020). For example, among animals, plants and fungi, terrestrial insects have the greatest average upward shift (i.e., + 36.2 m per decade), while semi-aquatic insects do not show any elevational shift, perhaps because freshwater habitats are heavily fragmented (e.g. dams) and thus difficult to colonize or because water provides microclimate buffering on warming rate, especially within mountain ranges where streams are fed by snow and glacier melt ((Vitasse *et al.* 2021). In terrestrial environments, trees strongly buffer ground level temperatures by preventing solar radiation to reach the ground and by limiting air fluxes (De Frenne *et al.* 2021). Thus, species living in forests' understory might experience climate change to a lesser extent than species inhabiting less buffered environments such as drylands, shrublands or grasslands (Rita *et al.* 2021; Wagner *et al.* 2021).

The size, number, and distance between patches of habitats affects insects' ability to track climate change (Platts *et al.* 2019; Wagner *et al.* 2021) because small and isolated patches are difficult to colonize or to recolonize after local extinction associated with extreme climatic events ((Oliver *et al.* 2015). The quality of habitat patches also varies within landscapes due to natural features (e.g., soil properties) and anthropogenic pollutants (e.g., heavy metals, plastics, pesticides, artificial light) that can affect insects' survival, reproduction, and dispersal ((Wagner *et al.* 2021). For example, cultivated areas are frequently sprayed with insecticides (Colin *et al.* 2020; Raven and Wagner 2021) and, with the combined effect of rising temperature, could become even more inhospitable to many insect species as climate warms (Raven & Wagner 2021); but see (Maino *et al.* 2018).

Among many land-use changes, urbanisation is perhaps the closest to climate change in terms of environmental modifications, because urban areas experience higher temperatures than adjacent rural or semi-natural areas. This is due to the urban heat island effect, a phenomenon caused by the thermal properties of artificial materials such as concrete and asphalt (e.g., low albedo, high emissivity) and by the lack of evaporative cooling associated with sparse vegetation, elevating the temperature in urban areas by up to 5°C relative to surrounding natural areas (Chapman *et al.* 2017). Urbanization is thus regarded as a potential unintentional global experiment to study and predict the effects of climate change on ecological and evolutionary dynamics (Lahr, Dunn and Frank 2018). But the effect of urbanization on insects' distribution is more complex than a simple 'fine-scale replicate' of climate change. The interaction of climatic conditions and urbanization is known to affect insects' spatial distribution at local to continental scale (Gippet *et al.* 2017; Cordonnier *et al.* 2020; Polidori *et al.* 2021). For example, some species colonize northern locations that are outside of their climatic niche by exploiting the warmer urban microclimate (e.g., the invasive mud-dauber wasp; (Polidori *et al.* 2021). Also, as drought events increase in frequency, some species might find refugia in urban areas by exploiting irrigated areas such as public parks and private gardens (e.g., ants in Arizona; (Miguelena & Baker 2019). Finally, as urban conditions favour heat tolerant species, it is expected that urban specialist species will expand their distribution outside cities as the climate warms (Menke *et al.* 2011). The effects of urbanization and climate change on insects' range shifts (at local to continental scale) might also depend on the background climatic conditions, as arid, temperate, or tropical areas will not experience the same relative climatic changes along urbanization gradients (Diamond *et al.* 2015).

3.3. Microclimates

Because insects are small, they experience environmental conditions at very fine spatial scale (i.e., ~10 cm around them; (Pincebourde and Woods 2020). Thus, insects could, in theory, exploit microscale variations in temperature and humidity by for example, moving around tree trunks or going deeper in the ground (Pincebourde and Woods 2020). Air and ground temperature can vary greatly over a few centimeters (up to ~15°C; (Pincebourde *et al.* 2016) because of differences in the amount of direct solar radiations, that are mainly due to natural and artificial vertical features such as trees and buildings (Napoli *et al.* 2016; Gippet, George and Bertelsmeier 2022). Very few studies have tested the effect of microscale shading conditions on insects' spatial distribution. Shades created by human buildings or experimentally have been shown to affect the foraging patterns of native and invasive ant species (Wittman *et al.* 2010; Gippet, George and Bertelsmeier 2022). However, to our knowledge, it is still unknown if insects can exploit shading conditions as microrefugia in response to climate change. Microclimatic conditions (e.g., temperature, water content, nutrients) can also vary depending on the depth of soil (Krab *et al.* 2010; Duffy *et al.* 2015). With climate warming, deep soil layers will heat less than upper layers and might thus offer microrefugia for many insect species (Duffy *et al.* 2015).

