UNIL | Université de Lausanne

Faculté de biologie
et de médecine

**Département d'Ecologie et Evolution**

# Impact of globalization on the spread of non-native insects

**Thèse de doctorat ès sciences de la vie (PhD)**

présentée à la

Faculté de biologie et de médecine
de l'Université de Lausanne

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Lausanne
2025

1434/2025

**UNIL** | Université de Lausanne
Faculté de biologie
et de médecine

**Ecole Doctorale**
**Doctorat ès sciences de la vie**

# Imprimatur

Vu le rapport présenté par le jury d'examen, composé de

| | | | | |
|---|---|---|---|---|
| **Président·e** | Monsieur | Prof. | Sven | **Bergmann** |
| **Directeur·trice de thèse** | Madame | Prof. | Cleo | **Bertelsmeier** |
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le Conseil de Faculté autorise le dépôt de la thèse finale de

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intitulée

## Impact of globalization on the spread of non-native insects

Lausanne, le 27 juin 2025

pour le Doyen
de la Faculté de biologie et de médecine

Prof. Sven Bergmann

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# Acknowledgments

First, I would like to thank my PhD supervisor: Cleo Bertelsmeier

Thank you so much for giving me the opportunity to join your group! Thank you for your support and guidance, first during my master's project, then throughout my PhD! You've always been very positive and supportive of my ideas, and you gave me so much freedom to explore the topics and questions I was interested in. You also provided precious ideas, advices and directions whenever I needed it. You were an amazing supervisor and I learned a lot thanks to you. I really enjoyed working with you during these past years, and I am looking forward to continuing the adventure! Thank you Cleo!

I would then like to thank Mark van Kleunen, Tim Blackburn and Sven Bergmann for accepting to be part of my thesis committee, for their constructive feedback and the interesting discussions.

I also thank all the members of the DEE, and in particular the former and current members of the Bertelsmeier group: Olivia Bates, Gyda Fenn-Moltu, Jelena Bujan, Jérôme Gippet, Tim Szewczyk, Sébastien Ollier, Tristan Klaftenberger, Eddie Pérochon, Zoé Sherpa, Lucie Aulus-Giacosa, Mathieu Leclerc, Rosaëlle Perreault, Tongyi Liu and Julian Melgar. Thank you for all the interesting discussions, the laughs, adventures and aperos. It is great being surrounded by such brilliant, kind and funny people!

I am also very grateful to all the members of the "MoRIS team", Jérôme Gippet, Bernard Kaufmann, Charles Rocabert and Serge Fenet, with whom I took my first steps in research on ants and invasion biology. Thank you for trusting me to work with you when I was a first year master student. I am very lucky to have met you! Special thanks to Jérôme, for believing in me and supporting me throughout my two master's projects and my PhD, and for everything you have done for me!

I would also like to thank the coauthors and collaborators of the different projects I have been involved in, as well as the students who helped collecting and digitalizing data.

I thank my friends, in France, Switzerland and beyond. I had so much fun and so many incredible adventures these past five years, and I am so grateful I got to share these with such amazing people!

Finally, I thank my family. My parents, for their unconditional support and for everything they have taught me. Thank you for being such wonderful parents. I also thank my beloved brother who, like my parents, had to put up with the various insects I used to keep in the house (and their occasional escapes...). I also thank my grand-parents, my aunts, uncles and cousins for being such inspiring people from whom I learned and discovered a lot growing up.

# Summary

With increasing global trade, thousands of species have been introduced, intentionally or accidentally, to new regions outside of their native range, and some of them have significant impacts on ecosystems and human societies. A better understanding of the human-mediated dispersal of species is therefore required in order to better predict and prevent future invasions. This thesis investigates the effects of globalization and human activities on the spread of non-native species, with a particular focus on insects, which are very successful and damaging invaders that are mostly transported and introduced accidentally. **Chapter 1** addresses the temporal dynamics of insect and plants invasions over the past centuries. We used a statistical model that accounts for temporal variations in sampling effort to estimate insect and plant invasion rates. We found that, once sampling bias is accounted for, the rate of insect and plant invasions did not continuously increase over the past two centuries, but fluctuated, following the two waves of globalization (~1820–1914, 1960-present). In **chapter 2**, we show that the rise and fall of European colonial empires strongly influenced the spread of non-native species, using ants as a model system. Our results indicate that, before 1960, countries that belonged to a colonial empire received a higher number of non-native ant species than those that did not, and that ants spread preferentially between countries that belonged to the same empire. After 1960, however, former colonial ties no longer had an effect on ant invasions. We also found that most non-native ant species originated from colonized countries, which contrasts with the "Imperialist dogma". **Chapter 3** explores the importance of secondary introductions (i.e., the bridgehead effect) in non-native insect dispersal. We found that 34% of insect interceptions at ports of entry in the United States between 1913 and 1984 originated from previously invaded regions, rather than from the species' native range. We found that the probability of secondary introduction increased over time, and was also linked to the size of the species' non-native range. Our results show that the bridgehead effect creates a positive feedback loop between transport and establishment, leading to an acceleration of invasions. Finally, **chapter 4** highlights the strong link between plant and insect invasions, and shows that non-native plant flows dating back to 1900 were the best predictor of geographical variation in current non-native insect flows. This time lag between plant and insect invasions leads to a substantial insect invasion debt globally. The estimated debt was most important in the Afrotropics and the Neotropics, suggesting that insect invasions are likely to strongly increase in those regions in the near future. Overall, this thesis improves our understanding of the socio-economic drivers of biological invasions, and highlights the need for more research on the human dimensions of invasions because biological theory alone cannot explain or predict the spread of non-native species.

# Résumé

Avec l’augmentation du commerce mondial, des milliers d’espèces ont été introduites, intentionnellement ou accidentellement, dans de nouvelles régions en dehors de leur aire de répartition d’origine, et certaines d’entre elles ont des impacts significatifs sur les écosystèmes et les sociétés humaines. Une meilleure compréhension de la dispersion des espèces par l’homme est donc nécessaire afin de mieux prédire et prévenir les invasions futures. Cette thèse examine les effets de la mondialisation et des activités humaines sur la propagation des espèces exotiques, en se focalisant principalement sur les insectes, qui sont des envahisseurs très efficaces, principalement transportés et introduits accidentellement et qui causent de nombreux dégâts. Le **chapitre 1** traite de la dynamique temporelle des invasions d’insectes et de plantes au cours des siècles passés. Nous avons utilisé un modèle statistique qui prend en compte les variations temporelles de l’effort d’échantillonnage pour estimer le nombre annuel d’invasions d’insectes et de plantes. Nous avons constaté qu’une fois le biais d’échantillonnage pris en compte, le nombre annuel d’invasions d’insectes et de plantes n’a pas augmenté de manière continue au cours des deux derniers siècles, mais a fluctué en suivant les deux vagues de mondialisation (~1820–1914, 1960-présent). Dans le **chapitre 2**, nous montrons que l’essor et le déclin des empires coloniaux européens ont fortement influencé la propagation des espèces exotiques, en utilisant les fourmis comme organisme modèle. Nos résultats indiquent qu’avant 1960, les pays appartenant à un empire colonial ont reçu un plus grand nombre d’espèces de fourmis exotiques que ceux qui n’en faisaient pas partie, et que les fourmis se sont propagées préférentiellement entre les pays appartenant au même empire colonial. Après 1960, cependant, les anciens liens coloniaux n’avaient plus d’effet sur les invasions de fourmis. Nous avons également découvert que la plupart des espèces de fourmis exotiques provenaient des pays colonisés, ce qui contraste avec le « dogme impérialiste ». Le **chapitre 3** explore l’importance des introductions secondaires (ou "l’effet tête de pont") dans la dispersion des insectes exotiques. Nous avons constaté que 34 % des interceptions d’insectes aux frontières des États-Unis entre 1913 et 1984 provenaient de régions déjà envahies, plutôt que de l’aire de répartition d’origine de l’espèce. Nous avons également constaté que la probabilité d’introduction secondaire augmentait au fil du temps et était également liée à la taille de l’aire de répartition exotique de l’espèce. Nos résultats montrent que "l’effet tête de pont" crée une boucle de rétroaction positive entre le transport et l’établissement, entraînant une accélération des invasions. Enfin, le **chapitre 4** met en évidence le lien étroit entre les invasions de plantes et d’insectes et montre que les flux de plantes exotiques remontant à 1900 étaient le meilleur prédicteur de la variation géographique des flux actuels d’insectes exotiques. Ce décalage temporel entre les invasions de plantes et d’insectes conduit à une dette d’invasion d’insectes substantielle à l’échelle mondiale. La dette estimée était particulièrement importante en Afrique et en Amérique latine, suggérant que les invasions d’insectes sont susceptibles d’augmenter fortement dans ces régions dans un avenir proche. Dans l’ensemble, cette thèse améliore notre compréhension des facteurs socio-économiques des invasions biologiques et souligne la nécessité de mener davantage de recherches sur les dimensions humaines des invasions, car la théorie biologique seule ne peut pas expliquer ni prédire la propagation des espèces exotiques.

# Introduction

## The reshuffling of biodiversity

All species are restricted in their geographical distributions. These range limits are determined by physical barriers preventing species dispersal, such as mountains or oceans, but also by interspecific interactions and the  species' adaptations to the environment within its range (Gaston, 2009). For thousands of years, however, humans have been moving species around the world, sometimes intentionally, for example for agricultural purposes, sometimes accidentally, as stowaways or contaminants on transported commodities (**appendix 3**; Hulme, 2009; Lenzner et al., 2018). These species transported by humans are sometimes able to establish self-sustaining population in the wild outside of their native range, and become new part of ecosystems. We know more than 37,000 such species today, and 200 new non-native species are discovered every year (Roy et al., 2024). This reshuffling of biodiversity with human-mediated transport is re-defining biogeography. Historically, species assemblages exhibited abrupt spatial transitions, called "biogeographic boundaries", characterized by sudden changes in community turnover. A well-known example of such boundary is the Wallace line separating the Indomalayan and the Australasian regions. These biogeographic boundaries have been shaped by geography, evolutionary history and environmental variations (Holt et al., 2013). As species are spreading to new regions outside of their native range, historical biogeographic boundaries are eroding, causing a global homogenization of species communities. This homogenization has been observed in terrestrial gastropods (Capinha et al., 2015), plants (Yang et al., 2021) and insects (Aulus-Giacosa et al., 2024).

Among the non-native species currently known, more than 3,500 have documented negative impacts on ecosystems and human societies (Roy et al., 2024), and are therefore called invasive species. Their impacts are manifold: invasive species affect native ecosystems by reducing species richness and abundance, altering phylogenetic diversity and trophic networks, changing animal behavior or affecting nutrient and contaminant cycling (Pyšek et al., 2020). They also impact human well-being and livelihoods by spreading infections and diseases, producing allergenic substances, affecting human safety by being venomous or poisonous, or impacting agriculture (Pyšek et al., 2020). Understanding the drivers of non-native species introduction and establishment is therefore important in order to prevent future invasions and limit their impact. In particular, there is an urgent need to investigate human-mediated dispersal of species, as the transport of propagules is the first and mandatory step of all invasion pathways (Catford et al., 2009).

# History of human-mediated dispersal of species

## Historical spread of non-native species

*Homo sapiens* might have started spreading out of Africa around 177 ka (Hershkovitz et al., 2018) and established in Middle East, Europe, Asia, and eventually colonized every continent. It reached Oceania probably between 65 ka and 50 ka (Clarkson et al., 2017; O'Connell and Allen, 2004), and the Americas around 15 ka (Marangoni et al., 2014). These first human migrations likely already involved the transport, accidental or intentional, of other species (**appendix 3**). For example, a head lice egg (*Pediculus humanus*) was found on a 10,0000 years old human hair in an archaeological site in Brazil, suggesting that this insect may have entered the New World with the first human colonists (Araújo et al., 2000).

Around 12 ka (thousand years ago), plant and animal domestication appeared (Larson et al., 2007), marking the beginning of the Neolithic Revolution and the transition from a lifestyle of hunting and gathering to the first agricultural communities. This led to a significant increase in human populations and an important range expansion. As human spread to new regions, they introduced various plant and animal species mainly for agricultural purposes but also as pets (Anderson, 2009; Larson et al., 2007). Invertebrate species associated with crops, livestock and pets also followed human expansion (**appendix 3**). For example, the squash bee *Peponapis pruinosa* followed the spread of their *Cucurbita* pollen hosts by native American societies from Mexico towards North America (López-Uribe et al., 2016). The emergence of agriculture also allowed the accidental spread of synanthropic species (i.e. undomesticated species that live in close association with humans), such as the house mouse. Native from the Indo-Pakistan subcontinent and neighboring Afghanistan and Iran, it became associated with humans as villages provided protection against predators and a constant food source due to grain storage. Its stowaway transport to Cyprus might have occurred as early as 10,8 ka. It then reached Eastern Europe 6.5 ka and Southern Europe 4 ka (Cucchi et al., 2020). Large scale grain storage might also have allowed the spread of several insects such as the grain weevil *Sitophilus granarius*. This flightless pest has been found in dispersed archaeological sites from early Neolithic Europe, suggesting human mediated dispersal with the spread of early farming (Panagiotakopulu and Buckland, 2017).

The first long distance trade routes emerged with the advent of ancient empires, during the Bronze and Iron Ages. A famous example of such trade route is the Silk Road in Eurasia (around 138 B.C.E – 1453 C.E.), along which various commodities were moved between Asia, Europe and East Africa. Inevitably, several species were accidentally transported along these routes (**appendix 3**). For example, the spread of the mealy peach aphid (*Hyalopterus arundiniformis*) from China to Europe coincided with the domestication and trans-Eurasian trade of peach via the Silk Road (Liu et al., 2022). Similarly, the introduction of the small cabbage white butterfly (*Pieris rapae*) from Europe to Asia might have been facilitated by the Silk Road (Ryan et al., 2019). The Roman Empire also led to numerous species introductions, some of which are now widely distributed in Europe such as the sweet chestnut or the common pheasant (Cassey et al., 2016; Conedera et al., 2004). In pre-Columbian America, exotic birds might have been bred and raised for the feather industry and pet trade, and merchants might have transported birds over long distances (Haemig, 1978). The Great-tailed Grackle (*Quiscalus mexicanus*) was introduced in the Valley of Mexico by the Aztec Emperor Auitzotl before the Spanish conquest, sometime between 1496 and 1502 (Haemig, 2012, 2011). There is evidence of other bird species introductions in the pre-Columbian era, such as the Red-legged Thrush (*Turdus plumbeus*) in the West Indies (Ricklefs and Bermingham, 2008), and the Tufted Jay (*Cyanocorax dickeyi*) in Mexico (Heamig, 1979).

Following the European discovery of the Americas in 1492, a global trade network connecting all continents emerged. This marked the beginning of the era of globalization, during which the increasing connectivity between continents resulted in a breakdown of natural dispersal barriers for many species, leading to an explosion of biological invasions.

### The era of Globalization

In the 16th century, the first Spanish and Portuguese trade routes connected the Old World to the Americas (Flynn and Giráldez, 1995). In the following centuries European countries expanded economically and politically into new regions. They established vast Empires covering most of the continents, leading to unprecedented demographic, economic and environmental transformations, with important movement of resources and humans globally (Flynn and Giráldez, 1995; Morrison, 2018; Thomas and Thompson, 2014). The Atlantic slave trade led to the transportation of more than 10 million people from Africa to the Americas (Lovejoy, 1989). Additionally, more than 50 million people left Europe for overseas territories between 1815 and 1930, generally in search of higher income (Baines, 1994). Many resources and commodities were also moved within colonial empires, and trade volumes doubled for countries belonging to these empires relatively to non-colonized countries, as preferential trade policies were established between European powers and their colonies (Mitchener and Weidenmier, 2008).

With the rise of colonial Empires, patterns of non-native species movement shifted from sporadic introductions within continents to frequent introductions between continents. As colonists settled to new territories, they intentionally brought plants and animals with them, mainly to make the land sustainable and economically productive, but also to provide sport for hunters and fishermen, for ornamentation of their gardens, to make their new colonized land feel more like home and enrich native faunas and floras (Osborne, 2000). These motivations led to the founding of Acclimatization Societies during the 19th and 20th centuries, which aimed to promote species introduction and establishment (Osborne, 2000). By 1900, more than fifty Acclimatization Societies had been created, most of them in the European colonies. These institutions were especially prevalent in the British territories where they introduced many bird species, in particular game animals such as ducks and pheasants, and ornamental birds such as passerines (Cassey et al., 2016; Dyer et al., 2017). During this period, collecting live exotic plants also became very popular, and many plant hunters collected plants for botanical institutions such as the Royal Botanical Gardens, Kew, in the United Kingdom, or the Leiden Hortus Botanicus, in the Netherlands (van Kleunen et al., 2018). These institutions played a key role in the intentional global exchange of plants, many of which are now established on several continents.

In addition to the numerous intentional introductions, many species might also have been accidentally introduced during the colonial era. Europeans unintentionally spread pathogens to the new territories, causing devastating epidemic outbreaks (Nunn and Qian, 2010). Many plant and insect species might have also been accidentally transported and introduced with other cargo or in ballast soil (Brown, 1878; Lindroth, 1957). For example, European colonization is thought to have facilitated the spread of the invasive ant *Wasmannia auropunctata* from South and Central America to the Caribbean islands in the 16th century (Foucaud et al., 2010). Likewise, *Solenopsis geminata*, another highly invasive ant species, might have been introduced from Mexico to Asia in the 16th century, and from there throughout the Old World, following historical Spanish trading routes (Gotzek et al., 2015). The effect of colonial empires on non-native species displacement is still visible today. The global distribution of non-native plants still bears the footprint of colonialism, as countries formerly belonging to the same Empire have greater floristic similarity (Lenzner et al., 2022; Yang et al., 2021).

This period was also marked by a major event in globalization history: the Industrial Revolution. The spread of the railroad network, but most importantly the development of steamships in the beginning of the 19th century led to an unprecedented increase in global trade (Baldwin and Martin, 1999; Hulme, 2021). This rise in global exchanges marked the beginning of the first wave of globalization (Baldwin and Martin, 1999; Federico and Tena-Junguito, 2017; World Trade Organization, 2013), which led to an acceleration of biological invasions (**appendix 3**; Bertelsmeier et al., 2017). Steamships were about two times faster than sailing ships to cross the Atlantic, which likely increased the chance of stowaway species to survive the journey, therefore facilitating their spread to new regions (Hulme, 2021). While solid ballast, such as soil or rocks, had been used for centuries to provide balance for ships, the development of watertight bulkheads around 1880 allowed the widespread use of ballast water tanks. These tanks were filled with water at the port of departure and emptied at the port of destination, inevitably translocating many fish, microorganisms and marine invertebrates to coastal seas, estuaries, and freshwaters (Davidson and Simkanin, 2012). However, little is known about these early accidental introductions as many of them might have gone unnoticed for decades or even centuries.

The first wave of globalization ended with the beginning of World War I. Between 1914 and 1945, the two world wars and the Great Depression led to strong reductions of international exchanges. It’s only around 1960 that trade openness resumed its upward trend, marking the beginning of the second wave of globalization (Baldwin and Martin, 1999; Federico and Tena-Junguito, 2017). Technological advances in transport continued, leading to bigger ships transporting a wider variety of commodities in greater volumes (World Trade Organization, 2013). World maritime trade increased from 500 million tons in 1950 to about 4,200 million tons in 1992 (Lundgren, 1996). The use of freight container around the 1960s vastly increased the efficiency of trade (Hulme, 2021). Moreover, the equipping of ships with refrigeration allowed the transport of fresh product, such as fruits, over long distances, providing opportunities for many pests and diseases to be transported around the world (Hulme, 2021). The use of wood packaging materials, such as dunnage, pallets, crates, and spools, facilitated the spread of wood boring and wood infesting organisms (Greenwood et al., 2023). Air freight and travel also developed quickly since the 1950s. Even though only 0.2% of the global tonnage of traded goods is transported by air, it is one of the faster-growing sectors in international trade (Hulme, 2021), and many potentially economically important non-native insects are transported with airline cargo (Caton et al., 2006). Moreover, air passenger miles increased from 28 billion in 1950 to 2.6 trillion in 1998 (World Trade Organization, 2013), and travelers baggage plays an important role in the introduction of non-native insects, weeds, pathogens and other pests (McCullough et al., 2006).

Although deliberate releases of non-native species in the wild have been declining after 1960 due to increasing awareness on their negative impacts (Hulme et al., 2008), the intentional transport of species to new regions has not ceased. Rather, their primary cause has changed, and wildlife trade has been increasing dramatically over the past decades (Harfoot et al., 2018). Millions of live animals are traded every year as pets, for food, traditional medicine, scientific research and other purposes (Michael Marshall et al., 2025; Romagosa, 2016), causing many biological invasions. The exotic pet trade has already led to the establishment of several hundred non-native vertebrates, as species manage to escape confinement or are released by their owner (Lockwood et al., 2019). Similarly, the import of live plants has been increasing steadily over the past decades and ornamental horticulture plays an important role in plant invasions (van Kleunen et al., 2018).

Overall, the increasing connectivity between world regions led to higher propagule pressure, resulting in an increase of species establishments (Lockwood et al., 2009). Since the Industrial Revolution, the rate of non-native species first records (i.e. the date at which an established species is first observed in a region outside of its native range) strongly increased and shows no sign of saturation for most taxa (Seebens et al., 2017).

## Insect invasions

### Insects are important invaders

Around 1 million insect species have been described so far, which represents about half of all currently described species worldwide (Li and Wiens, 2023), and it is estimated that several more million insect species are yet to be discovered (Stork, 2018). Insects are major components of most terrestrial habitats and include various trophic groups such as herbivores, pollinators, predators, parasites and detritivores. The number non-native insect species likely exceeds 10,000 (Roy et al., 2023), which is more than all other non-native animal taxa combined (Seebens et al., 2017), and some of them are among the most damaging invasive species worldwide (Global Invasive Species Database, 2024).