4. The role of dispersal

4.1. Natural dispersal

Dispersal ability is key to determining how insect species will cope with climate change. Highly mobile species might be more successful in shifting their ranges (Pöyry *et al.* 2009, Fig. 7). In

Europe for example, highly dispersive insects might be able to naturally spread from the continent to Great Britain as the climate becomes suitable (Hulme 2017). Conversely, species with limited dispersal might not be able to track the shifting climate and are therefore more likely to be limited by suitable niche space and risk extinction. Among butterflies, for instance, species with low dispersal capacities showed smaller altitudinal shift than more mobile species (Rödger *et al.* 2021).

In response to climate change, insect populations at expanding range boundaries might evolve greater dispersal capacities because dispersive individuals are more likely to establish new populations beyond their current range limits and transmit their genes. Descendants of these individuals will be more likely to found populations at range margins and therefore transmit traits favouring high dispersal rates (Parmesan 2006; Hill, Griffiths and Thomas 2011). This phenomenon has already been described in several insect species. For example, two bush cricket species show a higher proportion of long-winged (dispersive) individuals in populations at range margins in the United Kingdom (Thomas *et al.* 2001). Similar observations were made in Germany, where Roesel's bush-cricket (*Metrioptera roeseli*) has increased proportions of long-winged individuals in populations at the expanding range margin (Poniatowski, Heinze and Fartmann 2012). Likewise, populations of the European map butterfly (*Araschnia levana*) at the expansion front in Finland show higher frequency of the *Pgi-1* allele, associated with superior flight metabolic rate, compared to historical Estonian populations (Mitikka and Hanski 2010).

Rising temperatures may also affect insect dispersal directly, by increasing activity levels (Lantschner *et al.* 2014). Insects may be able to disperse over longer distances in regions with higher temperatures because of increased metabolic rate and extended flying period (Robinet and Roques 2010). For example, females of the winter pine processionary moth (*Thaumetopoea pityocampa*) showed increased flight activity with higher temperatures, allowing them to disperse over longer distances (Battisti *et al.* 2006). This likely facilitated the rapid increase in the altitudinal range limit of this species during the record hot summer of 2003 in Southern Europe. But temperature is not the only climatic factor affecting insect dispersal. For example, increased precipitation was shown to facilitate the spread of the invasive Argentine ant (*Linepithema humile*) in California (Heller *et al.* 2008). Moreover, the increased prevalence, intensity and duration of extreme climatic events (IPCC 2012) could facilitate species dispersal to new regions (Hellmann *et al.* 2008; Diez *et al.* 2012). Many insect species depend on wind currents for natural long-distance dispersal (Chapman, Reynolds and Wilson 2015; Leitch *et al.* 2021). More frequent storms could therefore increase the probability of insects moving over long distances and across physical barriers. It is likely that the cactus moth (*Cactoblastis cactorum*) benefited from the 2005 hurricane season to travel from the Caribbean to Mexico where it now has important ecological and economic impacts (Burgiel and Muir 2010). Similarly, the red palm mite (*Raoiella indica*) is thought to have spread throughout the Caribbean due to storms and hurricanes (Burgiel and Muir 2010).

4.2. Human-mediated dispersal

Climate change will not only affect natural dispersal. Many insect species are transported and introduced accidentally to new regions as contaminants or stowaways on traded commodities (Gippet *et al.* 2019; Meurisse *et al.* 2019). Consequently, more than 5,000 insect species have

established outside of their native range (Seebens *et al.* 2017). Climate change will likely alter patterns of trade and transport, and thus change the dispersal dynamics of introduced insects (Hellmann *et al.* 2008, Fig. 7). For instance, the opening of Arctic shipping routes due to the loss of sea ice might considerably reshape trade flows (Bekkers, Francois and Rojas-Romagosa 2018). Trade between Europe and Eastern Asia is expected to grow, which could increase introduction opportunities. The opening of the Arctic shipping routes will also greatly reduce sailing distances and travel time (Dellink *et al.* 2017; Bekkers, Francois and Rojas-Romagosa 2018), which could enhance the survival of insects during transport. Climate change will also affect the production of many commodities (Dellink *et al.* 2017) which could change global trade flows and thus the dynamics of insect dispersal. In particular, climate change will impact agricultural production. Changes in temperatures, precipitations and more frequent heat extremes may lead to crop yield loss in most part of the world (Dellink *et al.* 2017). Some productions might also be relocated as new regions become suitable for certain crops. International trade could therefore play a key role in compensating for these shifts in production potential (Huang, von Lampe and van Tongeren 2011), which may enhance unintentional insect introductions.