Invasive insects can have a wide range of ecological and economic impacts. First, they can displace native species through mechanisms such as predation or competition (Fortuna et al., 2022; Kenis et al., 2009). For example, the Argentine ant, *Linepithema humile*, which has invaded most of the continents, is known to displace native ants, other arthropods, birds, lizards, amphibians and mammals in its non-native range (Angulo et al., 2024). Invasive insects can also disrupt key insect–plant mutualisms, affect seed dispersal, change native pollination services and affect nutrient, carbon and hydrologic cycles (Clark et al., 2010; Kenis et al., 2009). Invasive insects are also infamous as pests damaging ornamental and agricultural plants (Oliveira et al., 2013; Paini et al., 2016) as well as forests (Fei et al., 2019). For instance, the box tree moth, *Cydalima perspectalis*, was recently accidentally introduced into Europe and is now threatening several *Buxus* species both in urban areas and forests all over the continent (Bras et al., 2022). Invasive insects are also important vectors of human, animal and plant diseases (Leta et al., 2018; Mellor et al., 2000; Morin et al., 2007). The human-mediated dispersal of the invasive tiger mosquito, *Aedes albopictus,* and the yellow fever mosquito, *Aedes aegypti,* have facilitated the spread of the arboviruses dengue, yellow fever, chikungunya and Zika (Kraemer et al., 2019; Leta et al., 2018). Many efforts and resources have been deployed to eradicate some invasive insect populations, not always successfully. Out of 316 eradication campaigns targeting 11 non-native ant species, 144 have been documented successful (Hoffmann et al., 2016). The size of the invaded area has an important effect on both the likelihood of success and the total cost of eradication, making it sometimes impossible if not attempted in the early stages of invasion (Brockerhoff et al., 2010). Overall, the global economic cost of insect invasions, including prevention, damage and response, is estimated to exceed 70 billion US dollars per year (Bradshaw et al., 2016). Understanding the drivers of these invasions is therefore urgent in order to prevent future non-native insect introductions. Yet, despite their obvious importance as invaders, non-native insects have received less attention than other taxonomic groups such as plants (Pyšek et al., 2008).

## Pathways of insect introduction

Because of their small size, insects are easily transported unnoticed with human activities (Meurisse et al., 2019). Unlike vertebrates, most non-native insects have been introduced accidentally (Saul et al., 2017). Accidental dispersal of insects by human activities can be classified in two types of pathways: contamination and hitchhiking (Gippet et al., 2019).

The contamination pathway corresponds to the transport of a cargo contaminated by insects, either because the cargo is their natural host, such as plants or mammals, or their immediate environment, such as soil or rocks (Gippet et al., 2019). Thousands of insect species are intercepted at country borders on contaminated commodities, mainly live plants, cut flowers, fruits, nuts, vegetables, wood and wood articles (Fenn-Moltu et al., 2022). A striking example of the importance of the contamination pathway in insect dispersal is the numerous insect introductions caused by the trade of live plants. In the US, about 60% of historical forest insect introductions most likely occurred via infested live plant imports (Liebhold et al., 2012). More than 40% of non-native insect introductions in Austria and Switzerland are estimated to be associated with the plant trade, mainly that of ornamentals (Kenis et al., 2007). In Great Britain, almost 90% of human-assisted introductions of invertebrate plant pests are believed to be associated with the plant trade, out of which 74% are linked to ornamental plants (Smith et al., 2007). The transport of soil, for example during road maintenance, was also shown to facilitate the spread of insects, such as the invasive fire ant *Solenopis invicta* (King et al., 2009).

The hitchhiking pathway refers to the transport of insects that attached to an object not directly related to their natural environment, such as shipping containers or cars (Gippet et al., 2019). Several cases of ants hitchhiking on vehicles were reported, sometimes including queens and brood (Hsu et al., 2024). Similarly, spongy moths sometimes lay eggs on surface of sea containers, ships, and road vehicles and are then transported while the vectors travel (Keena et al., 2008; McFadden and McManus, 1991).

Although insects are mostly transported by accident, there are sometimes introduced intentionally, as biological control agents, as food or even as pets (Gippet et al., 2019; Kumschick et al., 2016). Following their intentional release or escape from confinement, these insects have sometimes become invasive. For example, the Asian ladybird (*Harmonia axyridis*) has been voluntarily released in several countries as a biological control agent against aphids, and has now become invasive on four continents where it causes biodiversity losses and human nuisance (Brown et al., 2011; Chakir et al., 2016). In Japan, commercial colonies of European bumblebees (*Bombus terrestris*) were introduced since 1992 for crop pollination in greenhouses. However, it managed to escape and is now established and spreading in the country (Inari et al., 2005). Additionally, many insects, such as butterflies, ants and stick insects, are traded around the world as pets (Kumschick et al., 2016), and this market is growing quickly with the ever-increasing demand for exotic animals and the growing use of the internet to sale and purchase species (Gippet et al., 2023; Gippet and Bertelsmeier, 2021). Many of these traded species are known invaders or have a great potential to become invasive if they escape or are released by their owner, suggesting that the pet trade might become an important invasion pathway for insects in the future (Gippet and Bertelsmeier, 2021; Wang et al., 2023).

## Temporal dynamics of insect invasions

Globally, the annual number of non-native insect first records has been increasing dramatically since the Industrial Revolution (Seebens et al., 2017), suggesting an acceleration of insect invasions over time. However, non-native species first records reflect a combination of both species introductions and species discovery (McGeoch et al., 2023; Solow and Costello, 2004). As the sampling and recording of species occurrences strongly increased over the past centuries (Boakes et al., 2010), it likely influenced non-native species first record rate. This strong confounding effect can mask underlying dynamics of insect invasions, which means that non-native species first records don't necessarily reflect patterns of species introductions (Mangiante et al., 2018; McGeoch et al., 2023; Solow and Costello, 2004). For example, it was shown that the rate of non-native species first records can increase even in scenarios where the actual introduction rate remains constant or even decreases (Belmaker et al., 2009; Costello and Solow, 2003). This sampling bias might be particularly pronounced for taxa like insects as they are harder to detect, due to their small size, than other bigger and more "charismatic" taxa such as vertebrates (Bobeldyk et al., 2015). Moreover, as insects are mostly introduced accidentally, their detection might be particularly arduous as their presence might be harder to anticipate. Consequently, the global temporal dynamics of insect invasions remains largely unknown.

Other studies at finer spatial or taxonomic scales found varying rates of insect invasions over time. The rate of non-native ant detection worldwide fluctuated over the past two centuries, following variations in global trade openness (Bertelsmeier et al., 2017). In Europe, the observed spread of non-native insects accelerated after 1990, suggesting that the fall of the Iron Curtain have facilitated the spread of species (Roques et al., 2016). Important fluctuations were also observed in the annual number of non-native Hemiptera first recorded since 1850, with different dynamics between countries and regions (Liebhold et al., 2024; MacLachlan et al., 2021). In the US, the rate of forest insect detection differed between feeding guilds, but globally peaked between 1900 and 1930 and has been decreasing since, possibly because increasing mitigation and regulatory efforts may counter the escalation of international trade and travel (Aukema et al., 2010). Overall, the temporal dynamics of insect detection show important variations between taxa and regions, driven by the complex interplay between global trade dynamics, regulatory efforts, potential invader pool depletion, species characteristics and variations in sampling effort.

## Spatial dynamics of insect invasions

Insect flows from donor to recipient regions show a strong asymmetry, with some regions being overrepresented as donors while others are overrepresented as recipients (Isitt et al., 2024; Lantschner et al., 2020; Wong et al., 2023). For example, Europe has exported many insect species to North America, while the insect flow in the opposite direction is much smaller (Isitt et al., 2024). Global trade is widely recognized as the main driver of species establishment as it increases propagule pressure (Hulme, 2021; Lockwood et al., 2009). However, despite the logic of this process, evidence of the role of trade in explaining insect flows are surprisingly mixed. For example, value of imported goods does not predict insect flows between Europe, North America and Australasia (Isitt et al., 2024). Conversely, global flows of Scolytinae species were primarily driven by variations in trade among world regions (Lantschner et al., 2020). One possible explanation for these mixed results is that insect taxa might generally spread with a very particular type of commodity which may not be representative of general trade flows. For example, total and agricultural imports are poor predictors of non-native ant flows from donor regions to the US. Instead, ant flows are strongly associated with imports of plant and fruit, a subset of agricultural imports (Ollier and Bertelsmeier, 2022). Prior knowledge on the propensity of a particular insect taxa to be associated with a given type of commodity might therefore be required to use appropriate trade metrics (Chapman et al., 2017; Ollier and Bertelsmeier, 2022).

Other factors influencing insect flows have also been identified, such as the size of the species pool of the donor region (Liebhold et al., 2017) and climatic similarity between native and non-native areas (Yamanaka et al., 2024). As the invasion process includes multiple stages, such as transport, introduction and establishment (Blackburn et al., 2011), the factors influencing each of these stages might vary. For example, while biogeography and trade influenced insect flows during both the transport and establishments stages, the Gross National Income in the source country had an effect only at the transport stage, and environmental matching between the source and recipient region only influenced the establishment stage (Fenn-Moltu et al., 2023).

Species flows are usually visualized by connecting the native to the invaded area, as species are assumed to be introduced from their native range. However, the reality is more complex, as biological invasions often include “bridgehead effects”. Bridgehead effect is a phenomenon of secondary introduction, where a propagule comes from a previously invaded region rather than directly from its native range (Bertelsmeier and Ollier, 2021). These secondary introductions are very frequent in insect dispersal, which can distort our view of non-native species flows (Bertelsmeier and Ollier, 2021). Evidence for bridgehead effect comes from species interceptions on commodities at ports or airports. Among the insects intercepted at ports of entry in the US, the European Union, Japan and South Africa, 65% were coming from bridgehead countries (Worm et al., 2024). Similarly, the proportion of secondary interceptions of termites in the US that came from invaded regions was 46% (Blumenfeld and Vargo, 2020). For ants, 75.5% of the interceptions in the US were coming from the species' non-native range, and this proportion goes up to 87.8% for interceptions in New Zealand (Bertelsmeier et al., 2018). Secondary spread is therefore a key feature of the global dispersal of non-native insects. This could be because introduced population evolve higher invasiveness (Lombaert et al., 2010), or because they often establish in highly connected trade or transport hubs, enhancing their probability of being transported again.

These flows of species have led to the establishment of probably more than 10,000 non-native insect species (Roy et al., 2023). The number of established species strongly varies among countries, with North America, Europe, Japan, Australia and New Zealand being more invaded than other regions (Roy et al., 2023). These differences between regions are largely driven by global trade. Countries connected through trade networks for multiple commodities, but particularly live plant trade, were shown to receive more non-native plant pests (Chapman et al., 2017). More insect invasions are also observed in countries with higher GDP (Amano et al., 2016; Roy et al., 2014; Trombik et al., 2023), which is often used as a proxy for trade. Non-native insect richness also increases with countries' wealth (calculated by summing net foreign assets and produced, natural and human capitals) and population density (Pyšek et al., 2010) as well as with KOF index of globalization (which measures all economic, social and political dimensions of global connectivity); Amano et al., 2016). Within the trade network, certain countries emerge as central hubs for the early introduction of non-native species, which then facilitate their subsequent spread to adjacent countries. Hence, Italy and France have been identified as important gateways for insect invasions in Europe (Capinha et al., 2023).

At finer spatial spatial scales, the spread of insect is also driven by increasing connectivity and human movement. In New Zealand, non-native wasps were more abundant on islands that have been settled by humans (Schmack et al., 2020). The number of tourist arrivals and regional GDP were also important drivers explaining spatial pattern of non-native insect establishment in New Zealand between 2000 and 2014 (Edney-Browne et al., 2018). In the US, counties with higher economic activity and connectivity (measured as per capita income, population size, road length and distance to port) tend to receive more non-native insects (Cook et al., 2021; Liebhold et al., 2013). At the regional and landscape scales, the road network topology also shapes the spread of non-native insects, showing that transportation corridors act as introduction pathways (Prasad et al., 2010; Rocabert et al., 2024; Thomas et al., 2017). By facilitating the movement of propagules, globalization has a direct influence on the long-distance dispersal of insects between continents and countries, but also on their secondary spread through the landscapes.

Another important factor shaping the spread of insects is the distribution of non-native plants, as they create ecological niches for insects, especially herbivores that use these plants as host (**appendix 2**; Rodríguez et al., 2019). Humanity deeply transformed the world flora with the spread of agriculture, with crop areas representing 12% of the global land area (Ellis et al., 2010). Most agricultural crops are non-native where they are planted (Young, 2016), and they facilitate the spread of non-native insects that specialize on them (Paini et al., 2016). Similarly, planted forest now represent 7% of the total forest area and is continuously expanding, likely to reach 20% by 2100 (Brockerhoff et al., 2013). They often include non-native trees, which also favor the establishment of non-native insects. For example, *Hylurgus ligniperda*, a species of pine bark beetle, has spread through the southern hemisphere where pine plantations occur (Faccoli et al., 2020). In urban landscapes, plantings are often dominated by non-native plants. In UK gardens, for example, about 70% of plants are non-native (Loram et al., 2008). The presence of non-native trees in urban areas provide host for non-native tree pests, possibly facilitating their establishment (Augustinus et al., 2024). Around the world, more than 70,000 and 160,000 vascular plant species are grown in domestic and botanical gardens, respectively (van Kleunen et al., 2018). Many of them are non-native where they are grown, increasing the risk of non-native insect introduction and establishment (Wondafrash et al., 2021).

Non-native plants are also increasingly dominant in the wild, with many plants establishing self-sustaining populations as they escape from cultivation or are introduced accidentally (Lehan et al., 2013; Saul et al., 2017). As a result of human activity, more than 13,000 plant species have established outside of their native range (van Kleunen et al., 2015), and the number of non-native plants establishments is still increasing at a high rate (Seebens et al., 2017), and will likely continue in the future (Seebens et al., 2021, 2015). These plant invasions also facilitate the spread of non-native insects. For example, non-native insects feeding on Black Locust (*Robinia pseudoacacia*) were shown to follow the invasion of their host tree (Mally et al., 2021; Medzihorský et al., 2023). Globally, numbers of non-native insect species are linked to both native and non-native plant richness among world regions (Liebhold et al., 2018). Thus, while propagule pressure is widely recognized as an important driver of insect invasions, invasibility is also a major determinant of non-native insect distribution (**appendix 2**).

Finally, observed spatial patterns of species invasions are also influenced by sampling effort (Mangiante et al., 2018). Sampling is strongly unequal between world regions, with the tropics being disproportionately poorly sampled (Hughes et al., 2021). Many countries in Africa, South America and Asia have very few recorded non-native insects, which might partly be due to the lower trade in these countries resulting in less insect invasions, but also to the lack of available data (Roy et al., 2023).

## Thesis outline

The aim of my PhD is to improve our understanding of the impact of globalization on the spread of non-native species over the past two centuries, with a particular focus on the human-mediated dispersal of insects. In **chapter 1**, we investigated the temporal dynamics of insect and plant invasions, in particular we tested whether the two waves of globalization (~1820–1914, 1960-present) influenced insect and plant spread dynamics. As first record data are strongly biased due to the global increase in species observations, we used a statistical model that accounts for temporal variations in sampling effort in order to estimate insect and plant invasion rate over the past centuries.

In **chapter 2**, we explored how colonial empires influenced the number of accidental non-native species introductions, using ants as a model system. Ants are very successful invaders (Wong et al., 2023), and are easily unintentionally transported as contaminants of potted plants or fruits (Ollier and Bertelsmeier, 2022; Suarez et al., 2009). and are therefore and ideal model to test the accidental dispersal of insects during colonial times. We used generalized linear models to test the effect of colonial empires and of potentially confounding variables on the number of non-native ants established per country. We also tested whether ants have spread preferentially between countries that belonged to the same empire. Finally, we investigated the “Imperialist dogma”, which states that colonialism mostly facilitated the spread of European species (Jeschke and Strayer, 2005; Seebens et al., 2015), by testing whether non-native ants originated primarily from colonizer, colonized or non-colonized countries.

We then investigated the importance of secondary introductions (i.e., the bridgehead effect) on insect dispersal (**chapter 3**). We analyzed a dataset of insect interceptions at the US borders spanning from 1913 to 1984 and measured the proportion of secondary introductions. We then used logistic regression to test if the probability of secondary introductions increases with the size of the species' non-native range. We also tested if the probability of secondary introductions increases over time, which would suggest that bridgehead effect is accelerating the global spread of insects.

Finally, in **chapter 4**, we explored the link between plant and insect invasions. In particular, we tested whether plant invasions precede and promote insect invasions. We extracted data on non-native plant and insect first record date per world region as well as information on their native range. We then used generalized linear mixed models to test the predictive power of historical and current alien plant flows, from 1800 to 2010, on insect invasions at a global scale. We then used the observed time lag between plant and insect invasions to estimate insect invasion debt in each world region.

Throughout this thesis, I was also involved in the writing of scientific reviews on the impact of climate change on native and non-native insect distribution (**appendix 1**), the effect of the global proliferation of non-native plants on insect invasions (**appendix 2**) and on the spatiotemporal dynamics of insect invasions in an era of globalization (**appendix 3**).

**Table 1: Glossary of keywords used in this thesis**

| Keyword | Definition |
|---|---|
| Bridgehead effect | Phenomenon of secondary introduction where a species is introduced from a previously invaded region rather than directly from its native range |
| Establishment | The establishment of a self-sustaining population outside of the species’ native range |
| First record | The date at which a species is first observed in a region outside of its native range where it has established |
| Interception | The catching of a stowaway species at a country’s port of entry, generally on a contaminated commodity |
| Invasive species | A non-native species that have impacts on ecosystems and/or human societies |
| Native range | The natural geographic distribution of a species |
| Non-native species | A species that has been introduced, accidentally or intentionally, via human-mediated dispersal outside of its native range and has established a self-sustaining population. |
| Non-native range | Area outside of the species’ native range where is has been introduced by human activity |
| Propagule pressure | The total number of individuals introduced at a given location |

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# Summary of the results

**Chapter 1** explores the temporal dynamics of insect and plant invasions. We found that most of the increase in the number of non-native insect and plant first records over the past two centuries can be explained by increasing sampling effort. Once this bias is accounted for, we showed that the rate of insect and plant invasions did not continuously increase over the past two centuries, but greatly fluctuated, following variations in global trade openness linked to the two waves of globalization. This chapter highlights the urgency of better understanding the effect of socio-economic drivers to improve predictions of future invasions.

**Chapter 2** investigates in greater details the spatiotemporal dynamics of insect invasions over the past centuries and in particular the effect of European colonial empires on the spread of non-native species, using ants as a model system. Our results show that, before 1960, countries that belonged to a colonial empire received more non-native ant species than those that did not. Moreover, during that period, ant spread preferentially between countries that belonged to the same empire. After 1960, however, we found that former colonial ties no longer influenced the spread of non-native ants. Finally, this chapter challenges the "Imperialist dogma", as we found that colonized countries were the most important source of non-native ants. Overall, this chapter shows that the rise and fall of colonial empires shaped the spread of non-native ants.

In **chapter 3**, we address the role of the bridgehead effect in non-native insect dispersal by analyzing border interception records in the US between 1913 and 1984. We found that 34% of the interceptions originated from bridgehead regions. We also showed that the probability of secondary introduction increased over time and was linked to the size of the species' non-native range. This chapter shows that the bridgehead effect accelerates insect invasions by creating a positive feedback loop between transport and establishment.

Finally, **chapter 4** explores the link between plant and insect invasions. We found that current non-native insect flows are best explained by non-native plant flows dating back to 1900 compared to more recent plant flows, showing that plant invasions precede insect invasions. Historical plant flows were also a better predictor of insect invasions than general trade flows. Using the observed time lag between plant and insect invasions, we estimated that the insect invasion debt consists of 3,442 region-level introductions globally, representing 35% of the current number of insect invasions. This debt was particularly important in the Afrotropics and the Neotropics, suggesting that the number of insect invasions is likely to strongly increase in those regions in the near future. Overall, this chapter emphasizes that the spread of non-native plants is a major driver of insect invasions.

In each of these chapters, I designed the study, performed the analysis and wrote the manuscript, with inputs from my co-authors in these different steps.

# Chapter 1

# Insect and plant invasions follow two waves of globalisation

This work was published in Ecology Letters.

Received: 6 April 2021 | Revised: 10 May 2021 | Accepted: 27 July 2021
DOI: 10.1111/ele.13863

ECOLOGY LETTERS cnrs WILEY

LETTER

# Insect and plant invasions follow two waves of globalisation

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**Funding information**
Swiss canton Vaud; Swiss National Science Foundation (NSF); Fondation Sandoz-Monique de Meuron pour la relève universitaire

**Editor:** Jessica Gurevitch

**Abstract**

Globalisation has facilitated the spread of alien species, and some of them have significant impacts on biodiversity and human societies. It is commonly thought that biological invasions have accelerated continuously over the last centuries, following increasing global trade. However, the world experienced two distinct waves of globalisation (~1820–1914, 1960-present), and it remains unclear whether these two waves have influenced invasion dynamics of many species. To test this, we built a statistical model that accounted for temporal variations in sampling effort. We found that insect and plant invasion rates did not continuously increase over the past centuries but greatly fluctuated following the two globalisation waves. Our findings challenge the idea of a continuous acceleration of alien species introductions and highlight the association between temporal variations in trade openness and biological invasion dynamics. More generally, this emphasises the urgency of better understanding the subtleties of socio-economic drivers to improve predictions of future invasions.

**KEYWORDS**
biological invasions, globalisation waves, insects, invasion rate, sampling effort, temporal dynamics, trade openness, vascular plants

## INTRODUCTION

Since the Industrial Revolution, increasing global trade and human movement have facilitated the spread of thousands of species worldwide (Chapman et al., 2017; Early et al., 2016; Hulme, 2009). Some of these species, the so-called alien species, have managed to survive and reproduce outside of their native range without human assistance. Alien species can reduce local biodiversity and impair ecosystem functioning (Bellard et al., 2016; Cameron et al., 2016; Castro-Díez et al., 2019; Pyšek & Richardson, 2010), contribute to the homogenisation of floras and faunas (Capinha et al., 2015; Winter et al., 2009), cause agricultural losses (Paini et al., 2016) and affect human health and well-being (Bacher et al., 2018; Pyšek & Richardson, 2010). Over the past two centuries, development of new trade technologies and infrastructures has influenced the spread dynamics of alien species (Hulme, 2021). Trade and transport are likely to be important drivers of future biological invasions (Essl et al., 2020; Lenzner et al., 2020) and global species flows from donor to recipient regions might change following shifts in trade dynamics (Epanchin-Niell et al., 2021). Understanding how variations in global trade have influenced the spread of alien species in the past is, therefore, crucial to better predict invasion risk and prevent alien species introductions in the future.

It has been suggested that biological invasions have accelerated over the last centuries, driven by increasing global trade (Seebens et al., 2017). However, although globalisation of trade and transport has intensified dramatically since the Industrial Revolution, this increase was not continuous. Instead, the world experienced two major waves of globalisation (Baldwin & Martin, 1999; Federico & Tena-Junguito, 2017). It is a great challenge for invasion biology to understand how these two waves have affected invasion dynamics. So far, the two waves of globalisation have gone largely unnoticed in ecology, yet the economic literature recognises these waves as the dominant feature of global commerce during the last two centuries (Baldwin & Martin, 1999). The first globalisation wave occurred from ~1820 to 1914, powered by the decline in international transport costs due to the development of steamships and railroad network (Baldwin & Martin, 1999; Federico & Tena-Junguito, 2017; O'Rourke & Williamson, 2002), which led to an unprecedented rise in world trade. The first wave of globalisation ended with the outbreak of the First World War and the protectionist reactions to the Great Depression, which strongly reduced international trade (Baldwin & Martin, 1999; Federico & Tena-Junguito, 2017). The second wave of globalisation started after the Second World War, around 1960, as international trade increased almost continuously until the early 21st century, driven among other factors by the development of transportation networks (Baldwin & Martin, 1999; Federico & Tena-Junguito, 2017).

These important variations in the intensity of global exchanges are likely to have influenced biological invasions over the past 200 years—as suggested by a previous study on ants (Bertelsmeier et al., 2017). Yet, previous research on other taxa does not seem to confirm this. Indeed, for most taxa, the rate of alien species first records (i.e. the annual number of alien species first records per country) was relatively low in the 19th century and increased continuously until the end of the 20th century (Seebens et al., 2017). However, scientific activities recording species occurrences have also strongly increased over the past two centuries, and a variety of sources of species record data have emerged (Boakes et al., 2010). Consequently, alien species first record rates are likely to be strongly influenced by the global increase in species observations, which could mask underlying dynamics of biological invasions. Accounting for variations in sampling effort is, therefore, required to disentangle the invasion dynamics from sampling bias (Belmaker et al., 2009; Costello & Solow, 2003; Mangiante et al., 2018; Solow & Costello, 2004) and, thus, get a more precise understanding of the temporal dynamics of invasions and of the potential impact of the two waves of globalisation.

To address these questions, we performed a global temporal analysis of alien species first record rates, which accounted for variations in sampling effort over time. As a proxy for sampling effort, we used the first record rate of native species, sourced from the Global Biodiversity Information Facility (GBIF; https://www.gbif.org). GBIF aims at gathering all the information about species taxonomy and distribution worldwide from various sources not only museums, local and global databases, scientific publications but also geotagged smartphone photos from amateur naturalists in the more recent years (Heberling et al., 2021). It offers a global coverage of more than 1.6 billion occurrences for about 1.6 million species spanning several centuries. This makes GBIF data appropriate to account for temporal variations in sampling effort worldwide.

We used these data to build a null model of alien species first record rate to (i) estimate biological invasion dynamics after accounting for variations in sampling effort and (ii) test the link between invasions dynamics and temporal variations in trade openness as a measure of trade globalisation. To do that, we focused on insects and vascular plants as they are the taxa with the highest numbers of first records (7,918 and 16,348 alien species first records, respectively), and they cover the majority of biodiversity and alien species described so far (Scheffers et al., 2012; Seebens et al., 2017). Moreover, these two groups include many species transported and introduced unintentionally (Saul et al., 2017) and are, therefore, likely to be influenced by variations in international trade.

## MATERIAL AND METHODS

We used a null model that assumes that the rate of alien species introduction is constant over time and simulates the rate of first records per country using sampling effort as a predictor. To account for variations in sampling effort, we used the rate of native species first records per country as a proxy. To measure the link between sampling effort and alien species first records, we computed the correlation between the first record rate simulated with the null model and the observed first record rate. Then, we computed the null model residuals (i.e. difference between the simulated and observed alien species first records), which represent variations in first record rate unexplained by sampling effort, and thus reflect true biological invasion dynamics. Finally, we measured the correlation between the residuals and variations in world trade openness to test whether the spread dynamics of alien insects and vascular plants followed the two waves of globalisation. Our approach to analyse the residuals of a model with a single predictor to remove first the confounding effect of this predictor is commonly used in the literature (Brown et al., 2021; Sofaer & Jarnevich, 2017).

To confirm our results, we also used a second approach where we directly included trade openness as predictor variable in the model by defining the introduction rate as a function of world trade openness (described in more detail in the Supplementary Material S1). Moreover, we tested the effect of other economic indexes (world trade and GDP) in addition to trade openness as a measure of globalisation to one better explained biological invasions dynamics when sampling bias is accounted for (Supplementary Material S1).

## Alien species first record data

We extracted data for insects and vascular plants from the Alien Species First Records database (Seebens et al., 2017), which is a global data set of alien species first record dates per country for a wide range of taxonomic groups. It contains data from different sources including online databases, scientific publications, books and personal collections. As part of the Alien Species First Records database was not published online, we excluded from our analysis countries for which data were missing. For vascular plants, we excluded the United States, New Zealand, Germany, Italy and Mexico from our analysis. For insects, only Australia was excluded. We removed first records with the 'casual' status (i.e. records of non-established alien species) to consider only established alien species (i.e. species that established permanent self-sustaining populations). Finally, the analysis was restricted to first records between 1750 and 2000. We did not include data after 2000 as they are incomplete due to lags in the recording of new alien species (Seebens et al., 2017). This resulted in a total of 7,918 first records of 4,528 established alien insect species, and 16,348 first records of 6,030 established alien vascular plant species.

## Native species first record data

A total of 40,484,764 insect and 121,456,805 vascular plant records until year 2000 were sourced from GBIF (GBIF.org, 2020a,b). First, we removed records of fossil specimen. We also removed records of species listed in the Alien Species First Records database or in the Global Register of Introduced and Invasive Species (Pagad et al., 2018, accessed August 2020) to consider only native species records. We renamed synonym species using the R package *taxizedb* (Chamberlain & Arendsee, 2020) with the Integrated Taxonomic Information System. Then, for each species, the first record per country was extracted. This resulted in a total of 512,736 first records of 273,090 native insect species (~27% of known insect species) and 541,139 first records of 262,121 native vascular plant species (~80% of known vascular plant species) between 1750 and 2000.

## Model description and simulations

The null model is based on a statistical model described by Solow and Costello (2004), which estimates the rate of introduction of alien species from the discovery records. It defines the random variable $Yt$ as the number of alien species first records in year $t$. $Y$t has a Poisson distribution with mean

$$\lambda_t = \sum_{s=1}^{t} \mu_s p_{st}$$

where $\mu s$ is the number of alien species introduced in year $s$, and $pst$ is the probability that a species introduced in year $s$ is discovered in year $t$. This probability is given by

$$p_{st} = \pi_t \prod_{j=s}^{t-1} \left(1 - \pi_j\right)$$

where $\pi t$ is the probability of observing a species in year $t$, which is the sampling effort in year $t$.

The model requires three inputs: A model describing the introduction rate, the annual sampling effort (i.e. the probability of observing a species for each year) and the observed alien species first record rate. To build the null model, the parameter for the introduction rate was kept constant over time ($\mu t = \mu$). Contrary to previous studies where the probability of observation was estimated in the model (Costello et al., 2007; Solow & Costello, 2004), we assumed that this value corresponds to the sampling effort, and used the rate of native species first records from GBIF as a proxy. The probability of observing a species in year $t$ is, therefore, the proportion of native species first records in year $t$, given by

$$\pi_t = \frac{\beta_t}{\beta_{\text{Total}}}$$

where $\beta t$ is the number of native species first records in year $t$, and $\beta$Total is the total number of native species first records on the whole period considered. We used native species first records—rather than all native species records—as a proxy for sampling effort because it can directly be compared with alien species first records because these two variables measure similar quantities: the number of new species—either alien or native—recorded each year in each country. Native species first record rate can thus be used to predict the expected number of alien species first records in each year, assuming that the probability of recording a new species is independent of whether it is native or alien (Belmaker et al., 2009).

The model was implemented with JAGS, using the *rjags* package (Plummer, 2019) in R v.4.0.4 (R Core Team, 2021), which is a program for analysis of Bayesian models using Markov Chain Monte Carlo simulation. For insects and vascular plants, a null model was fitted to the observed alien record rate. A uniform distribution was specified as a prior for the introduction rate parameter ($\mu$). For each model, the value of $\mu$ was estimated with a 7,000 iterations Gibbs sampling with three chains. The first 4,000 iterations were discarded as burn-in. Chain convergence was verified with Gelman and Rubin's convergence diagnostic (Gelman & Rubin, 1992). This procedure allowed to estimate the value of $\mu$ and to simulate 9,000 $\lambda t$ values (3,000 iterations*3 chains) per year $t$ for insects and vascular plants. For each $\lambda t$, a value was sampled in a Poisson distribution of mean $\lambda t$, to obtain 9,000 simulated numbers of alien species first records per year $t$. Finally, 9,000 residuals (i.e. difference between observed and simulated number of alien species first records) were computed for each year.

### Linking invasion dynamics with world trade openness

World trade openness is a widely used economic index of the level of trade globalisation (but see Fujii, 2019 for a critical review). It measures the share of what is traded internationally compared with the overall market value of all final goods and services produced worldwide, and thus represents the importance of trade in the world economy. It is, therefore, an appropriate indicator to test whether broad variations in invasion rates follow large-scale variations in globalisation. Our aim was not to evaluate the relative contribution of different socio-economic aspects of globalisation at the scale of individual countries, as this question has been addressed in the recent literature (Amano et al., 2016; Chapman et al., 2017; Dawson et al., 2017), but to use a single, widely applied, index of globalisation that can be calculated for the past centuries.

Trade openness was computed as the sum of all country imports and exports divided by the sum of all country GDP for each year from 1827 to 2000. Annual trade and GDP data were extracted from the TRADHIST database (Fouquin & Hugot, 2016). To test the effect of the annual variations of trade openness on invasion dynamics, we first smoothed trade openness with a cubic spline (smoothing parameter = 0.7) to be able to compute the derivative of trade openness.

### Statistical tests

We used Pearson's product moment correlation coefficient to measure the correlation between time series (*cor.test* function in R). First, we tested the link between simulated (mean of 9,000 simulations from the null model) and observed first record rates for insects and vascular plants. We then measured the correlation between the null model residuals (mean of 9,000 residuals per year) of the two taxonomic groups. Finally, we tested the correlation of the residuals with world trade openness derivative for each taxonomic group.

## RESULTS

### Importance of sampling effort

Most of the variation in the observed alien insect and vascular plant species first record rates can be explained by variations in sampling effort, as indicated by a strong correlation between simulated and observed first record rates (Figure 1; Pearson's $r = 0.94$ and 0.93 for insects and plants respectively; $p$-value <0.001 for both groups).

### Estimated invasion dynamics

Insects and plants had similar estimated invasion dynamics (Pearson's $r = 0.81$, $p$-value <0.001), with important fluctuations over the last centuries following a two-wave pattern (Figure 2). The first wave of insect started in the 19th century as the observed first record rate between 1820 and 1870 was on average 143% higher than expected by the null model. For plants, the first wave of invasions was more spread out over time, as the rate of invasion was already important in the late 18th century. From 1750 to 1870, the observed alien plant first record rate was on average 39% higher than expected by the null model. The second wave of invasions started in the second half of the 20th century for both groups. The observed number of first records between 1970 and 2000 was 28% higher for insects and 22% higher for plants than expected by the null model. For both insects and plants, the two invasion waves were separated by a period of reduced invasion rates, roughly from 1900 to 1960, during which the observed first record rate decreased of 19% for insects and 20% for plants compared with the null model expectations. During that period, the rate of insect invasions remained relatively stable, whereas the rate of plant invasions resumed an upward trend after the Great Depression.

### Linking invasion dynamics with world trade openness

The invasion dynamics of insects and plants were strongly correlated to world trade openness derivative (Figure 3; Pearson's $r = 0.65$ and 0.75 for insects and plants respectively; $p$-value <0.001 for both groups). Trade openness derivative explained both the increases and decreases of the rate of invasions over the past centuries (Figure 3) and was the best economic predictor of biological invasion dynamics (Table S1).

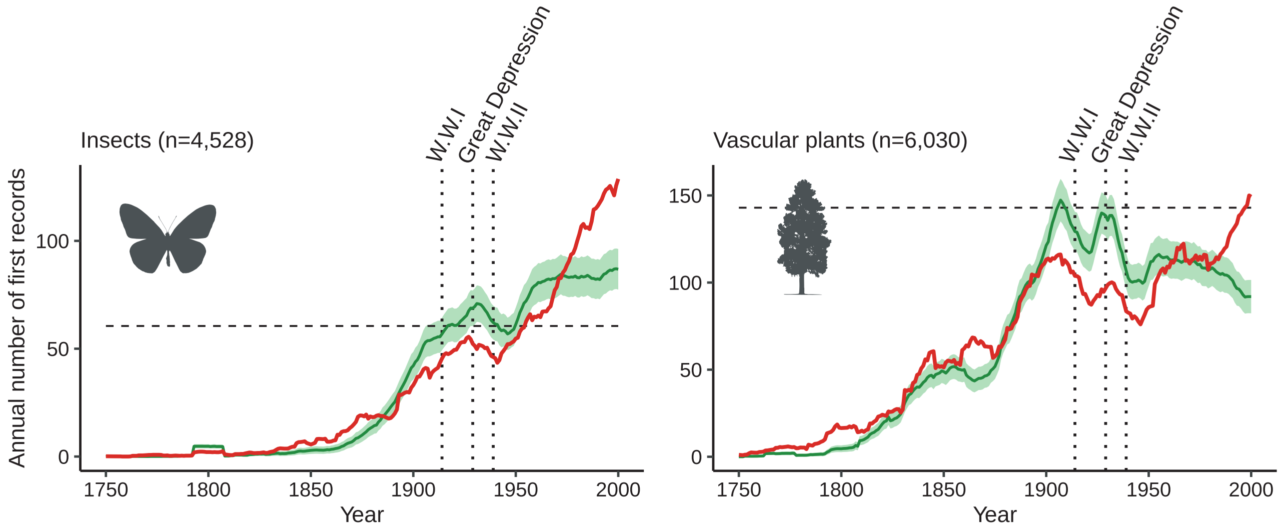

**FIGURE 1** Simulated (green) and observed (red) alien species first record rate. For each taxonomic group, the simulated number of first records was computed with a null model which assumes a constant introduction rate (horizontal black dashed line) and accounts for temporal variation in sampling effort. For each taxon, simulated means and standard deviations are based on 9,000 simulations. To ease visualisation, simulated and observed data are here represented with a 15-year moving average. Vertical black dotted lines represent dates of important events: The First World War (1914), Great Depression (1929) and Second World War (1939)

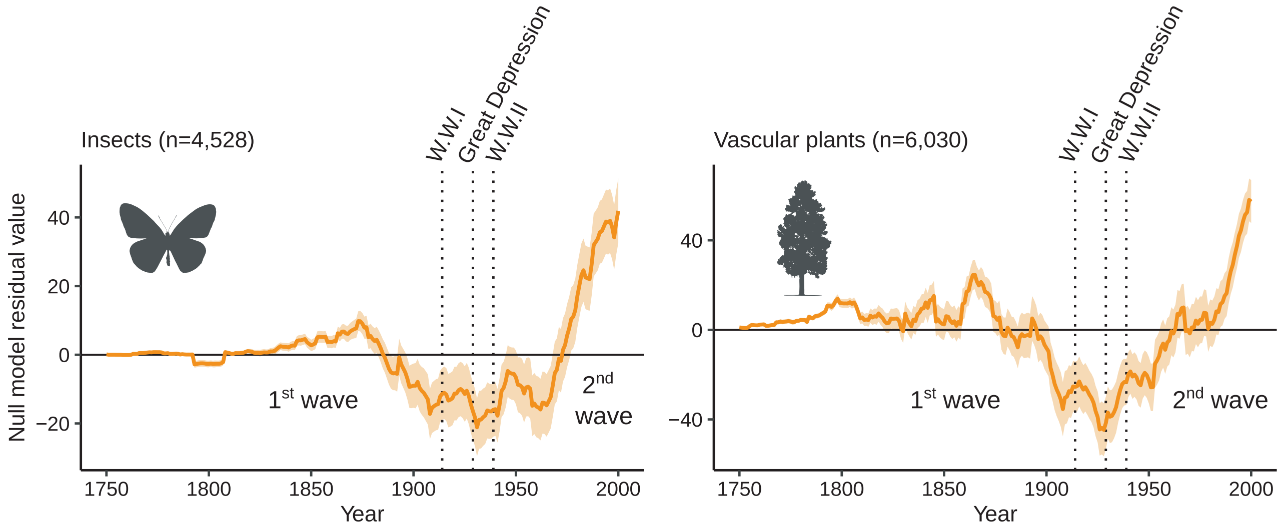

**FIGURE 2** Variations in biological invasion rate unexplained by the null model. Mean and standard deviation of 9,000 residual values by year from the null model (i.e. difference between the simulated and observed alien species first records; Figure 1). Positive and negative values indicate that the observed number of alien species first records is higher and lower (respectively) than expected by the null model, thus reflecting the variations of invasion rate overtime. To ease visualisation, residual values are represented with a 15-year moving average. Vertical black dotted lines represent dates of important events: The First World War (1914), Great Depression (1929) and Second World War (1939)

# DISCUSSION

The rate of insect and vascular plant invasion did not rise continuously over the past two centuries. Instead, we found that, once temporal variations in sampling effort are accounted for, the rate of invasions fluctuated over time and followed two distinct waves of invasions. These two invasion waves were linked to large-scale variations in world trade openness, which suggests that biological invasions accelerate when the economy becomes more globalised. Trade openness increased strongly between 1820 and 1870, marking the beginning of the first wave of globalisation, which was characterised by the expansion of the railroad network and the development of steamships (Baldwin & Martin, 1999; Federico & Tena-Junguito, 2017). This first wave of globalisation has led to an acceleration of insect and plant invasions during that period. However, when trade openness ceased accelerating between 1870 and 1914, plummeting after the outbreak of the First World War, the rate of n

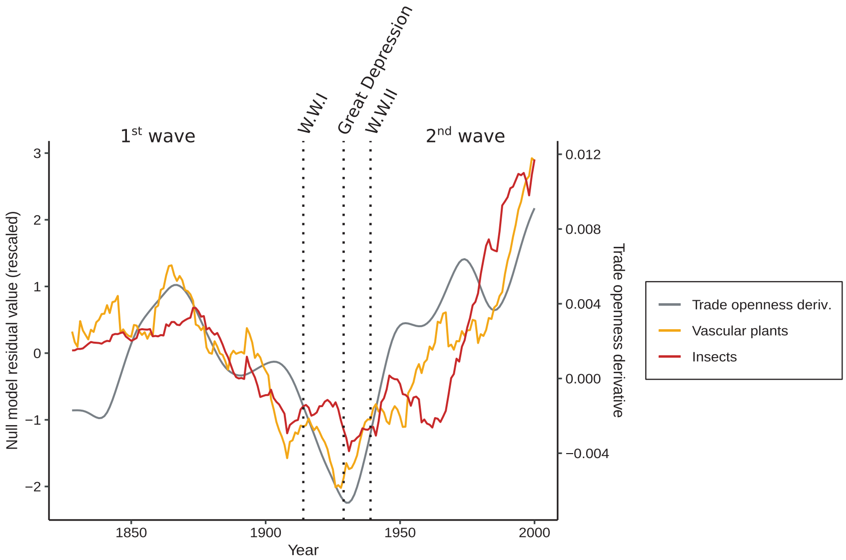

**FIGURE 3** Correlation between trade openness variations and biological invasion dynamics. Coloured lines represent the mean of null model residuals for vascular plants and insects from years 1828 to 2000. The grey line represents world trade openness derivative, that is, the derivative of ((exports+imports)/world gross domestic product). Null model residual values were scaled to a mean of 0 and a variance of 1 for visualisation purposes and are represented with a 15-year moving average. Dates of important events are indicated by the vertical black dotted lines: The First World War (1914), Great Depression (1929) and Second World War (1939)

decreased rapidly. The rate of plant invasions started to increase again after the Great Depression, while insect invasion rate stayed relatively low until the second half of the 20th century. For both groups, the rate of invasions exploded in the 1970s, after the world recovered from the Great Depression and the Second World War, reaching unprecedented levels of trade openness by the end of the 20th century. Hence, variations in trade openness explains both the increasing number of invasions during the two waves of globalisation and the lower invasion rate during the first half of the 20th century. Although plant and insect invasion rates followed large-scale variations in trade openness, the correlation is not perfect which suggests that other factors affected the spread of alien species at a global scale.

Interestingly, plant invasions had already taken off in the late 18th century, before the intensification of the first modern globalisation wave. This is probably a consequence of the numerous intentional introductions of alien plant species for ornamental purposes and food production that were already occurring at that time (van Kleunen et al., 2018). In addition, because plants can be transported as seeds (McNeill et al., 2011; Wilson et al., 2016), they may survive long journeys and depend less on fast transportation. By contrast, insects likely benefited from the advent of accelerated transportation in the 19th century to spread worldwide (Gippet et al., 2019), which could explain why the first invasion wave is more pronounced for insects than plants. But in contrast to plants, few records were available for both native and alien insect species before 1820; hence, no clear conclusion can be reached regarding insect invasions dynamics during that early period.

Our results demonstrate that the spread dynamics of insects and vascular plants—which represent the vast majority of described species (Scheffers et al., 2012) as well as the majority of known alien species (Seebens et al., 2017)—were linked to the two waves of globalisation. It is likely that other unintentionally introduced taxa, with similar introduction pathways as insects and plants, also follow the two waves of globalisation. However, dynamics may be different for intentionally introduced taxa, such as vertebrates, as their spread mostly depends on other pathways, like for example escape from zoos, farms or pet trade (Gippet & Bertelsmeier, 2021), introduction for biological control or through acclimatisation societies (Hulme et al. 2008), which are not directly related to globalisation dynamics.

Our findings also show that observed invasion dynamics are highly dependent on variations in sampling effort and, thus, highlight the importance of addressing this bias before reaching conclusions about temporal trends in global species accumulations. Even though we found that native species first records from GBIF could serve as proxy for sampling effort, this approach has some limitations. In particular, this proxy may underestimate sampling effort in the recent years because the pool of species remaining to be discovered decreases as new native species are recorded. As this pool reduces, the rate of native species first records inevitably tends to slow down even if sampling effort remains important. However, this is unlikely to have an impact for insects as only about 20% of all insect species have been described so far (Stork, 2018), which suggests that our proxy for insect sampling effort is appropriate and our results are robust for this group. For vascular plants, it that the majority of species have already been discovered (Joppa et al., 2011), which suggests that our approach could underestimate sampling effort for this taxonomic group in the more recent years. Consequently, the second wave of plant invasions may be less important than suggested by our results. But this issue would only affect the amplitude of the estimated second wave of invasions and not our conclusion concerning the global pattern of two waves of invasions.