Climate change will also affect the establishment probability of introduced insects (Robinet and Roques 2010; Hulme 2017). For example, it is predicted that climate suitability for pest arthropod species will increase in North-Eastern European countries but decrease in central European countries (Bacon *et al.* 2014). The Argentine ant (*Linepithema humile*) and the yellow crazy ant (*Anoplolepis gracilipes*) are two highly invasive species that are regularly intercepted at the British border. They have so far failed to establish there (at outdoor locations, but see Charrier *et al.* 2020), but this may change with warming climate (Hulme 2017). In Antarctica, insect establishment probability is low due to the harsh climatic conditions. But this region might become more susceptible to insect invasions in the future (Bergstrom 2022). More frequent extreme climatic events might also strongly disturb ecosystems, which could facilitate the establishment and spread of introduced species as they may have broader physiological tolerance than native species (Diez *et al.* 2012). Extreme climatic events can create “invasion windows”, for instance by generating resource pulses that introduced species can exploit more quickly than native species (e.g., thanks to more rapid growth and colonization). Heat waves and droughts can also cause significant stress to native communities and increase the mortality of native species, thus reducing biotic resistance (e.g., competition) against introduced species.

Finally, climate change might impact global trade as damage to trade infrastructures will increase with more frequent extreme climatic events (Dellink *et al.* 2017). Storms, extreme precipitations, and sea level rise may affect operations of airports, cause more frequent port closure, require the use of alternative shipping routes, affect sailing time and increase port and ship maintenance costs. Moreover, climate change will affect the global economy and potentially lead to lower GDPs, which is also likely to impact global trade (Dellink *et al.* 2017). These negative impacts of climate change on international trade and the world economy overall could also reduce the rate of insect invasions in the future as it is tightly linked to the level of trade globalisation (Bertelsmeier *et al.* 2017; Bonnamour, Gippet and Bertelsmeier 2021).

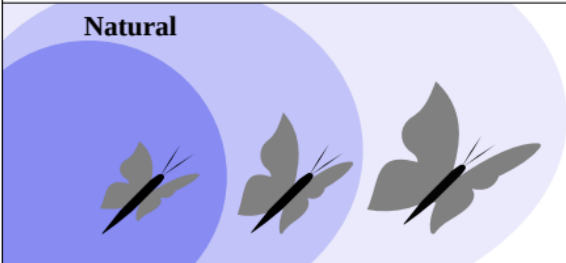
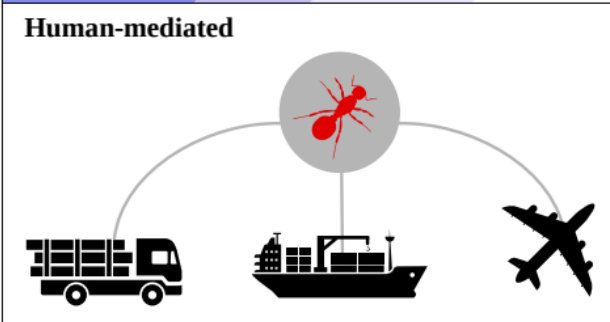
Dispersal type	Impact of climate change
<p>Natural</p> 	<ul style="list-style-type: none"> • Pressure on species with low dispersal ability • Selection for highly dispersive traits • Increased flight activity and metabolic rate • Changing host plant distribution • More frequent storm-driven dispersal
<p>Human-mediated</p> 	<ul style="list-style-type: none"> • Shifts in trade patterns • Changes in commodities • Impacts on trade infrastructures and the global economy • Changing climate suitability • Native ecosystem disturbance facilitating establishment

Figure 7. Impact of climate change on insect natural and human-mediated dispersal

5. Ecophysiological and life history traits

With ongoing climate change, species traits will be beneficial or limiting, creating both ‘winners’ and ‘losers’. Some traits relevant to responses to climate change are difficult to measure in the field and therefore current knowledge predominately relies on lab experiments, with sufficient data in some cases only for *Drosophila* species. Yet, some of these traits might hold the key to understanding persistence of insect populations in a changing environment. Given that traits are not as fixed as often assumed when predicting species distributions, we also address insects’ potential for adaptation and plasticity.

5.1. Thermal Traits

Critical thermal limits (CTs)—temperatures at which insects lose voluntary muscle control—have gained popularity in recent years for predicting species distributions (Lutterschmidt and Hutchison 1997; Rezende, Tejedo and Santos 2011). However, the data on insect CTs is biased towards 3 insect groups: *Drosophila*, Coleoptera and Formicidae, which comprise 95% of data on heat tolerance (Calosi *et al.* 2010; Diamond and Chick 2018a; Kellermann and van Heerwaarden 2019). Because of lower geographic variability and stronger phylogenetic signal in insect heat tolerance compared to cold tolerance (Addo-Bediako, Chown and Gaston 2000; Hoffmann, Chown and Clusella-Trullas 2013; Bujan *et al.* 2020) insect heat tolerance is expected to have low adaptive potential, which could be detrimental in a warming world. Tropical insects have narrower thermal ranges (CT_{max}-CT_{min}), and they are expected to be under higher extinction risk compared to insects from more variable, temperate climates (Diamond *et al.* 2012; Sunday *et al.* 2014; Diamond and Chick 2018b). However, in bumblebees, cold-adapted species are more sensitive to extreme heat events (Martinet *et al.* 2020). Thus, tropical species and cold specialist species are predicted to be most threatened by climate change.