Another limitation of our approach is that the invasion rate estimated from the null model does not reflect the exact rate of introductions because there is a time lag between the introduction of an alien species and the date of first observation (Aikio et al., 2010; Spear et al., 2021). However, estimating this time lag is very complex. It is likely to vary across taxa, as some species are better known or easier to detect than others. It might also change over time, as scientific knowledge and activity increase. Overall, such time lags may have been longer in the 19th century than in the more recent years, meaning that the first wave of invasions could have started earlier than estimated by our model. But overall, although this time lag could induce a temporal shift of the onset of the first invasion wave estimated in our analysis, it is unlikely to change the global dynamics of the two waves of invasions.

Our analysis show that biological invasions are strongly associated with temporal variations in world trade openness over the past two centuries, which we used as indicator of globalisation dynamics. Although the two globalisation waves consisted of a strong increase of international exchanges, their underlying trade flows strongly differed (Baldwin & Martin, 1999). The first globalisation wave was characterised by the hegemony of Great Britain and trade between the European countries and their colonies. The second wave was defined by the opening and dominance of the United States economy and the growing importance of emerging economies in global trade (Baldwin & Martin, 1999). Future research could explore in greater detail which countries were invaded and how alien species flows changed during the different phases of globalisation. This will be key to identifying the precise drivers of species introductions worldwide and will allow better predicting future invasions. This is especially important given that the future of globalisation, and consequently of biological invasions, remains highly uncertain. World trade openness has been decreasing since the 2007 financial crisis (Livesey, 2018; Witt, 2019) and the COVID-19 pandemic also slowed down international exchanges in 2020 (Enderwick & Buckley, 2020; Vidya & Prabheesh, 2020; WTO, 2020), potentially decreasing rates of new invasions as it happened after the first wave of globalisation.

Overall, our findings contest the widespread idea of an inexorable acceleration of biological invasions over the last centuries. Instead, we show that the world experienced two waves of invasions since the Industrial Revolution, which were associated with the two waves of globalisation. Even though it has long been recognised that human activity is responsible for the vast majority of biological invasions, most research has focussed on the role of habitat or species characteristics affecting invasion success, rather than on human-mediated dispersal (Catford et al., 2009; Ricciardi et al., 2017). Our findings emphasise the urgency to get a better understanding of how globalisation affects the accidental transport of invasive species because biological theory alone cannot explain current invasions, or predict those likely to happen in the future (Kueffer, 2017).

## ACKNOWLEDGEMENTS

We thank Natasha S. Vitek and two anonymous referees for their constructive comments which have greatly improved the manuscript. This work was supported by the Swiss canton Vaud, the Swiss National Science Foundation (NSF) and the Fondation Sandoz-Monique de Meuron pour la relève universitaire. Open Access Funding provided by Universite de Lausanne.

## AUTHORSHIP

A.B., J.M.W.G. and C.B. designed the study. A.B. performed the research. A.B., J.M.W.G. and C.B. all contributed to the writing of the paper.

## PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13863.

## DATA AVAILABILITY STATEMENT

Data and code used to perform the analysis and generate the figures are available at: https://doi.org/10.5281/zenodo.5153707.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Bonnamour, A., Gippet, J.M.W.&Bertelsmeier, C. (2021) Insect and plant invasions follow two waves of globalisation. *Ecology Letters*, 24, 2418–2426. https://doi.org/10.1111/ele.13863

## Supplementary Material S1

To test which economic index was the best predictor of insect and plant invasion dynamics when sampling bias is accounted for, we included different variables in the model: trade openness, world trade value (log-transformed), world GDP (log-transformed) and the derivative of each of these three indexes (i.e., variation of the index from one year to the other). Before computing the derivatives, each variable was smoothed with a cubic spline (smoothing parameter = 0.7). Derivatives were then rescaled between 0 and 1 to avoid negative values. Each variable was computed from 1828 to 2000 and the models were fitted over this period. We used the same model as described in the main text, but contrary to the null model, where the introduction rate is constant overtime, we here defined a linear relationship between the introduction rate and the economic index. The number of introductions in year *t* is thus given by $a*x_t$, where $x_t$ is the value of the economic index in year *t*. We also fitted a null model (i.e., with constant introduction rate) from 1828 to 2000 to compare the results with the "complete" models and thus test if biological invasions are dependent of the economic indexes. The simulations were performed following the same methodology as described in the main text. We then computed the root-mean-square error (RMSE) for each model. The results are presented in Table S1.

Table S1: Model RMSE comparison for each economic index and for the null model.

| | **trade openness derivative** | trade openness | log(trade) | log(GDP) | log(trade) derivative | log(GDP) derivative | null model |
|---|---|---|---|---|---|---|---|
| Insects | **16.2** | 17.7 | 17.6 | 17.6 | 17.7 | 23.6 | 18.4 |
| Vascular plants | **40.9** | 45.3 | 43 | 42.9 | 44.7 | 58.2 | 42.6 |

For both insects and plants, trade openness derivative is the best economic predictor of biological invasion dynamics over the last centuries. Including trade openness derivative in the model also improved the fit compared to the null model. This confirms the link between globalization and biological invasions dynamics, and that the rate of invasion did not continuously increase but fluctuated following the two modern globalization waves.

One limitation of this approach is that the model starts in 1828 since the economic variables are available from that date onwards. This can be a problem for plants as many were introduced before 1828, we thus lose information, affecting the fit of the model (null model RMSE = 32.4 and 42.6 for vascular plants when the null model starts in 1750 and 1828, respectively).

# Chapter 2

# European colonial empires accelerated ant invasions

This work is currently under review.

# European colonial empires accelerated ant invasions

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**Author contributions:**

A.B. and C.B. designed the study. A.B. performed the research. A.B and C.B. wrote the paper.

## Abstract

Between the 16th and the 20th centuries, European countries established vast colonial empires on all continents. These empires triggered profound environmental, demographic and economic transformations. It is likely that many non-native species have benefited from the newly emerged trade network between European countries and their colonies to spread to new regions, leading to an increase in invasions across countries that belonged to these empires. However, this hypothesis has not been tested, and it is still unknown whether colonial empires influenced non-native species richness and invasion dynamics over the last centuries. Here, we show that prior to 1960, countries that belonged to a colonial empire received a higher number of non-native ant species than those that did not. During that period, ant species native to parts of an empire spread preferentially to other countries within the same empire. However, after 1960 former colonial ties had no longer an effect on ant introductions. We also found that colonized countries were the most important source of non-native ants, contradicting the “Imperialist dogma”. Overall, our findings show that ant invasion dynamics were shaped by the rise and fall of European colonial empires, transitioning from empire-centered invasions before 1960 to a truly global spread of species in the more recent decades.

**Keywords:** Biological invasions; colonial empires; globalization; non-native ants; non-native insects; spatiotemporal dynamics

## Introduction

Thousands of species have established populations outside of their native range (Seebens et al., 2017), and some of them have become invasive and cause important damage to ecosystems (Cameron et al., 2016; Kenis et al., 2009) and human societies (Bradshaw et al., 2016; Paini et al., 2016). Many drivers of these invasions have been identified such as global trade (Chapman et al., 2017; Fenn-Moltu et al., 2022; Hulme, 2021), pollution (Crooks et al., 2011), land use (Chytrý et al., 2009; Liu et al., 2023), climate change (Walther et al., 2009) or species traits (Mathakutha et al., 2019; van Kleunen et al., 2016). However, it has become increasingly clear that we need to understand how human history has shaped the number and distributions of invasive species today (Bertelsmeier et al., 2017). A very important feature of global trade relationships and human societies of the past centuries has been neglected so far: European colonial history.

In 1922, about a quarter of the planet's land area was under British control (Murphy 2009). At this time, the British empire included more than 450 million people, a quarter of the world's population (Murphy 2009). Between the 16th and 20th century, other European powers, such as Spain, Portugal, France or the Netherlands, also established vast empires covering all continents. Colonialism led to unprecedented environmental, demographic and economic transformations. European countries extracted resources from their colonies, such as minerals, metals or timber, leading to important alterations of the environment (Morrison 2018). Landscapes in the colonies were also profoundly transformed by large plantations of sugar cane, cotton, tobacco, tea or rice (Morrison 2018). The construction of infrastructures allowing movement of people and commodities led to the depletion of colonies' natural resources such as forests (Das 2011). Colonialism also led to important human movements (Thomas & Thompson 2014). It is estimated that more than 10 million people were shipped from Africa to the Americas by the Atlantic slave trade (Lovejoy, 1989). Additionally, between 1815 and 1930, more than 50 million migrants left Europe for overseas territories, often looking for higher income (Baines 1994). Colonial empires also had a strong influence on global trade. Although globalization is often assumed to be contemporary, it has in fact a long history. In the 16th century, the Spanish trade routes were already connecting the New World to the Old World, and an important commercial network already existed between Europe, Africa and Asia (Flynn & Giráldez 2004). In the following centuries, a wide range of commodities were moved between European countries and their colonies. Preferential trade policies were established between European powers and their colonies, which doubled trade volumes for countries that belonged to a colonial empire relatively to those that did not (Mitchener & Weidenmier, 2008). Species were also intentionally moved between colonizers and their colonies. For example, birds were intentionally introduced within the British empire during the 19th century, in particular for game purposes (Dyer *et al.* 2017). Plant species were also moved inside colonial empires, mainly for food production but also as ornamental plants, resulting in increased floristic homogenization among countries formerly belonging to same empire (Yang *et al.* 2021; Lenzner *et al.* 2022).

However, it is still unknown how colonial empires influenced the number of non-native species introductions, in particular of accidentally introduced species. Certain taxa, such as insects, are mainly transported and introduced unintentionally, as stowaway or contaminants on traded commodities (Saul *et al.* 2017; Gippet *et al.* 2019). As these species often spread unnoticed, it is particularly difficult to predict and prevent their introduction, and limit their expansion. Given that non-native insects outnumber all other non-native animals (Seebens et al., 2017), these accidentally introduced species represent an important share of the global pool of non-native species. Moreover, they are among the worst invaders (Global Invasive Species Database, 2024). The cost of invasive insects already exceeds US$70.0 billion per year globally (Bradshaw et al., 2016), and is likely to keep rising in the future as insect invasions are expected to continue to increase (Bonnamour et al., 2023). It is therefore crucial to better understand past and current insect invasion dynamics. Due to the intensified movement of goods and people in colonial empires, many insects may have been transported unnoticed and introduced accidentally, resulting in an increasing rate of invasions in countries that belonged to these empires. But this hypothesis has not yet been tested.

Here, we investigated the impact of colonial empires on the global spread of non-native species over the past two centuries, using ants as a model system. Over 300 ant species have already been accidentally introduced outside of their native range, and some of them have become very successful invaders (Bertelsmeier 2021, Wong *et al.* 2023). Ants are easily unintentionally transported as contaminants of traded commodities such as potted plants or fruits (Ollier and Bertelsmeier, 2022; Suarez et al., 2009), and are therefore an ideal model to test the effect of colonial empires on accidental species introductions. Finally, ants are, relative to other groups of insects, a well-studied taxon, with good data on their spatial distribution over time (Bertelsmeier et al., 2017; Guénard et al., 2017; Kass et al., 2022).

We used dates of first record per country for 36 non-native ant species to compare invasion dynamics over the past two centuries between countries that belonged to a colonial empire and those that did not. In this analysis, we first used generalized linear models (GLMs) to test the effect of colonization and of potentially confounding variables (precipitation, temperature, insularity, country size, imports and sampling effort) on the number of non-native ants established per country. We modeled non-native ant establishment over two different periods: before 1960, which corresponds to the time of European colonization, and after 1960, which corresponds to the post-World War II wave of globalization, less tied to colonial powers. We then investigated the "Imperialist dogma" according to which colonialism has facilitated mainly the spread of European species from the imperialist European countries to their colonies, rather than vice versa (Jeschke and Strayer, 2005; Seebens et al., 2015). To do that we examined the native areas of these species in order to test if colonizers, colonies and non-colonized countries acted as most important donors of non-native ant species introduced elsewhere. Finally, we tested whether non-native ant species have spread preferentially between countries that belonged to the same colonial empire.

## Methods:

### *Data*

#### Ant distribution and establishment

We extracted 1,240 dates of first record at the country-level for 36 non-native ant species from 36 published sources (see Supplementary references), which were all regrouped in a previous study (Bertelsmeier et al., 2017).  We used these dates of first record as a proxy for the dates of species establishment. We focused on these 36 species as their spread over the past centuries has been well documented, which makes them good model species to study the effect of colonial empires on biological invasions. Species native ranges were defined based on the Global Ant Biodiversity Informatics database (GABI; Guénard et al., 2017).

#### Colonial ties

Data on colonial ties for eight European colonial empires (British, Spanish, French, Portuguese, Dutch, German, Belgian and Italian empires) were sourced from the Colonial Dates Dataset (COLDAT) (Becker, 2020). COLDAT aggregates information on the spatial extent and duration of European colonial empires from four older colonial empire datasets, and therefore constitutes the most complete and accurate dataset on the evolution of the geographic reach of European empires. COLDAT provides information on the start and end dates of colonial ties for all contemporary nation states (i.e., all members of the nation state system on December 31, 2016) (Correlates of War Project, 2017). As COLDAT aggregates information from various databases, maximum (i.e. last date mentioned across all sources) and mean values are given for each start and end dates of colonial ties. In this study, we used the mean values as they provide more accurate measurements of colonization dates (Becker, 2020).

### Trade data

We extracted import data for plants and fruits for the years 1962 (i.e., the earliest date for which plant and fruit trade data are available) and 2000 from the United Nations Comtrade database (https://comtradeplus.un.org). Import data for the year 1962 was only available for 131 countries. We considered only plant and fruit imports as these are the main pathway of ant introductions (Ollier and Bertelsmeier, 2022). We therefore extracted import data for the categories 06, 07 and 08 of the United Nations Harmonized Commodity Description and Coding System (2017 version).

### Environmental variables

We downloaded climate data for the period 1970-2000 at a 10-arcminute resolution from Worldclim version 2.1 (Fick and Hijmans, 2017) using the geodata R package (Hijmans et al., 2022). We extracted precipitations (in mm per year), minimum and maximum temperature (i.e., minimum temperature of the coldest month and maximum temperature of the warmest month in °C). We then averaged each variable at the country level. Country size was extracted from the Global Administrative Areas (GADM) database version 4.1 (https://gadm.org).

### Sampling effort

We used the number of ant occurrences per country as a proxy for sampling effort. We extracted ant occurrences from the Global Biodiversity Information Facility (GBIF.org, 2023). We excluded occurrences of the 36 ant species we focused on in this study. We then separated occurrences over two periods: before 1960, and between 1961 and 2000, resulting in 161,364 occurrences before 1960 and 631,590 occurrences after 1960. We then used the number of ant occurrences per country before and after 1960 as a proxy for sampling effort for each respective period.

*Modeling*

To test the effect of European colonization and of potentially confounding anthropogenic and environmental variables on the probability of non-native ant establishment, we fitted two GLMs of the proportion of non-native ants established per country before and after 1960. We used quasibinomial GLMs (to account for overdispersion) with a logit link.

We first fitted a GLM of the proportion of non-native ants established per country prior to 1960, out of *m* species. For each country, *m* is computed by subtracting to 36 the number of ant species (among the 36 species included in the analysis) that are native in this country (because a species cannot be introduced in its native range). We included as explanatory variables plant and fruit import value of the year 1962 (i.e., the earliest date for which plant and fruit trade data are available; log transformed), mean precipitation (square-root transformed), minimum and maximum temperature, country size (log transformed), insularity (binary variable), sampling effort (i.e. the number of ant occurrences per country before 1960; log transformed), and whether or not the country ever belonged to a European colonial empire (binary variable).

We then fitted a second GLM of the proportion of non-native ants established per country after 1960, out of a pool of *m* species. For each country, *m* is computed by subtracting to 36 the number of ant species that are native in this country (as in the previous model) as well as the number of ant species established in that country prior to 1960, because a species cannot be observed more than once in a country (i.e. first record date). Therefore, if a species has established in a country before 1960, it is no longer part of the pool of potential invaders for this country after 1960. Predictor variables were the same as in the first model, with the exception of plant and fruit import value, for which we used data of the year 2000 (compared to 1962 in the first model), and sampling effort, for which we used occurrences after 1960 (compared to before 1960 in the first model). For both models, predictors were rescaled to a mean of 0 and a variance of 1 to allow coefficient comparison within each model. For both models, the analyses were restricted to the 131 countries for which historical trade data were available. We also reran the second model (i.e. after 1960) with all 186 countries for which data were available, and found similar results (Supplementary figure 1).

We used half normal plots to check model residual distribution using the R package hsp (Moral et al., 2017). We also checked for spatial autocorrelation in the model residuals with the sf (Pebesma, 2018) and spdep packages (Bivand, 2022). Spatial autocorrelation can lead to biases in coefficient estimates in statistical models (Dormann, 2007). To do so, we built a spatial weight list between neighboring countries. Countries were considered as neighbors if the distance between their centroids was less than 3000km (the shortest distance for which all countries in our analysis have at least 1 neighbor). We then used a permutation test on the model residuals to compute Moran’s I, and found no spatial autocorrelation for both models (Moran’s I=0.045 and p=0.069 before 1960; Moran’s I=0.016 and p=0.22 after 1960).

### *Spread of non-native ants within colonial empires*

We tested whether ants have spread preferentially between countries within the same colonial empires as their native range. We hypothesized that, if an ant species is native in a country that belongs to a colonial empire, then this species might be more likely to be introduced to other countries of the same empire. To test this hypothesis, we calculated the expected number of establishments of each ant species in the empires where the species is native somewhere, assuming random spread before and after 1960, and compared to the observed number. We excluded countries that have never been colonized in order to consider only the spread of species inside European colonial empires, resulting in 136 countries for analysis. We considered a species as native to a given empire if at least one country in which the species is native has belonged to that empire (which does not mean that we consider the species as native in every country of this empire, but simply that this species is native somewhere in this empire). Hence, if a country A is colonized by the British in 1890, then the species native in country A will be considered as native in the British empire from the year 1890 onward. We did not include date of decolonization in this analysis; once a country where a species is native has been colonized, this species is considered native in this empire until the end of the studied period, even if that country no longer belonged to this empire at some point. We used this approach as there can be an important time lag between a species introduction and its detection. Hence, a species can be transported between two countries of an empire, but be observed long after, when the countries no longer belong to this empire. This is particularly true for very ancient invasions. For example, many ant species have probably been introduced in the Portuguese and Spanish empires between the 15th and 18th centuries (Gotzek et al., 2015; Wilson, 2005), yet they were not observed before the 19th century.

For each species, we computed the expected number of first records in the empires where this species is native in some part of these empires, under the assumption that species have spread randomly between countries (i.e., the species have the same probability of being established in all the countries of the different empires). For each year t when the species has been first recorded in a new country outside of its native range, we computed the probability that the species established in a country that belongs to an empire where the species is native somewhere. This probability $p_t$ is given by

$$p_t = \frac{s_t}{k_t}$$

where $s_t$ is the number of countries where the species can be introduced in year t (i.e. where the species is not native and not established at year t-1) and that belong to an empire where the species is native somewhere, and $k_t$ is the total number of countries where the species can be introduced in year t (i.e., all countries where the species is not native and has not established at year t-1).

We then computed the expected number of establishments, before ($n_1$) and after 1960 ($n_2$), in the empires where the species is native somewhere, under the assumption that the species spread randomly. This was done by summing all probabilities $p_t$ for all $t<1960$ and all $t>1960$ as follows

$$n_1 = \sum_{t \in Y | t < 1960} p_t \quad \text{and} \quad n_2 = \sum_{t \in Y | t > 1960} p_t$$

where Y is all the years when the species has been first recorded in a new country. We then compared for each species, and for both periods, the observed to the expected number of establishments in the empires where the species is native using Wilcoxon signed rank tests.

## Results and discussion

We found that colonial empires strongly shaped the spread of non-native ants. Before 1960, countries that belonged to a colonial empire received more non-native ant species than non-colonized countries (quasibinomial GLM, t=2.63, p<0.01; Figure 1 and 2). During that period, non-native ants were twice as likely to establish in a country that belonged to a colonial empire compared to a country that did not (Figure 2B). While previous studies had shown that colonial empires influenced non-native species composition (Yang *et al.* 2021; Lenzner *et al.* 2022), their effect on the number of non-native species was still unknown. Here, we show that colonial empires facilitated ant invasions, leading to an increase of non-native ant richness in countries that belonged to these empires. Interestingly, we found that this effect changed over time. After 1960, former colonial ties had no longer an effect on ant invasions as we found no difference in the rate of invasions between countries that had belonged to an empire and those that had not (quasibinomial GLM, t=-1.68, p=0.095; Figure 1 and 2). This clear change in the temporal effect reflects the dynamics of global trade over the past centuries. While movement of goods and people were centered on European empires during the colonial era, decolonization following World War II led to a restructuring of global exchanges, with a strong increase of trade in developing countries and a dramatic rise of connectivity between regions (World Trade Organization, 2013). Our results show that this reconfiguration of global trade led to important changes in ant invasion dynamics, transitioning from invasions centered on European empires to a more global spread of species with no effect of former colonial ties (Figure 1 and 2).

Interestingly, we found that European colonies were the main source of ant invasions, contradicting the “Imperialist dogma” (Jeschke and Strayer, 2005; Seebens et al., 2015). Instead, we found that there were more non-native ant introductions of species originating from the colonies than from colonizer (Wilcoxon test, W=715, p<0.01; Figure 3A) or non-colonized countries (Wilcoxon test, W=4179, p<0.0001). Even after correcting for native ant richness, colonies have still exported more non-native ants than colonizer (Wilcoxon test, W=715, p<0.01; Figure 3B) and non-colonized countries (Wilcoxon test, W=4040, p<0.0001). While many vertebrates and plants were introduced from Europe during colonial times (Dyer et al., 2017; Jeschke and Strayer, 2005; Lenzner et al., 2018), only one of the 36 ant species of this study was native to a European colonizer country. Our results show that colonial empires also facilitated the accidental spread of many species from the colonies during the imperialist era, while it had been assumed that they mostly dispersed European species at that time.

We found that, before 1960, ants spread preferentially between countries of the same colonial empire. Our hypothesis was that, if an ant species is native in a country that belongs to a colonial empire, then this species might be more likely to be introduced to other countries of the same empire. To test that, we calculated for each species, before and after 1960, the expected number of establishments (under the assumption that ants have spread randomly between countries of the different empires) in the empires where the species is native somewhere (i.e., in at least one country belonging to that empire). We then compared the expected number to the observed number of establishments in the empires where the species is native somewhere, for both periods. We found that, before 1960, ants that were native in one part of an empire spread preferentially to other countries of the same empire, with 17% more establishments than expected, rather than to countries belonging to other empires (Wilcoxon signed rank test, V=422, p<0.001; Figure 4). This can be explained by the fact that trade strongly increased between regions that belonged to the same empire (Mitchener and Weidenmier, 2008). Thus, if a species was native to one part of an empire, it might have benefited from this increased connectivity to spread to other regions within this empire. This is consistent with previous studies showing that colonial ties facilitated the exchange of plants between countries belonging to the same empire (Lenzner et al., 2022; Yang et al., 2021).  However, we found that this effect was not constant over time. After 1960, there were no longer any differences between the observed and expected number of establishments in those empires (Wilcoxon signed rank test, V=174, p=0.52; Figure 4), which is consistent with global trade dynamics. After decolonization, trade flows quickly eroded between the colonies and the colonizer country, as well as between former colonies (Head et al., 2010). This might explain why former colonial ties had no effect on ant invasions in the more recent decades.

Plant and fruit import value was an important predictor of ant invasions both before (quasibinomial GLM, t=2.87, p<0.01) and after 1960 (quasibinomial GLM, t=3.27, p<0.01; Figure 2). Import is widely recognized as the primary driver of biological invasions (Hulme, 2021; Liebhold et al., 2012) as it increases propagule pressure, thus facilitating species establishment (Lockwood et al., 2009). In line with what was shown in previous analysis (Ollier and Bertelsmeier, 2022), our results show that imports of fruits and plants was an important driver of historical and recent ant invasions.
Insularity was also an important factor explaining ant invasions during both periods (quasibinomial GLMs, t=4.95 and p<0.0001 before 1960; t=2.91 and p<0.01 after 1960; Figure 2). Islands are known to be hotspots of non-native species (Aulus-Giacosa et al., 2024; Dawson et al., 2017), possibly because the available niche space on islands is not saturated by native species, or because native island biotas may be competitively inferior to mainland species, which could facilitate non-native species establishment (Denslow, 2003; Essl et al., 2019; Moser et al., 2018). Island economies are also strongly dependent upon imports (Deidda, 2016). Islands might therefore be highly connected to distant regions with different species assemblages, thus increasing the risk of non-native species introductions. Finally, climatic variables had no effect in the models, with the exception of maximum temperature after 1960 (quasibinomial GLM, t=2.72, p<0.01; Figure 2). This limited effect of climate could be due to the fact that many non-native ants establish in urban

areas, near or inside buildings or greenhouses, where the microclimate can highly differ from the macroclimate (López-Collar et al., 2024).

One limitation to our study is that there is no record of ant invasions before 1793, despite the fact that some empires, such as the Spanish or Portuguese empires, were very important between the 16th and the 18th centuries. This is very likely due to the absence of sampling of insect species at that time (Bonnamour et al., 2021). Many ants might have been introduced before 1793, but remained undetected for a long time due to low searching effort. For example, *Solenopsis geminata* might have started to spread from Mexico to Eastern Asia then throughout the Old World in the 16th century, following Spanish trade routes (Gotzek et al., 2015). However, this species was first observed outside its native range only in 1851 in India (Wetterer, 2011). Similarly, *Wasmannia auropunctata* might have spread from South and Central America to the Caribbean islands following European colonization in the 16th century (Foucaud et al., 2010), but it was not observed outside its native range before 1863, in Cuba (Wetterer, 2013). This absence of records before 1793 should not affect our conclusions as these very early introductions have likely been recorded before 1960, so it would not influence the results of our GLMs as we combined all introductions prior to 1960 in the models. We also accounted for this bias in our analysis of the preferential spread of species within empires by not including dates of country decolonization in the analysis (see Methods for details).

Insect first records are often biased spatially, as some countries are better sampled than others (Hughes et al., 2021), and temporally, as searching effort strongly increased over the past centuries (Boakes et al., 2010). These biases can mask underlying dynamics of invasions when studying a high number of species for which data on their distribution and spread are incomplete (Bonnamour et al., 2021). In this study, we focused on 36 well-known ant species for which we have good spread data over time, thus limiting these biases. However, there might still be important differences of sampling effort between countries, in particular between those that belonged to a colonial empire and those that did not. To correct for this bias, we included the number of ant occurrences per country, before and after 1960, as a proxy for sampling effort in the models for each period respectively. This variable was a highly significant predictor of the number of non-native ant establishments recorded during both periods (quasibinomial GLMs, $t=4.66$ and $p<0.0001$ before 1960; $t=5.31$ and $p<0.0001$ after 1960; Figure 2). It should be acknowledged that we here focus only on 36 ant species out of the global pool of more than 300 non-native ants (Bertelsmeier, 2021). But our sample includes the most invasive and widespread ant species and is therefore representative of global ant invasions. Further research is now required to investigate the effect of colonial empires on other accidentally introduced taxa like ants, as they also likely benefited from colonial trade network to spread to new regions.

Overall, our findings suggest that European colonial empires facilitated the accidental spread of non-native species. They generated numerous accidental species introductions before 1960, leading to higher richness of non-native ants in countries that belonged to these empires. We also found that these empires facilitated the spread of many species from the colonies, which contrasts with the “Imperialist dogma”. While historical ant invasions were tightly linked to colonial empires, they became truly global in the more recent decades, with no more effect of former empires. Our results therefore demonstrate that the rise and fall of colonial empires strongly shaped ant invasion dynamics.

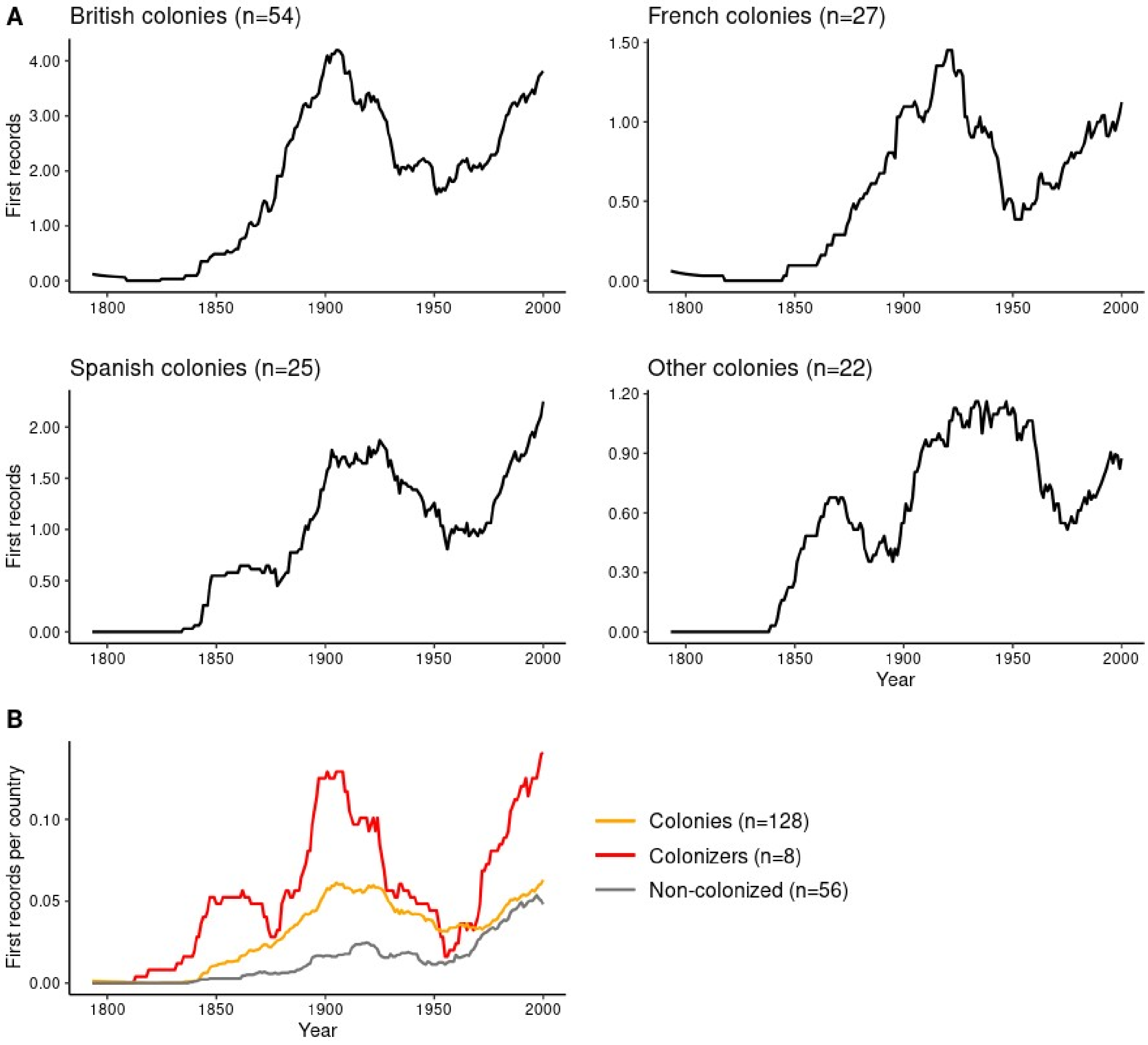


**Figure 1**: **Temporal dynamics of ant invasions.** (A) Annual number of non-native ant first records in colonized countries. For these plots, if a country was colonized by several European countries, it was assigned to the empire it belonged to for the longest time. (B) Annual number of first records corrected by the number of countries in the different groups. The number of countries in each group is given in parenthesis. Data are here represented with a 30-year moving average.

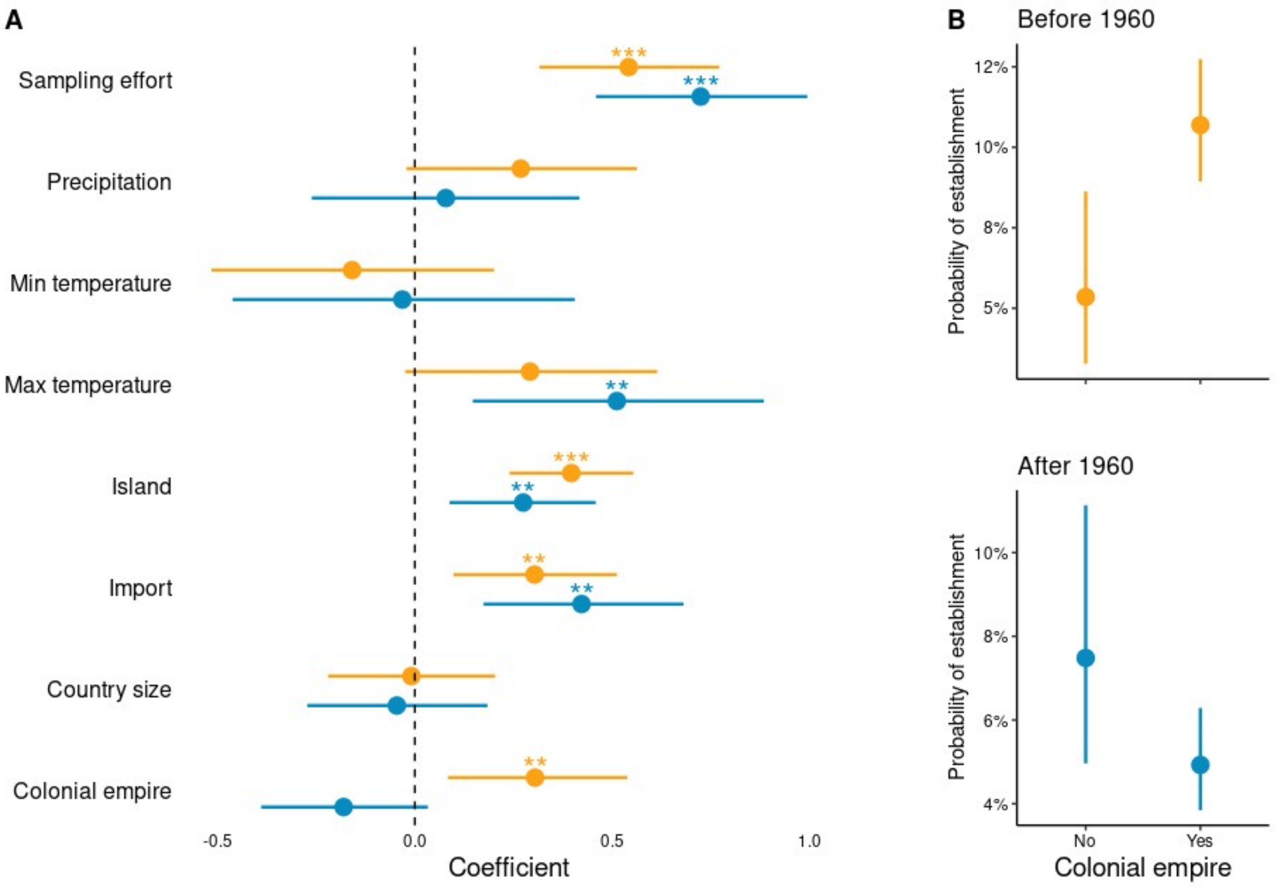
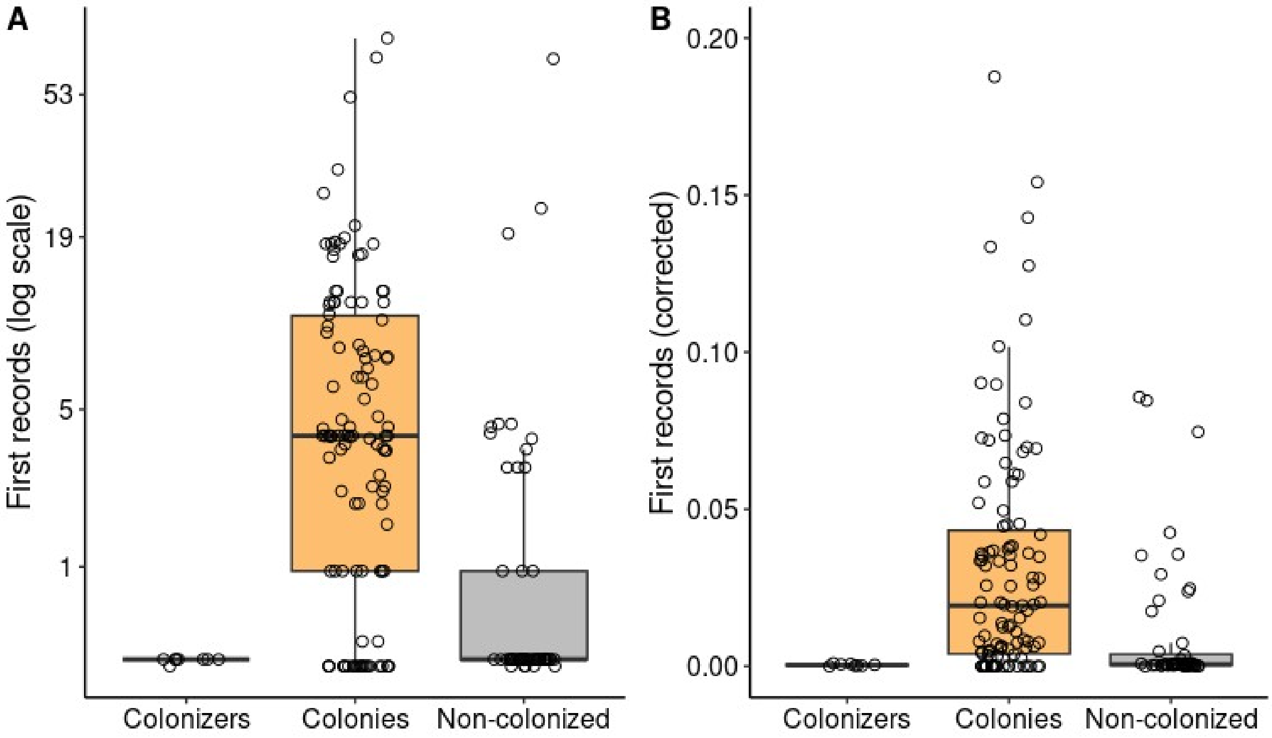


**Figure 2: Predictors of ant invasions before and after 1960.** A) Predictors of the proportion of non-native ants established per country before (orange; quasibinomial GLM, McFadden's $R^2=0.54$) and after 1960 (blue; quasibionomial GLM, McFadden's $R^2=0.42$). Dots and error bars represent GLM estimates and 95% CI. Explanatory variables were standardized to a mean of 0 and a variance of 1 to allow intra-model coefficient comparison. Significance code: ***: $p<0.001$, **: $p<0.01$, *: $p<0.05$. B) Marginal effect (with 95% CI) of belonging to a colonial empire on the probability of non-native ant establishment according to quasibinomial GLMs, before (top panel) and after 1960 (bottom panel).



391 **Figure 3: Origin of non-native ants.** (A) Number of establishments of ant species native from colonizers, colonies and non-colonized countries. Each dot is a country. When a species was native from more than one country, its number of first records was divided between all of them. (B) Number of establishments divided by the native ant richness per country. Four outliers are not shown on panel B, see Supplementary figure 2 for the full figure.

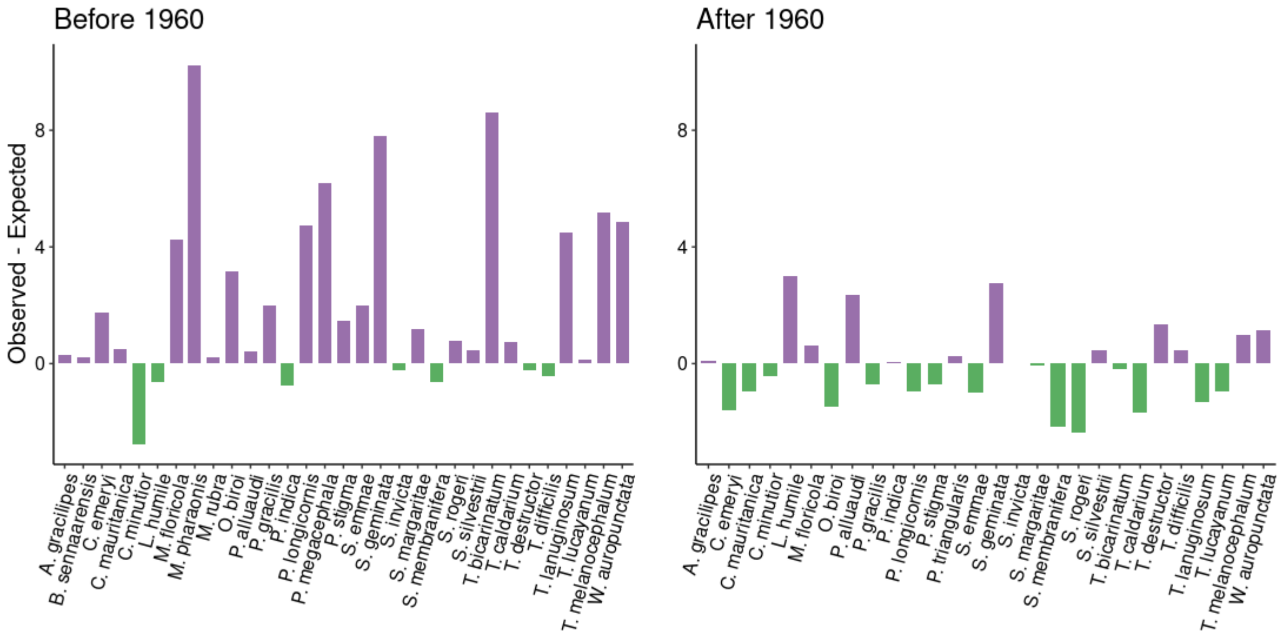


**Figure 4: Preferential spread of ants within empires.** Difference between the observed number and expected number of establishments (under a null model assuming that non-native ants spread randomly between countries of the different empires) in the colonial empires in which the species is native somewhere, showing that ants have preferentially spread to countries within the same empire as their native range before 1960 (left), but not afterwards (right).

**Data availability:**

Data and code used to perform analysis and generate figures will be archived in a public repository.