Thermal sensitivity of insect reproductive organs is also crucial to determine fitness under climate change. Temperatures that sterilize (Parratt *et al.* 2021) *Drosophila* males better predicted global species distributions than critical thermal limits (van Heerwaarden and Sgrò 2021). Additionally, temperature can differentially impact insect ovarian development across their geographic range (Everman *et al.* 2018). To assess which insect taxa are reproductively challenged by temperature, it would be necessary to measure optimal reproductive temperatures for a wide range of species and populations, in turn helping us better understand species distributions.

5.2. Desiccation Resistance

Climate change increases the frequency of severe droughts, particularly in the tropics (Dai 2011). Therefore, desiccation resistance—the ability to withstand water stress – is especially important for small insects. Generally, larger species of fruit flies (Gibbs and Matzkin 2001), tiger beetles (Schultz and Hadley 1987), and ants (Hood and Tschinkel 1990) are more resistant to desiccation compared to smaller species. Insects from dry areas adapted to withstand desiccation lose water slower than their mesic counterparts (Gibbs and Matzkin 2001). Given that tropical insects are not exposed to desiccation stress, they have low desiccation resistance and low adaptive potential for this trait, as shown in *Drosophila* (Hoffmann *et al.* 2003; Rajpurohit, Nedved and Gibbs 2013). However, the tropics are not uniform and in the same tropical forest drier tropical canopy holds species able to withstand drought stress longer than their understory counterparts (Bujan, Yanoviak and Kaspari 2016). Increase in drought frequency in the future is expected to limit the spread of some introduced insects, such as Argentine ants whose spread depends on soil moisture (Holway, Suarez and Case 2002; Couper *et al.* 2021). Yet, other introduced species like pollinator bees in Fiji, which show higher desiccation resistance than native pollinators (da Silva *et al.* 2021), or the larger grain borer (*Prostephanus truncates*) that can acclimate its desiccation resistance (Mutamiswa *et al.* 2021).

5.3. Dispersal ability

Dispersal ability is expected to be key to withstanding climate change (Berg *et al.* 2010). Generally insect populations at the range edges have traits that favour dispersal, such as higher proportion of long-winged morphs linked to increased flight ability (Simmons and Thomas 2004). However, there is mixed evidence that warming increases wing size and consequently dispersal ability in flying insects. Wing sizes of a social wasp decreased in response to warming (Polidori *et al.* 2020) but also increased with elevation in introduced *Drosophila suzuki* (Jardeleza *et al.* 2022). While stable environmental conditions are assumed to be one reason for evolution of flightlessness in insects (Wagner and Liebherr 1992), this trait might now be disadvantageous.

5.4. Voltinism

Number of generations produced per year—voltinism—is negatively correlated with latitude in many insect taxa (Musolin 2007; Zeuss, Brunzel and Brandl 2017). Thus, warmer areas promote multiple insect generations. Climatic warming increased voltinism in European butterflies and moths which now reproduce more frequently, giving them a potential evolutionary advantage, as insects with faster reproductions cycles have higher chances of adaptation to novel conditions (Altermatt 2010). But this is risky, as some species, like the European wall brown butterfly, have been known to fall into “developmental traps” risking

extinction if they fail to predict climates of the upcoming season (van Dyck *et al.* 2015). Some species might have an advantage by producing more generations per year, which is best demonstrated in introduced insects in which multi-voltinism enables faster spread. For example introduced populations of gypsy moths develop faster due to temperatures and length of the growing season (Faske *et al.* 2019). Multivoltine introduced insects spread on average 72.9 km/year, and univoltine insects only 16.9 km/year (Fahrner and Aukema 2018), highlighting a worrying competitive advantage in the face of warmer climates in introduced species that can increase the number of generations per year (Tobin *et al.* 2008; Ziter, Robinson and Newman 2012).

5.5. Adaptation vs. Plasticity

Species can alter their traits in two ways to persist under novel environmental conditions: through plasticity and evolutionary adaptation. Adaptations to novel environmental conditions are beneficial trait changes that are underpinned by genetic changes resulting in increased fitness (Bertelsmeier and Keller 2018). However, direct experimental tests of adaptive potential of introduced and native populations are rare (Chevin and Lande 2011; Colautti and Lau 2015), and the presence of adaptation is usually inferred (Bertelsmeier and Keller 2018). Adaptive responses of insects to climate change are not limited to thermal tolerances but can involve changes in melanism (Brakefield and de Jong 2011), voltinism (Altermatt 2010), morphology (Huey *et al.* 2000), desiccation resistance (Tejeda *et al.* 2016), and dispersal ability (Hill, Griffiths and Thomas 2011).