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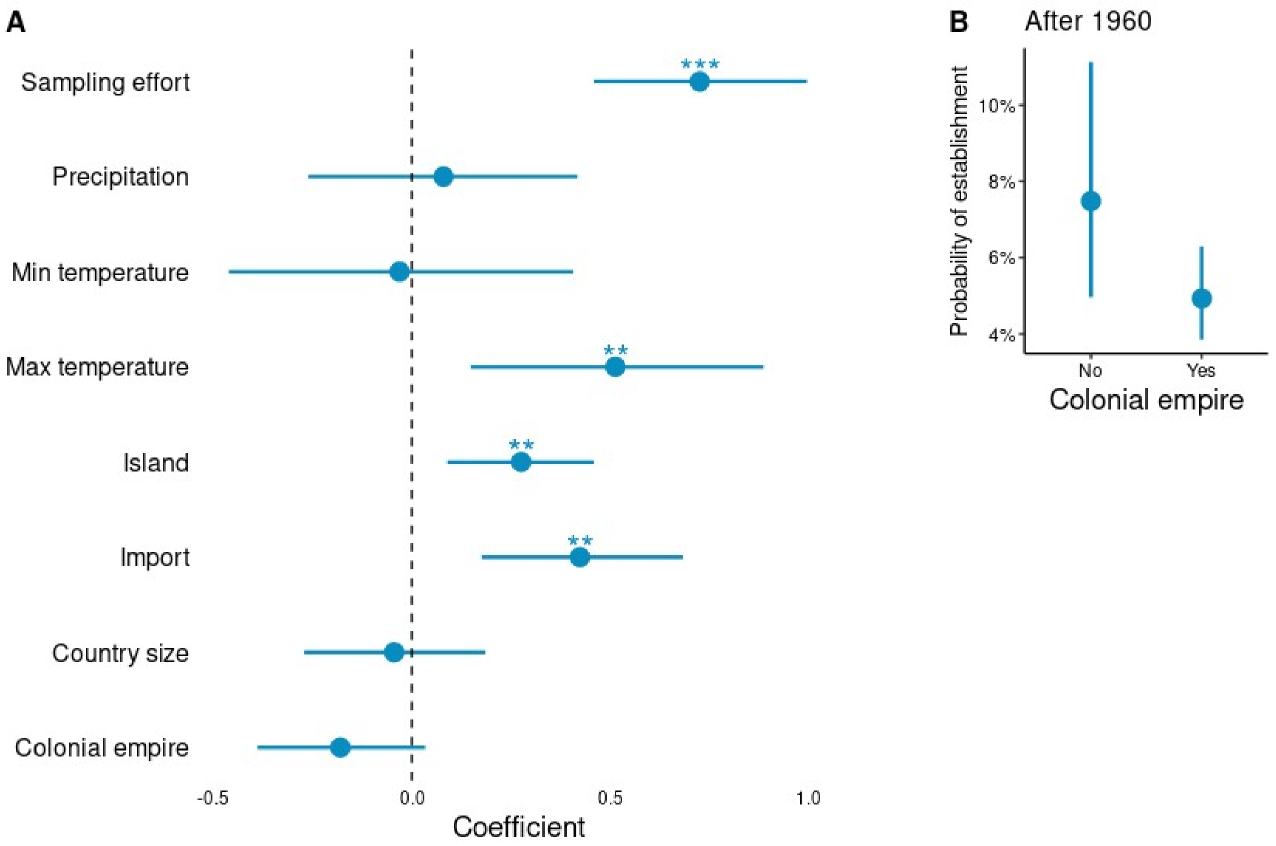
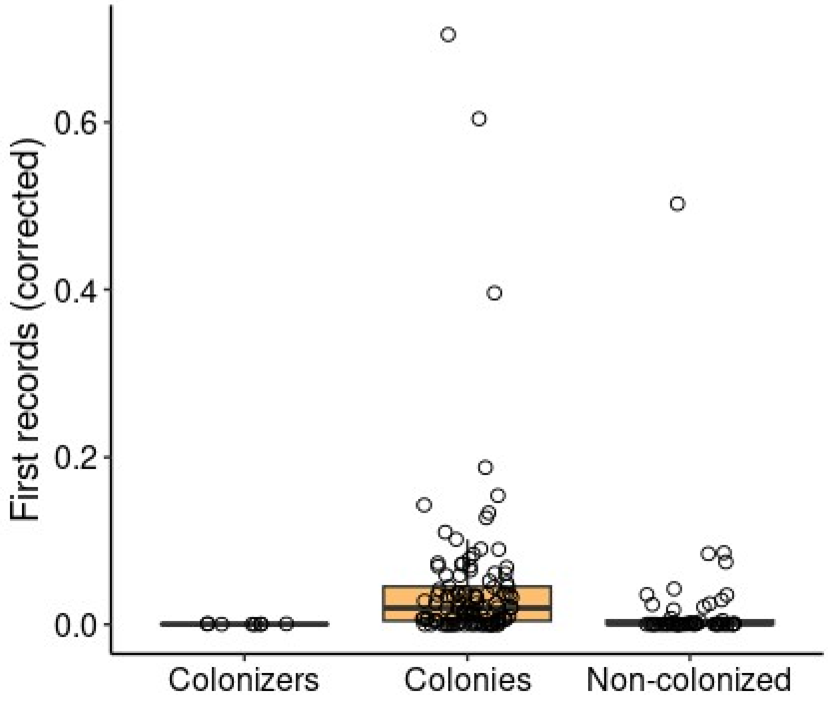
## Supplementary information



**Supplementary figure 1:** A) Predictors of the proportion of non-native ants established per country after 1960 when 186 countries are included in the model (quasibionomial GLM, McFadden's $R^2$=0.42). Dots and error bars represent GLM estimates and 95% CI. Explanatory variables were standardized to a mean of 0 and a variance of 1 to allow intra-model coefficient comparison. Significance code: ***: p<0.001, **: p<0.01, *: p<0.05. B) Marginal effect (with 95% CI) of belonging to a colonial empire on the probability of non-native ant establishment after 1960 according to the quasibinomial GLM (with 186 countries).



**Supplementary Figure 2: Origin of non-native ants.** Number of establishments of ant species native from colonizers, colonies and non-colonized countries divided by the native ant richness per country.

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# Chapter 3

# The increasing frequency of secondary spread over time accelerates insect invasions

This work is not published.

# The increasing frequency of secondary spread over time accelerates insect invasions

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## Abstract

Due to the globalization of trade and transport, many species have been accidentally introduced outside of their native range, and some of them have managed to establish self-sustaining populations. Non-native species can spread to a new region either directly from their native range (primary introduction) or via a previously invaded region (secondary introduction). The phenomenon of secondary spread has been called ‘bridgehead effect’ and is recognized as a major driver of global invasions. As more and more species are introduced to new regions and spread further within these regions, the frequency of secondary transport might increase over time, thereby creating a positive feedback loop between transport and establishment. But so far, it is unknown if the frequency of bridgehead effects increases over time.

To test this, we analyzed a dataset of 231,251 border interceptions of 1,939 insect species in the United States between 1913 and 1984. Overall, 34% of the interceptions originated from a country where the intercepted species had previously been introduced, with strong variations among countries. Using logistic regression, we found that the probability of secondary introduction increased by 6% between 1913 and 1984. Moreover, the probability of secondary introduction was strongly linked to the species’ non-native range size. Our results show that bridgehead effects accelerate biological invasions over time by creating a positive feedback loop where invasion begets invasion.

## Introduction

With increasing global trade, many species are transported and introduced, intentionally or accidentally, to new regions outside of their native range (Dawson et al., 2017; Hulme, 2021, 2009). There are at least 37,000 non-native species that have established self-sustaining populations in these new locations, and a subset of them, more than 3,500 species, have been classified as invasive based on their impacts on people and nature (Roy et al., 2024). They threaten global biodiversity by contributing to many plant and animal extinctions (Blackburn et al., 2019) and impact human societies by damaging agriculture, forestry, human health and infrastructures (Pyšek et al., 2020). The number of non-native species first records (i.e. the date at which a species is first observed in a region where it has established outside of its native range) is still increasing at a high rate (Seebens et al., 2017), and is likely to continue in the future (Seebens et al., 2020). As the movement of propagules is the first step of the invasion process, a better understanding of human-mediated dispersal of species is required in order to limit the number of invasions in the future (Catford et al., 2009).

Accidental human-mediated dispersal often involves complex introduction routes, with frequent jump dispersal to noncontiguous regions, multiple introductions from the native area, admixture between distant non-native populations, and sometimes back-introduction into the native range (Garnas et al., 2016). Pattern of non-native species movement also include recurrent secondary introductions where non-native populations act the source for subsequent introductions. This phenomenon of secondary spread has been called “bridgehead effect” (Lombaert et al., 2010), and plays a key role in biological invasions. For example, the invasion of the Harlequin ladybird (*Harmonia axyridis*) in Europe, South America and Africa was caused by the introduction of individuals from an invasive population in North America (Lombaert et al., 2010). Bridgehead effect was also shown to facilitate invasion of many other arthropods, such as termites (Blumenfeld et al., 2021), seed bugs (Lesieur et al., 2019), mealybugs (Correa et al., 2019), moths (Bras et al., 2022), spider mites (Boubou et al., 2012) and crabs (Darling et al., 2008), but also of nematodes (Esquibet et al., 2024), plants (Keller et al., 2012; Vallejo-Marín et al., 2021) as well as microorganisms (Fontaine et al., 2021). Due to its major role in the spread of invasive species, the bridgehead effect has been identified as one of the priority areas to advance invasion study and management in the future (Ricciardi et al., 2021, 2017).

Secondary introductions are very frequent in non-native species dispersal. The majority of insect introductions (65%) in the US, the European Union, Japan and South Africa was found to originate from bridgehead countries (Worm et al., 2024). For ants, 75%-87% of species intercepted at the US and New Zealand borders were coming from countries outside of their native range (Bertelsmeier et al., 2018). Similarly, 46% of termite interceptions in the US came from invaded regions (Blumenfeld and Vargo, 2020). These studies have measured bridgehead frequency as a static value by regrouping all interceptions across a given period, and did not investigate potential variations over time. However, the bridgehead frequency may have increased over time, as non-native species spread and increase their non-native range, thereby mechanically increasing their probability of doing secondary introductions. If it is the case, it would indicate that bridgehead effect is increasing the global movement of insects over time, creating a positive feedback between transport and establishment leading to an acceleration of invasions. But this hypothesis has not been tested yet.

Accidental introductions cannot be observed directly, as species are often transported unnoticed as hitchhikers or contaminants on traded commodities (Gippet et al., 2019; Meurisse et al., 2019). However, border interceptions of species at air and maritime ports provide a window into the ongoing accidental dispersal of species and can be considered proxies for unobserved introductions (Turner et al., 2021). Border interceptions have therefore been used to estimate the proportion of primary and secondary introductions in human-mediated species movement. In this study, we analyzed a dataset of 231,251 interceptions of 1,939 insect species at the US borders spanning from 1913 to 1984. Using information on insect native range, we calculated the overall proportion of secondary introduction in the interceptions. This unique dataset of interceptions covering more than 70 years also allowed us to test whether the probability of bridgehead effect increased over time, which would suggest that it contributes to the acceleration of biological invasions. We also tested the link between the size of the species' non-native range and the probability of secondary introduction to confirm that the potential increase of bridgehead frequency over time is due to the positive feedback between establishment and transport.

## Methods

### *Interception data*

We used a dataset of 433,229 insects interceptions at ports of entry (maritime, land and air) between 1913 and 1984 in the US. We restricted our analyses to interceptions recorded at the species level and for which information on the species' native range was available (see section below), representing a total of 231,251 interceptions of 1,939 insect species. As parts of the dataset are still in the digitalization phase, interceptions are missing for certain years (Figure 1). This data will be included in the analysis before this chapter is submitted to a journal. As most of the interceptions have already been digitalized, and the missing data represent short periods of time, the currently available data is likely representative of the global trend of the total dataset and can therefore be analyzed despite some missing information.

Each interception event includes information on the identity of the taxon, the country of origin of the interception and the year when the interception was observed. As there have been variations over time in the names of recorded species, we used a taxonomic cleaning script modified from Blake and Turner (2021) to standardize species names. The script uses the R package *taxize* (Chamberlain et al., 2025) with the GBIF API (GBIF.org, 2025). Taxon names that did not match with GBIF taxonomic backbone were searched in 9 additional databases (Catalogue of Life, Integrated Taxonomic Information System, National Center for Biotechnology Information, Wikispecies, The Interim Register of Marine and Nonmarine Genera, Encyclopedia of Life, Aphid Species File, Index to Organism Names and uBio NameBank). As countries also changed names over the last century, we used the R packages *rangeBuilder* (Title, 2024) and *countrycode* (Arel-Bundock et al., 2024) to standardize country names using ISO code 3166.

### *Native and non-native distribution data*

Data on insect native ranges were extracted from Turner et al. (2021). Native range data for additional species was manually searched in scientific papers, online databases and websites. We thus obtained native range data for 28% of the species, representing 93% of the interceptions. Native range data was used at the scale of biogeographic regions (Asian Palearctic, European Palearctic, Afrotropics, Neotropics, Indomalaya, Nearctic, Australasia and Oceania), using a system modified from Wallace's designation (Wallace, 1876). Species non-native range was sourced from the Alien Species First Records Database (Seebens, 2023; Seebens et al., 2017), which includes the first record date in each country where the species was introduced.

### *Analysis and modeling*

To identify whether an interception was a secondary or primary introduction, we checked whether the origin country was part of the biogeographic region where the intercepted species is native. If the origin country was part of the insect's native range, then the interception was considered as a primary introduction. Otherwise, it was considered as a secondary introduction.

To test if the probability of secondary introduction increased over time, we fitted a generalized linear mixed model (GLMM) with a logit link and a binomial distribution. We used the type of each interception (i.e. primary or secondary introduction) as a binary response variable and the year of the interception as explanatory variable. We included the species and the country of origin of the interception as random effects on the intercept of the model. We then fitted the same GLMM, but using the the size of species' non-native range (defined as the number of countries where the species had been recorded outside of its native range up to the year of the interception; log-transformed) as explanatory variable, rather than the year of the interception, in order to test if the probability of secondary introductions increases with the size of the species' non-native range. We checked residual distribution and dispersion for both models using the R package *DHARMa* (Hartig et al., 2024). All analysis were performed in R v.4.4.2 (R Core Team, 2024).

## Results and discussion

We analyzed 231,251 interceptions of 1,939 insect species at the US borders between 1913 and 1984. The annual number of interceptions increased over time (Figure 1), which likely reflects the increasing effort to examine imported commodities. Interceptions mainly originated from Latin America, Asia and Europe (Figures 1 & 2), which is consistent with previous analysis of interceptions of ants at the US border (Bertelsmeier et al., 2018). Mexico, Hawaii and Japan were the most important sources of interceptions in our data (Figure 2 & 3). Overall, we found that 34% of the interceptions were coming from outside of the species' native range, with strong variations between regions (Figure 3). Some countries, such as Mexico, mainly exported native species, while others, such as Australia or Pacific Islands, exported almost exclusively non-native species (Figure 3), possibly because there are many established non-native species in these regions.

Using interception data spanning more than 70 years, we found that the proportion of secondary introductions increased by 6% between 1913 and 1984 (binomial GLMM, z=17.04, p<0.0001; Figure 4B). This increase is due to the ongoing expansion of non-native species in new regions, as we found that the probability of secondary introductions increases with the size of the species' non-native range (binomial GLMM, z=17.79, p<0.0001; Figure 4A), confirming the findings of a previous study (Bertelsmeier et al., 2018). Our results demonstrate that bridgehead effects are a self-accelerating process leading to an increasing rate of invasions over time. As a species spreads to new regions, its probability of being transported again increases, thereby also increasing its probability of establishing in new regions and spreading further. While secondary introductions have already caused several biological invasions (Blumenfeld et al., 2021; Bras et al., 2022; Correa et al., 2019; Vallejo-Marín et al., 2021), the increasing proportion of bridgehead effects over time suggests that the movement of insects from bridgehead regions will continue to rise in the future, and so will the rate of invasions caused by secondary introductions.

Increasing bridgehead effect will also further distort our view of global flows of non-native species (Bertelsmeier and Ollier, 2021). Studies on species flows usually link the native to the non-native range of the species (Bonnamour et al., 2023; Isitt et al., 2024; van Kleunen et al., 2015), suggesting that species are exclusively introduced from their native range. However, as species spread to new continents, their probability of being introduced from a bridgehead region also increases, which makes species flows (from the native to the non-native range) less reliable over time to investigate actual species introduction routes (Bertelsmeier and Ollier, 2021). With secondary spread becoming more frequent over time, understanding species movement might get increasingly difficult, and future species introductions might be harder to predict and anticipate.

In this study, we found 34% of secondary introductions, which is lower than what was found in other studies on insect interceptions. The proportion of secondary introduction observed in ants during the same period (1914-1984) in the US was 75%, and 87% in New Zealand between 1955 and 2013 (Bertelsmeier et al., 2018). This difference with our results could be explained by the fact that ants may be particularly likely to be accidentally picked up and transported from their non-native range. Ants have complex social structures and can become very abundant and dominant in invaded regions where they sometimes form supercolonies covering vast areas and excluding many other ant species (Angulo et al., 2024). Ants may therefore be more likely to be introduced from bridgehead regions, and may not be representative of other insect groups. Another study across diverse insect taxa found that 65% of the interceptions were coming from the species' non-native range (Worm et al., 2024). This study was at the global scale, which could partially explain the difference in bridgehead frequency observed with our analysis focused on the US. Also, Worm *et al.* (2024) analyzed interceptions from a more recent period (1997-2020). As we showed in this analysis, the frequency of bridgehead effect is increasing over time, it is therefore not surprising that we found lower proportion of secondary introductions compared to studies focusing on more recent interception data.

The 34% proportion of secondary introductions measured in this study is a conservative estimate as we used native range data at the scale of biogeographic regions. It is likely that some species might be native only in part of a biogeographic region, and that interceptions coming from other parts of this region should therefore be considered as secondary introductions for that species. The frequency of secondary introductions may therefore be higher than we estimated here, but this bias is unlikely to affect our finding about the overall increase in bridgehead proportion over time.
Another potential limitation is that some of the origins of the interceptions may be erroneous. For example, a commodity can be transported through several ports before arriving at its destination in the US, and the last port of transit may have sometimes been recorded as the origin of the commodity by the inspectors, without being the actual source of the commodity and the intercepted species. Additionally, erroneous source of interceptions could be due to contamination of a container while it was in transit in an intermediate port, or because the container was not completely cleaned and might therefore still contain contaminant organisms from a previous shipment. However, these scenarios should be rare and they are therefore unlikely to impact our results.

Overall, our findings show that bridgehead effect plays an important role in the global dispersal of insects. We found that the probability of a species to do secondary introductions is linked to the size of its non-native range. We also showed that the frequency of secondary introductions is increasing over time, which confirms that bridgehead effect creates a positive feedback loop between transport and establishment in the invasion process. Our results show that secondary introductions are accelerating the global spread of species over time.

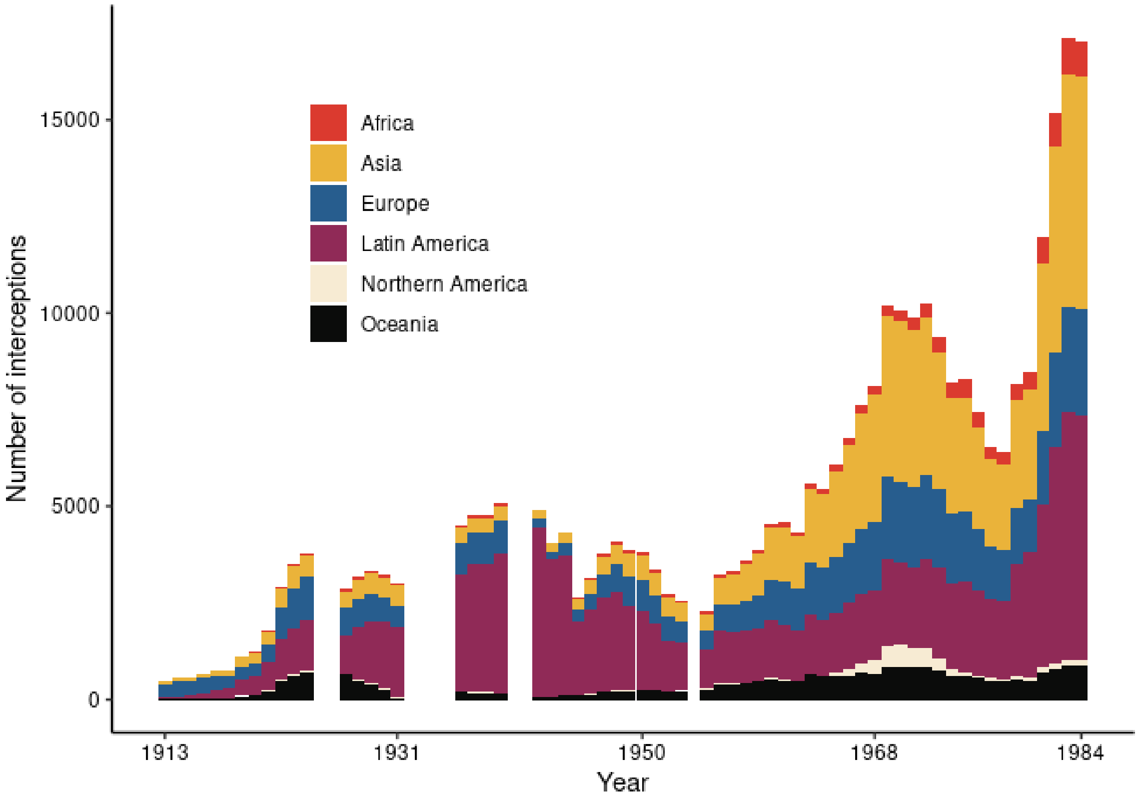

Figure 1: Number of insect interceptions in the US over time originating from the different continents. Gaps in the data are due to the ongoing digitalization of the intereception records.

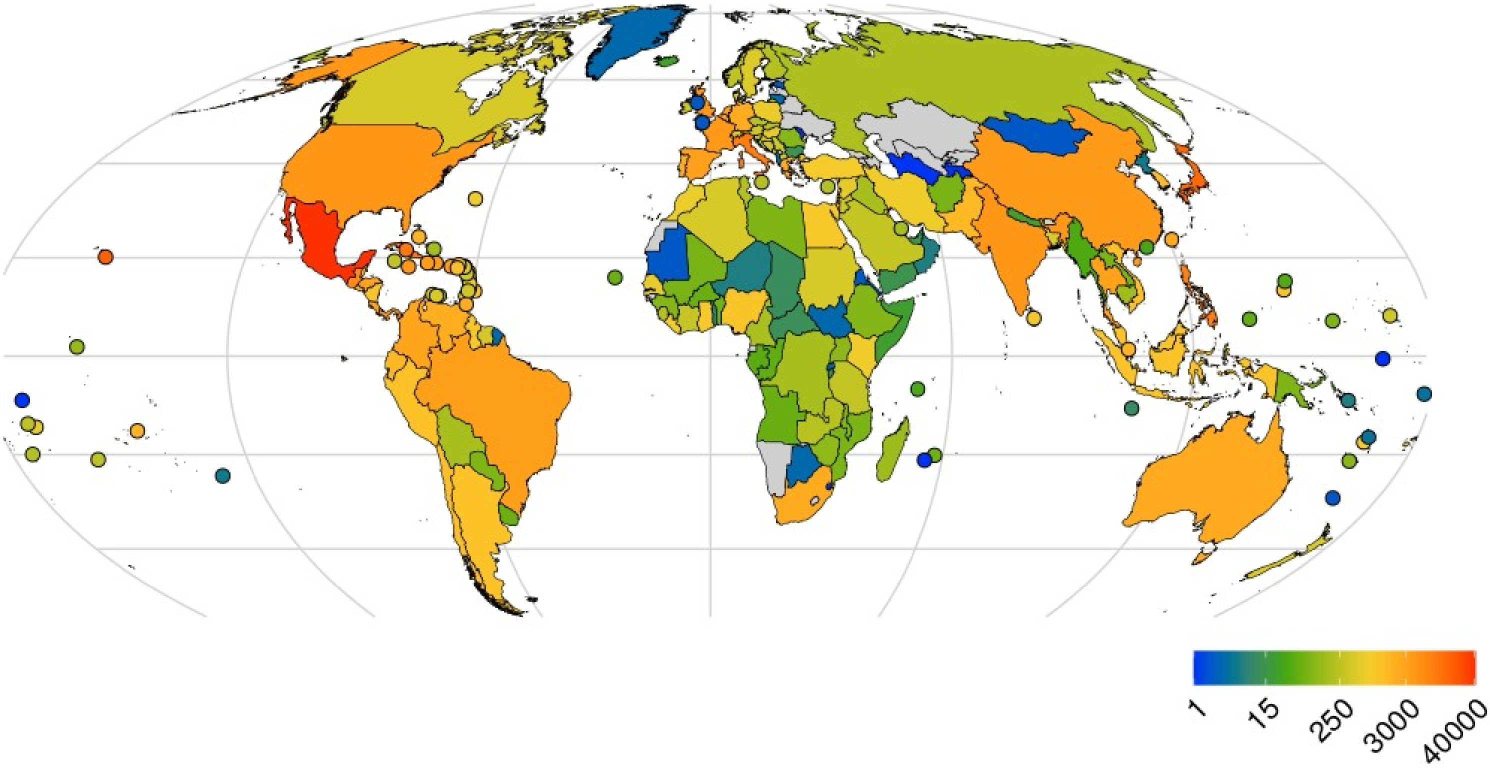

Fig 2: Number of insect interceptions at US ports of entry originating from each country (log scale).