In the absence of adaptation, species may benefit from phenotypic plasticity – the potential of one genotype to express multiple phenotypes (Agrawal 2001). For example, phenotypic plasticity can include changes in morphology, diet, and physiology under new environmental conditions. When insects are faced with extreme heat, thermal plasticity enables them to withstand temperature changes and provides a competitive advantage over insects with static thermal tolerances (Rodrigues and Beldade 2020). Some studies suggest there is a trade off between basal thermal tolerance and thermal plasticity (Esperk *et al.* 2016). However a recent meta-analysis shows this evidence to be equivocal (van Heerwaarden and Kellermann 2020). A plastic phenotype can be costly, either because of timing costs associated with developmental stages or costly production of heat shock proteins. Therefore, phenotypic plasticity is assumed to be lost in a stable environment (Sgrò, Terblanche and Hoffmann 2016).

Introduced insects may benefit from short term phenotypic changes when they arrive in novel environments. In plants, introduced species showed higher phenotypic plasticity than native species (Davidson, Jennions and Nicotra 2011), but in springtails there were little differences between introduced and native populations (Janion-Scheepers *et al.* 2018). A frequently studied type of phenotypic plasticity is acclimatization—a reversible physiological change which enhances performance (Angilletta 2009). Some introduced insects are able to acclimate (Nyamukondiwa, Kleynhans and Terblanche 2010; Coulin *et al.* 2019; Bujan *et al.* 2021) but considering the impact of introduced, insects our knowledge on the extent of phenotypic plasticity in introduced insects is lagging behind.

6. Species interactions and responses to climate change

6.1. Interactions regulate ability to track climate change

Climate change impacts virtually every type of biotic interaction among species in a community (Table 1) by altering the conditions that species experience (Tylianakis *et al.* 2008). In turn, these interactions determine how species respond to changing environmental conditions (e.g., Davis *et al.* 1998a, b). Moreover, community composition is not static. Climate change and human activities are reshuffling species distributions, creating new communities worldwide (e.g., Schweiger *et al.* 2010, Alexander *et al.* 2016). New interactions emerge in these novel communities, while others no longer take place. Interactions at all trophic levels are implicated: herbivores, predators, parasitoids and pathogens, hyperparasitoids and tertiary predators, and their prey or host species. Insect endosymbiont functions are also potentially altered by rising temperatures (van Baaren, le Lann and JM van Alphen 2010). The nature and relative importance of interactions depend on the climatic conditions, which has important implications for determining species' current and future distributions (Wisz *et al.* 2013). Warmer range-edge responses in particular depend strongly on biotic interactions (Paquette and Hargreaves 2021), potentially due to stronger negative interactions in warmer and more productive ecosystems (e.g., Vamosi *et al.* 2006, Roslin *et al.* 2017, Hargreaves *et al.* 2019), or interactions being relatively more important under benign climatic conditions (Dobzhansky 1950).

Table 1: Main types of interactions between species, and their impact on each partner. Impacts are either positive (+), neutral (0) or negative (-).

Type of interaction	Response	
	Species 1	Species 2
Mutualism	+	+
Commensalism	+	0
Neutral	0	0
Predation/parasitism	+	-
Amensalism	-	0
Competition	-	-

6.2. Range shifts disrupt interactions

Species' range shifts driven by climate change are often not synchronized within a community (Schweiger *et al.* 2010; Urban, Tewksbury and Sheldon 2012). Biotic interactions are thus disrupted by shifts either in space or time, which can have considerable impacts on species' fitness. These impacts can be positive, offering a release from negative interactions in the new range (Fig. 8a). The enemy release hypothesis, which was originally formulated in the context of biological invasions, predicts that introduced species are more successful in new areas where their native enemies are absent (Keane and Crawley 2002). So far, support for this is mixed (Heger and Jeschke 2014; Mlynarek 2015), and may be more relevant for species under strong enemy effects in their historic range (Prior *et al.* 2015). Similarly, range shifts of native species may disrupt enemy interactions. Subsequent fitness increases in the new range could facilitate tracking suitable climatic conditions (Fig. 8a). This has been illustrated in grassland communities, where less spatial overlap between predatory spiders and their grasshopper prey due to differential responses to warming allows the grasshoppers to increase their feeding (Barton 2010).