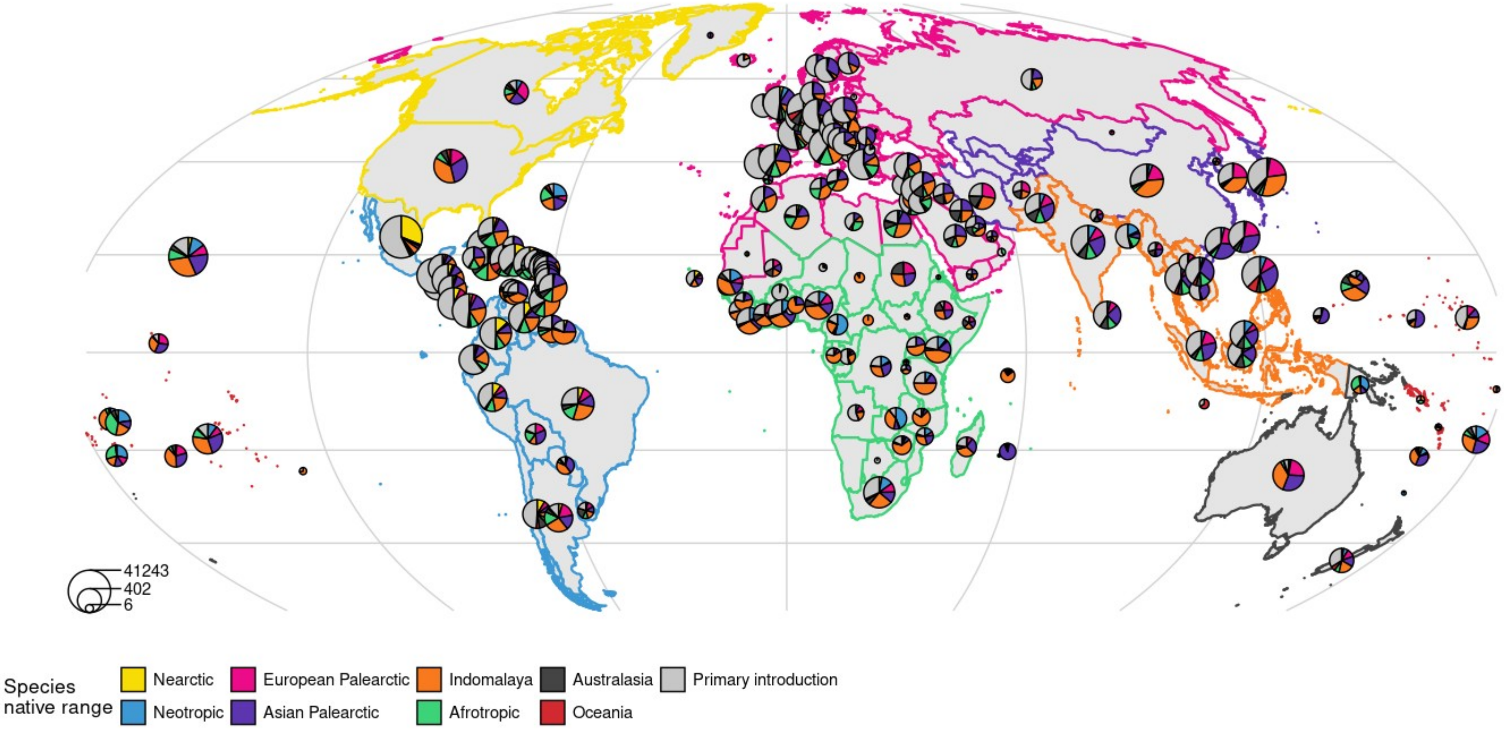

Figure 3: Origins of insects intercepted at US ports of entry. The pie charts represent the proportion of primary (in gray) and secondary (in color) introductions coming from each country. The colors represent the native range of insects exported through secondary spread. The size of the pie charts is linked to the number of interceptions coming from each country.

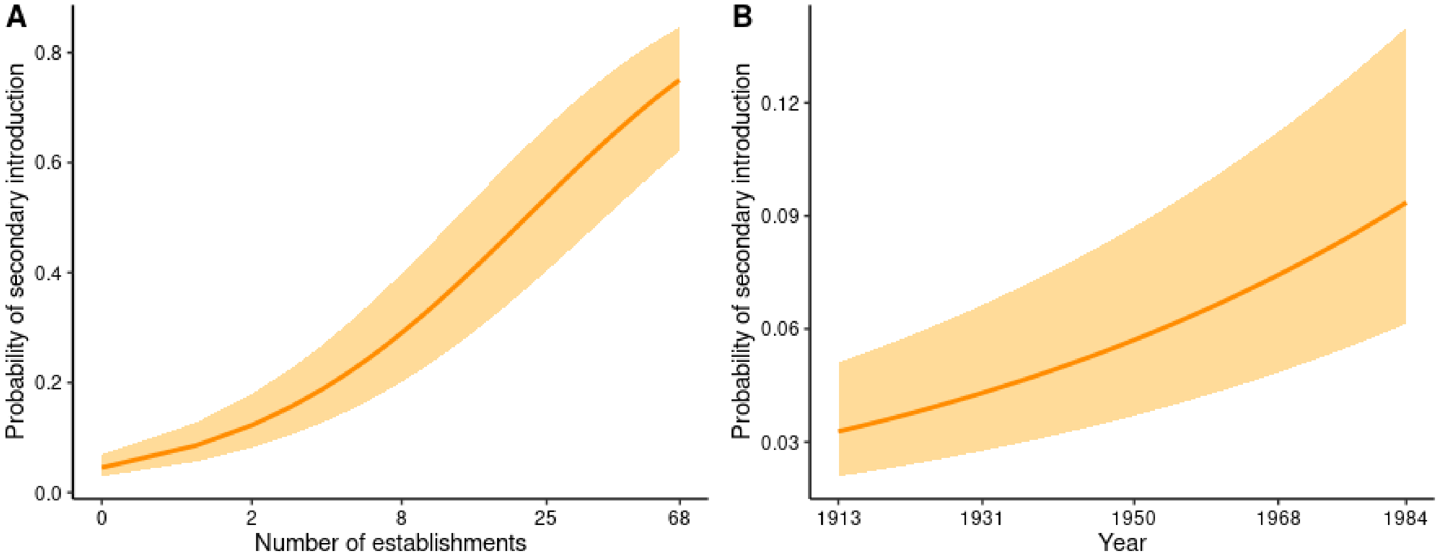

Figure 4: Increasing frequency of bridgehead effect (A) with species' non-native range size (i.e. the number of countries where the species has established up to the year of the interception) and (B) over time. Marginal effects with 95% confidence intervals estimated with binomial GLMMs.

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# Chapter 4

# Historical plant introductions predict current insect invasions

This work is published in PNAS.

PNAS RESEARCH ARTICLE | ECOLOGY

# Historical plant introductions predict current insect invasions

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Edited by Daniel Simberloff, University of Tennessee at Knoxville, Knoxville, TN; received December 23, 2022; accepted April 20, 2023

**Thousands of insect species have been introduced outside of their native ranges, and some of them strongly impact ecosystems and human societies. Because a large fraction of insects feed on or are associated with plants, nonnative plants provide habitat and resources for invading insects, thereby facilitating their establishment. Furthermore, plant imports represent one of the main pathways for accidental nonnative insect introductions. Here, we tested the hypothesis that plant invasions precede and promote insect invasions. We found that geographical variation in current nonnative insect flows was best explained by nonnative plant flows dating back to 1900 rather than by more recent plant flows. Interestingly, nonnative plant flows were a better predictor of insect invasions than potentially confounding socioeconomic variables. Based on the observed time lag between plant and insect invasions, we estimated that the global insect invasion debt consists of 3,442 region-level introductions, representing a potential increase of 35% of insect invasions. This debt was most important in the Afrotropics, the Neotropics, and Indomalaya, where we expect a 10 to 20-fold increase in discoveries of new nonnative insect species. Overall, our results highlight the strong link between plant and insect invasions and show that limiting the spread of nonnative plants might be key to preventing future invasions of both plants and insects.**

nonnative insects | nonnative plants | time lag | invasion debt | species flow

## Significance

Invasive insects severely impair ecosystem functioning and impact human societies. It is therefore urgent to better predict and prevent future invasions. Using statistical models, we show that nonnative plant introductions are a major driver of insect invasions, and that insect invasions lag behind plant invasions. In the near future, new insect invasions are estimated to increase by 35% worldwide based on recent nonnative plant introductions. The Afrotropics, the Neotropics, and Indomalaya are the regions most at risk of future invasions. Our results highlight that limiting the introduction and spread of nonnative plants will be key to preventing future insect invasions.

With increasing globalization, many species are transported and introduced outside of their native range, where they sometimes succeed in establishing self-sustaining populations. Some of these nonnative species are called invasive, either because they have very good spread capacities or because they strongly impact ecosystems and human societies (1). With now more than 7,000 species established outside of their native range, insects outnumber all other nonnative animals (2), and some insects are among the most damaging invaders worldwide (3). Insects are evolutionarily extremely successful and diverse. They include herbivores, predators, pollinators, and detritivores, and are major components of every biome with the exception of most marine habitats. Invasive insects have a wide range of ecological impacts, outcompeting native species, disrupting key insect–plant mutualisms, affecting native seed dispersers, changing native pollination services (4), and potentially causing species extinction (5). Many invasive insects are also important pests damaging agricultural and ornamental plants (6) as well as forests (7). A striking example is the box tree moth, *Cydalima perspectalis*, which was accidentally introduced in Europe and threatens Buxus trees all over the continent (8). Nonnative insects can also spread infectious diseases in humans and livestock (9, 10). The two invasive mosquitoes *Aedes aegypti* and *Aedes albopictus* are efficient vectors of several human arboviral diseases such as dengue, zika, chikungunya, and yellow fever, and the distribution of these two species will continue to expand in the coming decades (11). Overall, the economic cost of nonnative insects is estimated to exceed US$70.0 billion per year globally (12) and is likely to increase in the future as many new insect invasions can be expected due to ongoing global exchanges. It is therefore urgent to better understand the drivers of insect introductions to better predict future invasions and limit their impact.

One possible predictor of future insect invasions are current plant invasions. Plant introductions may precede insect invasions because insects have tight relationships with plants, with many insect species feeding or living on plants (13). Consequently, many insects are transported accidentally on plant products (14–16). The trade of live plants for horticultural and ornamental purposes is therefore an important pathway of nonnative insect introductions (17–20). In Great Britain, almost 90% of invertebrate plant pest introductions are associated with the plant trade, in particular with ornamental plants (18). Nonnative plant diversity is also an important driver of insect invasions (21) as they can facilitate the establishment and spread of nonnative insect species, in particular those that rely on plants as hosts (22–25). Nonnative plants can also promote invasions of

Author contributions: A.B. and C.B. designed research; A.B. performed research; A.B., R.E.B., A.M.L., H.F.N., A.R., R.M.T.,T.Y., and C.B. collected data; A.B. analyzed data; and A.B., R.E.B., A.M.L., H.F.N., A.R., R.M.T., T.Y., and C.B. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2221826120/-/DCSupplemental.

Published June 5, 2023.

pollinators and plant visitors (26, 27). While it has been shown that areas with higher numbers of native and nonnative plant species also harbor higher numbers of invasive insects (21), it remains unknown whether insect invasions follow plant invasions. If this hypothesis is correct, current plant invasions might be used to predict future insect invasions.

Time lags between drivers of invasions and actual nonnative species establishment have been previously identified. For many taxa, the current distribution of nonnative species is better explained by socioeconomic indicators from the year 1900 than to those from 2000 (28), suggesting an important historical legacy (29). This time lag between cause and effect suggests that socioeconomic activities lead to an "invasion debt" (28), caused by past socioeconomic processes. Invasions may be delayed when a species has been present in low numbers in its introduced range for a long time before starting to spread. For example, this may happen if past environmental conditions did not yet allow the species to spread. This is different from "future invasions" which refers to the introduction of species by future trade activities. Here, we tested the predictive power of lagged vs. current nonnative plant flows (from years 1800 to 2010) for nonnative insect invasions at a global scale. We not only focused on species classified as invasive, but included all nonnative insect and plant species in our analysis. We built generalized linear models of nonnative insect flows between biogeographic regions, using data of nonnative plant and insect first record dates per region and information on their native range. As global trade dynamics strongly influence biological invasions (30–32), we also included lagged and current trade flows in the models. In this analysis, we i) tested the predictive power of lagged vs. current nonnative plant flows and confounding variables on insect invasions, ii) quantified the time lag between plant and insect invasions, and iii) estimated insect invasion debt in each biogeographic region based on the observed time lag.

## Results

**Patterns of Insect and Plant Invasions.** The greatest number of recorded insect introductions so far has occurred in the Nearctic, Oceania (mostly Hawaii), Europe, and Australasia (Fig. 1*A*). In comparison, records of nonnative insect species are much more limited in the Asian Palearctic, the Neotropics, the Afrotropics, and Indomalaya. But nonnative insect richness in these regions is likely to be largely underestimated as these regions are undersampled (33). Similar invasion patterns were observed for plants through 1900, with Europe, the Nearctic, and Australasia being the main recipients of historical plant introductions (Fig. 1*C*). Since 1900, many nonnative plant species have been recorded in the Afrotropics, Oceania, and Asia (Fig. 1*B*). The current distribution of nonnative insects is therefore more correlated to the distribution of nonnative plants from 1900 (linear model $R^2 = 0.57$) rather than 2010 (linear model $R^2 = 0.48$).

**Time Lag between Plant and Insect Invasions.** We used generalized linear mixed models (GLMMs) to test the predictive power of historical and current nonnative plant flows on nonnative insect flows between biogeographic regions. We found that current nonnative insect flows were best explained by nonnative plant flows up to 1900, as indicated by the lowest AIC [AIC = 627.5; Nakagawa's $R^2 = 0.95$ (34), Fig. 2*A*], rather than by more recent plant flows. The relationship between plant and insect flows is shown in *SI Appendix*, Fig. S1. An AIC difference ($\Delta$AIC) >2 indicates that the weaker model has low comparative support, and models with $\Delta$AIC >10 have no support (35). Here, the model with plant flows through 1900 was significantly better than the model with plant flows through 2010 ($\Delta$AIC = 11.7). Accounting for unequal sampling between regions did not change these dynamics (*SI Appendix*, Fig. S3*A*). We then tested for the

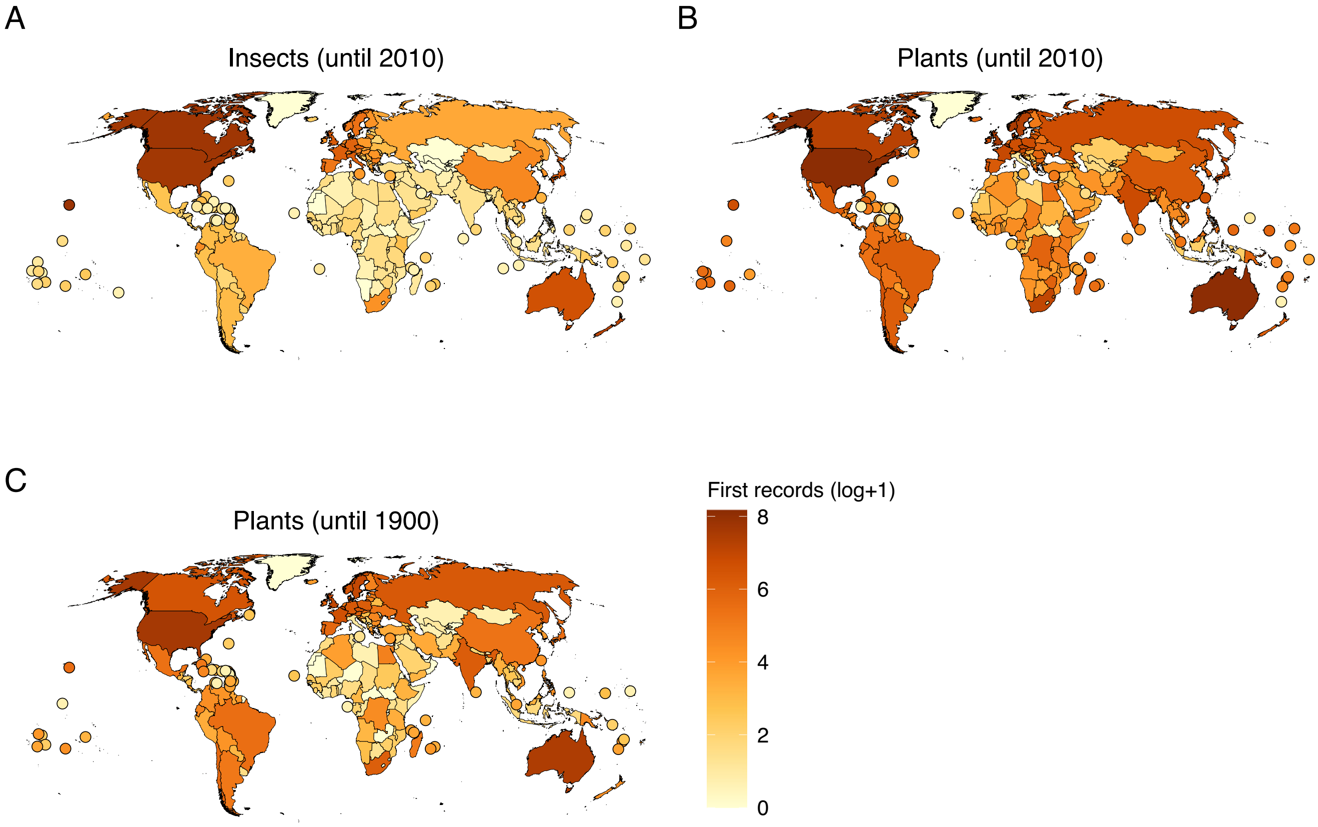

**Fig. 1.** Number of first records (log-transformed) of nonnative insects (*A*) and plants (*B* and *C*) per country.

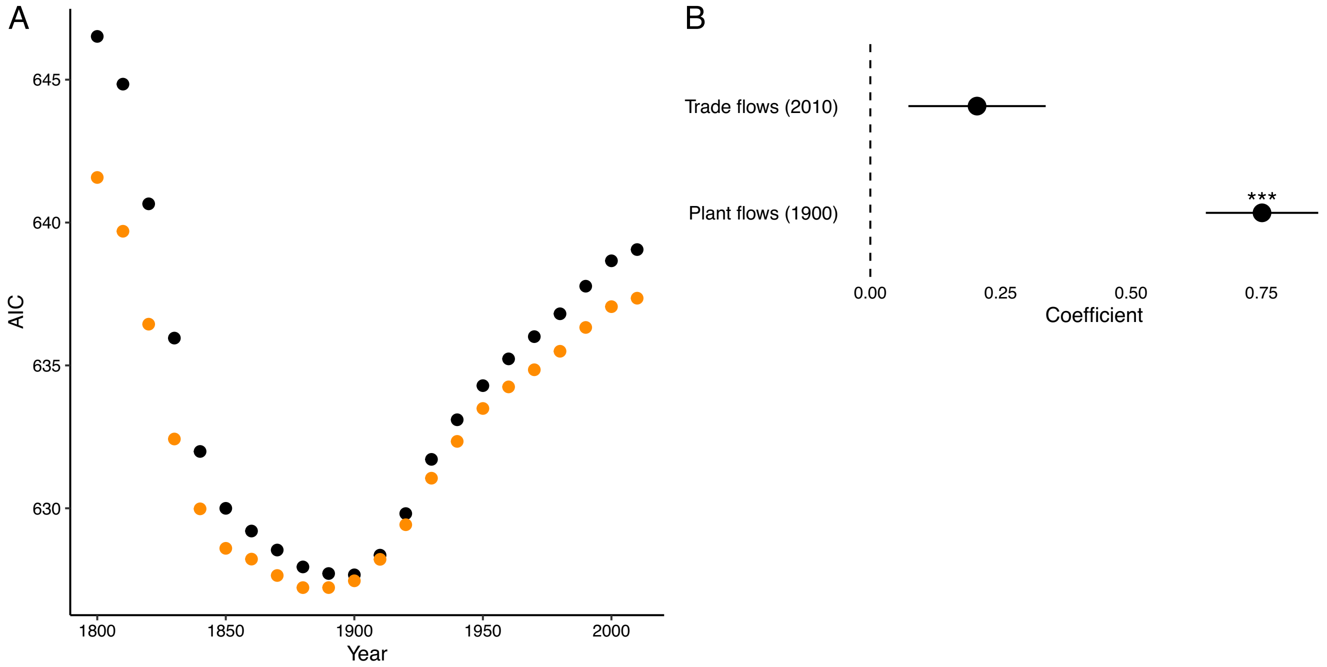

**Fig. 2.** (*A*) Fit of the GLMMs of current nonnative insect flows between each region as a function of nonnative plant flows (based on cumulative values up to the year shown on the *x* axis) as a predictor (black) and including general trade flows of 2010 as a second predictor (orange). AIC values were averaged using a 30-y sliding window for visualization. (*B*) Estimates of trade flows (2010) and nonnative plant flows (1900) as predictors for current (2010) nonnative insect flows in GLMM. Explanatory variables were standardized to a mean of 0 and a variance of 1 to allow coefficient comparison.

potentially confounding effect of trade flows on insect invasions. We found a similar time lag between plant and insect flows when trade flows of plant products and general trade flows of 1900 and 2010 were included in the models (Fig. 2*A* and *SI Appendix*, Figs. S3*B* and S4*A*). Finally, nonnative plant flows were a better predictor of nonnative insect invasions than general trade flows and plant product trade flows (Fig. 2*B* and *SI Appendix*, Fig. S4*B*).