Disrupting interactions can also have negative impacts. Species may be prevented from colonizing climatically suitable areas if their interaction partners are absent (Fig. 8b). For example, eggs of the butterfly *Aporia crataegi* survive at higher elevations with increased warming, but upward colonization is restricted by the lack of host plants (Merrill *et al.* 2008). Future projections indicate increasing range mismatch between host-plant-limited European butterflies and their hosts, restricting their climate-tracking ability (Schweiger *et al.* 2010).

6.3. Range shifts create new interactions

If interacting species' distributions change in synchrony, or if they find new partners, interactions can facilitate spread (Fig. 8c). For example, *Polygonia c-album* has undergone the fastest range expansion of any resident butterfly species in Britain (Warren *et al.* 2001), likely due to a shift in larval host preferences (Braschler and Hill 2007). The effects of global change on insect mutualisms are highly variable however, making general patterns difficult to detect (Vidal *et al.* 2021). Range shifts can also be restricted by novel interactions. Competition may slow species spread into suitable habitats (Urban, Tewksbury and Sheldon 2012) (Fig. 8d) and can negatively impact species in the recipient community. For example, numbers of migratory butterfly species in southern Britain are increasing with rising temperatures, posing a competitive threat to less mobile and more specialized native insects (Sparks *et al.* 2007).

Insects may join existing interaction networks in their new range, for example as pollinators or seed dispersers. This has been observed for introduced species (e.g., Aizen *et al.* 2008, Traveset *et al.* 2013), and may also be the case with naturally dispersing species. New species can fundamentally alter network structure, transferring links from generalist native to super-generalist introduced species (Aizen, Morales and Morales 2008). Novel networks with many links may be more stable, making them more resistant to certain types of disturbance, and more vulnerable to others (Aizen, Morales and Morales 2008; Traveset *et al.* 2013). Novel species can also, to some extent, replace lost or declining native pollinators (Gross 2001; Dick, Etchelecu and Austerlitz 2003), and can either partly compensate for negative impacts of climate change on pollinator networks, or intensify them (Schweiger *et al.* 2010).

6.4. Hitchhiking pathogens and interactions across trophic levels

The effects of climate change are likely to be stronger at higher trophic levels (van Baaren, le Lann and JM van Alphen 2010). Predators, parasitoids and hyper-parasitoids must locate and exploit their prey or hosts. Many of these interactions are temperature-dependent, and vulnerable to environmental change (Hance *et al.* 2006). Additionally, as insect distributions change, parasites and pathogens may hitch a ride, forming their own novel interactions. Introduced bees and bumblebees have been shown to transmit pathogens to less-resistant native species, and even less virulent ones can be lethal to new hosts when combined with environmental stressors (Arbetman *et al.* 2013; Vilcinskis 2019). The co-introduction of parasites and pathogens with their hosts can also impact human health. For example, introduced mosquito species pose significant threats to public health due to the diseases they transmit (e.g., Schaffner *et al.* 2013), and climate change may increase their invasion potential (Iwamura, Guzman-Holst and Murray 2020).

6.5. Novel interactions can facilitate additional species establishing

Species may also form interactions, or create environmental conditions that promote the establishment of additional species as they spread. For instance, introduced insects are often key pollinators of introduced plants (Simberloff and von Holle 1999; Olesen, Eskildsen and Venkatasamy 2002; Stout, Kells and Goulson 2002; Goulson 2003), potentially facilitating their spread (Morales and Aizen 2002). The hemlock woolly adelgid, *Adelges tsugae*, reduces light interception by the forest canopy, indirectly creating conditions favouring introduced plants (Eschtruth *et al.* 2006). Such interactions can have knock-on effects on community composition (e.g. Brightwell and Silverman 2010), potentially also in response to species shifting their range due to climate change.

At the community level, facilitation between several introduced species may lead to increasing establishment rates or accelerating impacts, termed “invasional meltdown” (Simberloff and von Holle 1999; Simberloff 2006). While this concept is based on species invasions, the same processes could occur following natural dispersal induced by climate change. It is challenging to show experimentally that mutualisms increase the populations of both partners at a regional scale, due to ethical considerations and the complexity of factors involved, but the circumstantial evidence is often strong (Simberloff 2006). On Christmas Island, populations of the introduced ant *Anoplolepis gracilipes* increased dramatically after the introduction of scale insects. The ants protect the scales from predators and parasites, and also devastate populations of the native land crab *Gecarcoidea natalis*. *G. natalis* no longer controls ground cover plants, and sooty mould growing on honeydew causes canopy dieback, altering forest community composition (O’Dowd, Green and Lake 2003; Abbott 2004). In turn, the absence of *G. natalis* has facilitated the establishment of Giant African Land Snails, *Achatina fulica* (Green *et al.* 2011). In the face of global change, restoring “pristine” interaction networks is likely impossible. The question is whether these novel communities can absorb new species, while simultaneously sustaining complex interactions between native species (Roubik 2000; Traveset and Richardson 2006).

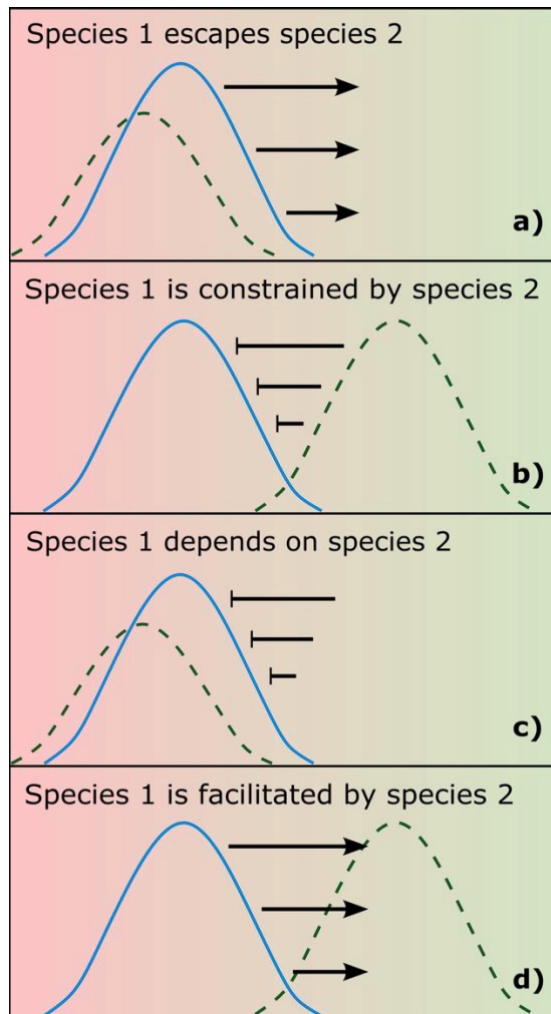


Figure 8: Interactions determine species' climate-tracking ability, impacting the distributions of focal species (blue line) and their interaction partners (dashed green line). The gradient indicates changing climate and habitat suitability. a) species track climate change through enemy release, b) species lag behind climate change due to enemy interactions in their new range, c) species lag behind climate change due to mismatched range shifts between interaction partners, or d) species track climate change through facilitation by existing or new partners. Adapted from (HilleRisLambers *et al.* 2013).

7. Predicting the distribution of species under climate change

Different approaches can be used to make predictions about future species distributions under climate change. Most use species occurrences in combination with climate data to model species' climate niches and project potential future distribution under future climatic conditions (Guisan and Thuiller 2005; Gallien *et al.* 2010; Mammola *et al.* 2021). But the complexity of models can range from simple correlational models to process-based mechanistic models. Here, we discuss the use of correlational models (7.1), hybrid models and semi-mechanistic models (7.2), and mechanistic models (7.3) in predicting the future distributions of insect species under climate change

7.1 Correlational models

The simplest and most widely used model type are species distribution models (SDMs; also called ecological niche models (ENMs)) (Evans, Diamond and Kelly 2015). These correlative models use the present-day occurrence point locations of a species to determine the current environmental conditions experienced by the species, and then map areas where these climatic conditions are expected to occur in the future (Dormann 2007; Evans, Diamond and Kelly 2015; Hill and Thomson 2015). An underlying assumption of these models is that future distributions will reflect the current realized niches of species. Although all SDMs link species occurrences with climatic data, there are many different algorithms that can be used to model

this species-environment relationship. Options range from statistical models such as general linear models (GLMs), for example in recent predictions of future distributions of hoverflies (*Syrphidae*) in the Balkans (Radenković *et al.* 2017), to other machine learning models such as neural networks (e.g., boosted regression trees, for example seen in a study of Odonata species (Jaeschke *et al.* 2013)). One of the most commonly used SDM method is 'Maxent'; an easy-to-use machine learning approach (Phillips, Anderson and Schapire 2006). For example, a recent study on 18 meso-American bumblebee (*Bombus*) species used a Maxent SDM to predict area losses of up to 67% by 2050 of their current range along with altitudinal shifts upwards (Martínez-López *et al.* 2021). However, there is no single 'best' model type (Carvalho, Rangel and Vale 2017). Multiple model outputs may have statistically good predictive outputs (usually evaluated using TSS or AUC scores), while predicting significantly different distributions. A widely used solution to deal with this variation in individual model outputs is to combine them by averaging across models. The contribution of individual models to a final 'ensemble model' can be weighted based on evaluation statistics (Thuiller *et al.* 2016; Hao *et al.* 2019). Recent examples of ensemble models include studies on future distributions of aquatic insects (Timoner *et al.* 2021) and introduced bee species in Hawaii (Tabor and Koch 2021).

7.2 Hybrid/Semi-mechanistic models

There are several extensions to classic SDMs that can inform models with additional biologically relevant information. For instance, hybrid or niche-population models can predict distributional changes by integrating population-level responses (Aragón, Baselga and Lobo 2010; Zurell *et al.* 2016). A recent study on Japanese stag beetles (*Allomyrina dichotoma*) used estimated dispersal distances based on kernel densities and found that models incorporating dispersal constraints performed better than simpler models, ultimately predicting large reductions of stag beetle ranges by 2070 (Zhang and Kubota 2021). Another study on butterflies included population-specific distributions, site-specific species richness, as well as species-specific growth rates to incorporate dispersal into their predictions (Isaac *et al.* 2011).

Other traits are more commonly used to inform predictions of insect distributions by semi-mechanistic models. The semi-mechanistic modelling tool 'CLIMEX' (Jung, Lee and Jung 2016; Kriticos *et al.* 2016) is used in a large number of studies to predict future distributions under climate change, with recent applications including studies on the orders Coleoptera (Zhou *et al.* 2021), Lepidoptera (Guo *et al.* 2021), Hemiptera (Falla *et al.* 2021), Hymenoptera (Byeon *et al.* 2020) and Diptera (Kim, Park and Kim 2020). CLIMEX uses laboratory-based growth, phenology and stress information on a specific species to create an ecoclimatic index (EI) which is used to quantify habitat suitability in different areas and under different climatic scenarios (Jung, Lee and Jung 2016; Kriticos *et al.* 2016; Byeon, Jung and Lee 2018).

7.3 Mechanistic Models

Currently, the most 'complex' models employed to predict insect species distributions under climate change are mechanistic models (Evans, Diamond and Kelly 2015; Maino *et al.* 2016). These models can predict which regions will remain suitable under climate change by modelling species-specific responses to climate based ecophysiological data and vital rates, sometimes even including life-stage specific growth and death rates in response to climate (Kearney 2006; Kearney and Porter 2009).

Physiological based demography models (PBDMs) base predictions on physiological, phenological and demographic responses in space and time. For example, the range expansion of the pest species *Bemisia tabaci* has been predicted under climate change with a PBDM using estimates of developmental rates, temperature-dependent mortality rates, age-specific fecundity (Gilioli *et al.* 2014). PBDMs can ultimately incorporate mechanistically both demographic and physiological responses to climate (Gutierrez and Ponti 2014). It is important to note, however, that eco-physiological limits and growth rates measured under laboratory conditions may not represent the realised limits of a species in the field. Moreover, physiologically based models do not account for biotic and dispersal constraints (Soberón and Peterson 2005). But other mechanistic models can explicitly incorporate dispersal into estimates of distribution and abundance, for example which was done in a study that used a random-walk model to predict distributional changes of the European grasshopper *Chorthippus albomarginatus* (Walters *et al.* 2006). However, detailed models incorporating empirical data on dispersal are rare for insects.

Another type of mechanistic model estimates “degree-days”, i.e., the number of days within a certain climate range needed for a species development. This phenological model type is particularly interesting for insects because many species go through multiple life stages with different climatic optima, and potentially impacted differently by climate change. For example, brood and early life cycles are known to be particularly sensitive to climate. Degree-day models are calibrated using data from physiological experiments measuring developmental response curves under different temperatures (Lemoine 2021), to estimate ‘degree days’ across a season. Degree-day models have been used to predict the spread of the introduced potato beetle (*Leptinotarsa decemlineata*) in Scandinavia (Pulatov *et al.* 2014). This approach allows researchers to delimit when daily temperature is above the species’ threshold for survival or development, and therefore using a combination of timing of first to second generation development as well as generational numbers per years. Degree-day models have also been used to predict brood survival and oviposition rates in the introduced Argentine ant *Linepithema humile* (Abril *et al.* 2009). Such phenological models have in some cases even been shown to outperform SDMs, for example as was seen in a study on in U.K. butterfly species (Buckley *et al.* 2011), and even more complex physiological-based mechanistic models (Bryant, Thomas and Bale 1997; Buffo *et al.* 2007), as was exemplified in a study of the pine processionary moth in Italy (Buffo *et al.* 2007).

7.5 Future of modelling

Overall, a combination of data availability and expert knowledge can help determine which approaches are best for a particular species. In the absence of expert knowledge, employing multiple model types, from correlative to mechanistic, across various future environmental predictions will allow us to predict future species distributions with increased confidence (Violle *et al.* 2014; Benito Garzón, Robson and Hampe 2019; Mammola *et al.* 2019, 2021).

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