**Insect Invasion Debt.** We estimated insect invasion debt in each biogeographic region based on the observed time lag between plant and insect flows. We used the coefficient of the best linear model (i.e., with nonnative plant flows of 1900) to predict the expected nonnative insects flows between regions given the total flows of plants observed until 2010. We then computed the insect invasion debt as the difference between the expected flows of nonnative insects and the observed flows (Fig. 3*B*). We found a global debt of 3,442 insect introductions across all biogeographic regions (Fig. 3*B*). So far, a total of 9,952 insect introductions (7,592 species) have been recorded from the eight regions (Fig. 3*A*). The number of known insect invasions can therefore be expected to increase by 35% worldwide in the near future. The invasion debt was greatest in the Afrotropics (869 species), the Neotropics (809 species), and Indomalaya (776 species). Few nonnative insects have currently been recorded in these regions. Our results suggest that the number of nonnative insect species is expected to increase almost 10-fold in the Afrotropics and the Neotropics, and about 20-fold in Indomalaya over the coming years (Fig. 3). The smallest debt was found for Oceania (the estimated debt is null for this region) and the Nearctic (16 species), which have already received many nonnative insect species. The debt was relatively high in the European Palearctic (417 species) and Australasia (317 species) despite the fact that many nonnative insects have already been introduced in these regions (Fig. 3). Finally, the Neotropics are expected to be the greatest source of insect invasions in the future (904 exported species), followed by the European Palearctic (732 species, Fig. 3*B*).

## Discussion

Current interregional nonnative insect flows are best explained by nonnative plant flows through 1900 compared to more recent plant flows, indicating that plant introductions precede invasions of nonnative insect species that use these plants as host (24, 25, 36). There are several potential explanations for the extensive time lag. First, nonnative host plants must increase in abundance and start spreading, which can be protracted, before nonnative insects are able to establish and spread in turn. In addition, repeated introductions of a given plant species are probably necessary before an insect species that is sometimes transported on this plant species (14–16, 19) reaches a sufficient propagule pressure to establish a self-sustaining population. Since only some, but not all, plants are transporting insects, a high number of plant introduction events may be necessary before an insect species can establish, which might also contribute to the extensive time lag. Furthermore, our analyses included all nonnative insect species belonging to various feeding groups, and only the spread of herbivores (25) and pollinators (26, 27) may be directly facilitated by plants. However, following the establishment of herbivores and pollinators, invasions of predators and parasitoids may be indirectly facilitated. This “trickle up” effect of trophic influences may also contribute to time lags between plant and insect invasions.

The observed time lag could also partly be explained by the fact that establishment of new insect species may be recorded later than for plants because plants tend to be better sampled than insects. Indeed, insects are highly underrepresented in biodiversity databases, while plants are usually well sampled (37). Established insects might stay at low abundance for several decades, a phenomenon described as “sleeper populations” (38), and might therefore remain undetected for an extended period (38, 39). For example, MacLaughlin et al. (40) reported a median delay between establishment and discovery of about 80 y for plant-feeding Hemiptera which are small and easily overlook

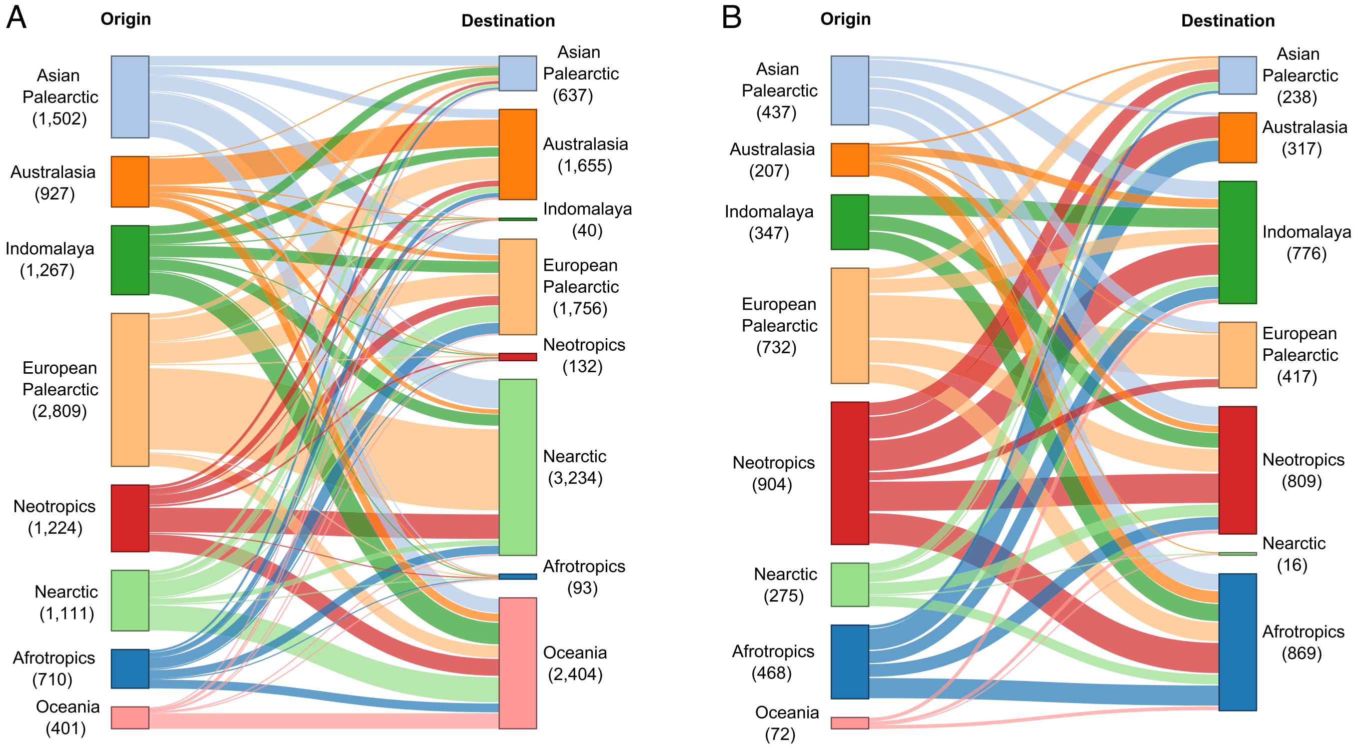

**Fig. 3.** Observed flows of nonnative insects through 2010 (*A*) and estimated insect invasion debt (*B*). The number of species is given in parenthesis for each origin and recipient region.

that the actual time lag between plant and insect establishment may be shorter than we observed. Nonnative plants are also often introduced intentionally for horticultural and ornamental purposes (41, 42), while insects are mostly transported accidentally, as contaminants or stowaways (43, 44), and might therefore be more difficult to detect as their presence may be less expected. This again suggests that we may overestimate the true time lag between plant and insect invasions.

Using this observed time lag between plant and insect establishment, we estimated the insect invasion debt in each biogeographic region. We found a substantial debt of 3,442 region-level insect introductions worldwide, suggesting a potential increase of 35% of new reports of insect invasions over the coming years. While insect invasions have so far mainly been recorded in the European Palearctic, Nearctic, Australasia, and Oceania, the most important debts were found for the Afrotropics (869 species), the Neotropics (809 species), and Indomalaya (776 species). The number of discoveries of insect introductions is expected to increase almost 10-fold in the Afrotropics and the Neotropics, and 20-fold in Indomalaya. This is of particular concern given that the number of plant invasions in emerging economies is also predicted to continue accelerating in the coming years (45), which could further promote future insect invasions. It should however be emphasized that the nonnative insect fauna already established in these regions is largely underestimated as these regions tend to be poorly sampled (33). For instance, a high proportion of insect species intercepted by biosecurity services at ports of entry and arriving from Africa and South America are not yet recorded as established in these regions (46). The insect invasion debt may therefore be partly attributed to species that are already established but not recorded, and partly to future species establishments. A previous study also predicted an increase of arthropod invasions by 2050 in Africa, South America, and Tropical Asia (47), yet at a slower rate than what our results suggest. However, this previous study used records of historical arthropod invasions to anticipate future trajectories, and might therefore underestimate future invasions due to the incompleteness of nonnative arthropod records in these regions. It should also be noted that our estimate of insect invasion debt is based on the number of plant introductions, but other factors such as biosecurity measures and national policies on imports also influence insect invasions. Moreover, we assume that the slope of the relationship between plant and insect invasions is constant over time. Our analysis therefore provides an assessment of insect invasion debt per region, but further research is required to precisely estimate invasion risk as well as the insect taxa most likely to be introduced in the different regions.

Although a high number of insects have already established in the European Palearctic and Australasia, we found an important debt in these regions. Most future insect introductions in the European Palearctic are expected to be intracontinental, which is consistent with the many intracontinental plant introductions observed in this region (*SI Appendix*, Fig. S2) (48). The debt for Oceania was null, and very small for the Nearctic, as many insects have already established and have been recorded in these regions. But this does not indicate that insect species will no longer be introduced in these regions, since importations of commodities and the introduction of new nonnative plants in the future are likely to promote new insect invasions, if the potential source pool of emergent nonnative species is not depleted. Previous research has indicated that this should not be the case for nonnative insects in North America (47), while plant invasions may saturate in this region (47), suggesting that, beyond the estimated invasion debt, many new nonnative insects may fail to establish.

Many insects from the European Palearctic have been introduced to the Nearctic. In comparison, fewer insects have been introduced in the opposite direction. Mattson et al. (49) argued that there may be fewer niches for invasive insects in Europe due to the lower host plant diversity in this region caused by the Pleistocene/Holocene glaciations. Although this in dispute (20), it could explain this asymmetry in insect invasions. However, a similar asymmetry can be observed for nonnative plants (*SI Appendix*, Fig. S2), with more introductions from the European Palearctic to the Nearctic than in the opposite direction, possibly due to European colonialism (29). Our results therefore suggest that the asymmetry in insect invasions might be driven by the asymmetry in plant invasions.

Our analysis highlights the role of plant invasions in driving insect invasions. Interestingly, we found that general trade flows and plant-related trade flows did not explain additional variation in insect invasions once nonnative plant flows were included in the model. This shows that although global trade is a strong driver of biological invasions (30–32), it cannot explain all geographical variations in insect invasion frequencies and suggests that geographical variation in habitat invasibility plays an important role (21). Previous invasions might be important in determining invasion dynamics.

A potential limitation of our approach is that it does not account for "bridgehead effects." The bridgehead effect is a phenomenon of secondary spread where nonnative insects arrive to a new region from a previously invaded region, rather than directly from the native range (50). This phenomenon has a strong impact on the spread of nonnative insects (50–53). If a high proportion of species are established in several continents, bridgehead effects tend to be more frequent which can distort our global view of nonnative species flows (54). But in this analysis, the majority of nonnative insect and plant species were recorded in only one biogeographic region (*SI Appendix*, Fig. S5), which suggests that recorded nonnative species flows largely reflect actual introduction routes. Moreover, it appears that insects follow similar invasion patterns as the plants with which they have coevolved within their native range, regardless if they were introduced directly from their native range or from a bridgehead region. Our aim was not to predict the exact future spread routes, but rather to anticipate future flows of nonnative insects from donor to recipient regions.

Our analysis revealed an important time lag between plant and insect invasions at a global scale. Further research could investigate this time lag at the scale of individual insect species for which the host plant species are known. Our data did not include georeferenced records and therefore we cannot confirm that nonnative insects and plants are actually co-occurring, but previous studies suggest that it is very likely to be the case (25–27). Future studies might also assess the effect of nonnative plants which have been planted for agriculture, forestry, or horticulture but have not managed to establish populations in the wild yet. These species are not represented in our data, but may also contribute to the spread of nonnative insects specializing on those plants (24, 55). Similarly, many invasive insects may be associated with ornamental plants used in urban landscapes (56).

Time lags between plant and insect invasions may vary among taxonomic groups, feeding guilds, and also among regions. Understanding what drives these time lags would inform efforts to better predict and manage future insect invasions. Future research could also investigate the effect of nonnative plant abundance, rather than just species richness, on nonnative insect establishment. It is likely that the probability of insect establishment increases as nonnative plants spread and increase in abundance in a given region.

Overall, we have shown that global insect invasions lag behind plant invasions. Given patterns of recent plant introductions, insect invasions are expected to rise in tropical regions, which could strongly impact local economies and threaten biodiversity. Our study highlights that nonnative plants can have indirect environmental consequences by facilitating insect invasions. Including the risk of insect introduction in invasion risk screening tools might therefore be necessary when assessing the potential impact of nonnative plants. Targeting plant imports (57) and limiting the establishment and spread of nonnative plants might also help to reduce invasions of insect in the future.

## Materials and Methods

**Nonnative Species Flows.** Records of insect establishments and plant naturalizations were compiled for each of the eight world biogeographic regions (Asian Palearctic, European Palearctic, Afrotropics, Neotropics, Indomalaya, Nearctic, Australasia, and Oceania) using a system modified from Wallace's designation and snapped to country borders (*SI Appendix*, Fig. S6). We extracted data of nonnative insect and vascular plant first record dates per country or region from online datasets (2, 58–61). We also used information on insect and plant nonnative range from the Global Register of Introduced and Invasive Species (GRIIS) (62) together with dated occurrences from the Global Biodiversity Information Facility (GBIF; https://www.gbif.org) (63, 64) to extract additional nonnative species first records. We cleaned species synonyms using the R package *taxizedb* (65) based on the GBIF taxonomic backbone. We then merged these datasets of nonnative species first records. When the different data sources indicated different first records dates for a given species in a given country, we used the earliest date. It resulted in 16,486 establishment records of 7,592 nonnative insect species and 54,020 naturalization records of 10,560 nonnative plant species made prior to 2010. We did not include data from the most recent years (2011 to present) as they are incomplete because of the delay in the publication of new nonnative species records (2, 66). Most of the extracted first records were at the country level. As we analyzed species flows at the region level, we only kept the first record date per biogeographic region for each nonnative insect and plant species.

Data on insect native ranges were sourced from Turner et al. (60). Data on plant native ranges were extracted from the World Checklist of Selected Plant Families (67). We thus obtained information on native ranges of 90% of nonnative insect and 85% of nonnative plant species. We then used the nonnative species first records per biogeographic region and their native ranges to reconstruct flows of nonnative species between pairs of origin and recipient region. Flows were quantified as the number of species introduced from one region to another region. When a species was native to more than one region, we weighted the flows of this species by the number of regions where it is native from.

**Trade Data.** Data on general trade flows were extracted from the TRADHIST database (http://www.cepii.fr/CEPII/en/bdd_modele/bdd_modele_item.asp?id=32). TRADHIST gathers more than 1.9 million bilateral trade flows between 319 administrative entities from 1827 to 2014. It includes data from various sources such as government publications, books, and academic articles. We computed general trade flows between biogeographic regions as the sum of trade values between countries of each region pair for the years 1900 and 2010. Data on plant product trade flows for the year 2010 were extracted from the United Nations Comtrade database (https://comtradeplus.un.org) using the R package *comtradr* (68). We followed the same traded commodity classification as Fenn-Moltu et al. (15) for plant products.

**Modeling.** Statistical models were used to test the role of various candidate predictors for their ability to explain current (2010) insect flows among biogeographical regions. We first tested the predictive power of historical and current nonnative plant flows on nonnative insect flows, using generalized linear mixed models (GLMMs) with a zero truncated negative binomial distribution. Current insect flows were computed as cumulative species invasions between each of the 64 pairs of biogeographic regions recorded for years prior to 2010. Plant flows were calculated for each of the same pairs of regions but as cumulative naturalizations in decadal steps, from 1800 to 2010. We did not investigate the association between individual plant and insect species, but we tested the correlation between the number of insect and plant species that were moved from a donor to a recipient region.

We used an iterative approach: We first fitted a model of current insect flows (i.e., cumulative flows of insects until 2010) as a function of nonnative plant flows until the year 1800 (i.e., cumulative flows of plants until 1800; log-transformed to normalize their distribution). We then fitted separate models for each subsequent decade starting with 1810 and ending with 2010, using the plant flows until each decade as the predictive variable (log-transformed), while keeping the same response variable across all the models (i.e., insect flows until 2010). We did not test plant flows prior to 1800 because few nonnative plants have been recorded before that date (2). This resulted in 22 GLMMs predicting current insect flows as a function of plant flows cutoff at each decade (from 1800 to 2010). We also included origin and destination of the nonnative species flows as random effects on the intercept for each model. The models were evaluated using AIC scores.

For each decade $x$ (with $1800 \leq x \leq 2010$), the model can be summarized as:

Insect flows (through 2010) ~ Plant flows (through year $x$) + (1|origin) + (1|destination)

To test for the predictive power of lagged and current trade flows on nonnative insect flows, we then repeated the same modeling approach, but added general trade flows (log-transformed) as a predictor in the models. We tested the effect of general trade flows of 1900 and 2010. As trade data were not available for all regions for 1900, 13 pairs of origin–destination regions were removed from the models with trade flows of 1900. To allow comparison between the different modeling approaches, we also reran the previous models (i.e., without trade flows and with trade flows of 2010) after removing the same 13 pairs of biogeographic regions from the models. As insects are mostly transported on plant products (14, 15), we also tested the effect of plant product trade flows of 2010 on insect invasions, using the same modeling approach. We did not test the effect of lagged plant product trade flows as detailed data on traded commodities are only available for the recent years.

Another important factor influencing observed patterns of invasions is sampling effort (31, 69). To control for unequal sampling between regions, we repeated the same modeling approach but included, as an additional predictor variable, the number of all native insect occurrences per square kilometer as a proxy for sampling effort (*SI Appendix, Materials and Methods*).

**Estimating Insect Invasion Debt.** We used the coefficient of the best model (i.e., with nonnative plant flows until the year 1900, Fig. 2*A*) to predict the expected flows of nonnative insects given the total flows of nonnative plants observed until 2010. We then subtracted the current nonnative insect flow (i.e., the total flow of nonnative insect species discovered up to 2010) from the predicted flow of nonnative insects, and thereby obtained the insect invasion debt. We therefore used a single predictor, current nonnative plant flows, to estimate the insect invasion debt. We also assume that the slope of the relationship between plant and insect flows is constant over time.

All analyses were performed with R 4.1.2. (70).

**Data, Materials, and Software Availability.** Previously published data were used for this work (2, 46, 59–63, 67). Code used to perform analysis and generate figures is available at: https://doi.org/10.5281/zenodo.7945261 (71).

**ACKNOWLEDGMENTS.** This work was supported by the Swiss canton Vaud, the Swiss NSF (SNSF grant 310030_192619), and the Fondation Sandoz-Monique de Meuron pour la relève universitaire. Additional support was from Grant EVA4.0, No. CZ.02.1.01/0.0/0.0/16_019/0000803 financed by Czech Operational Programme Science, Research and Education, and Grant 21-IG-11132762-241 financed by US Forest Service International Programs.

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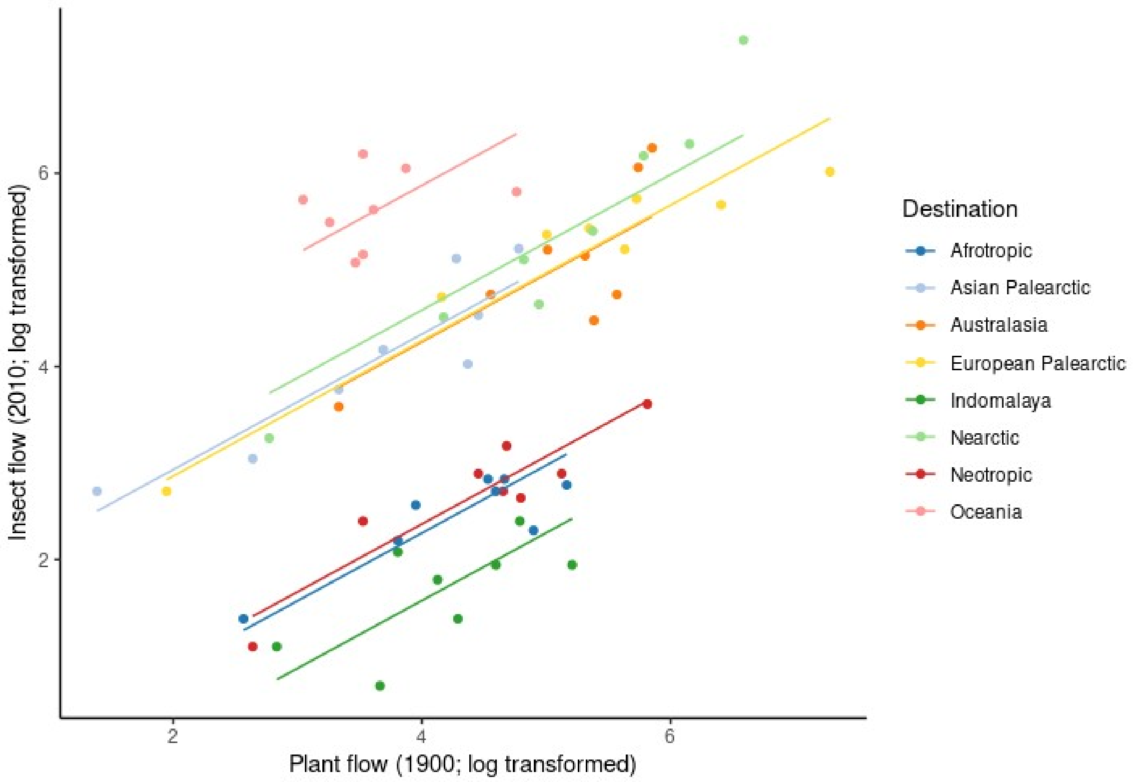
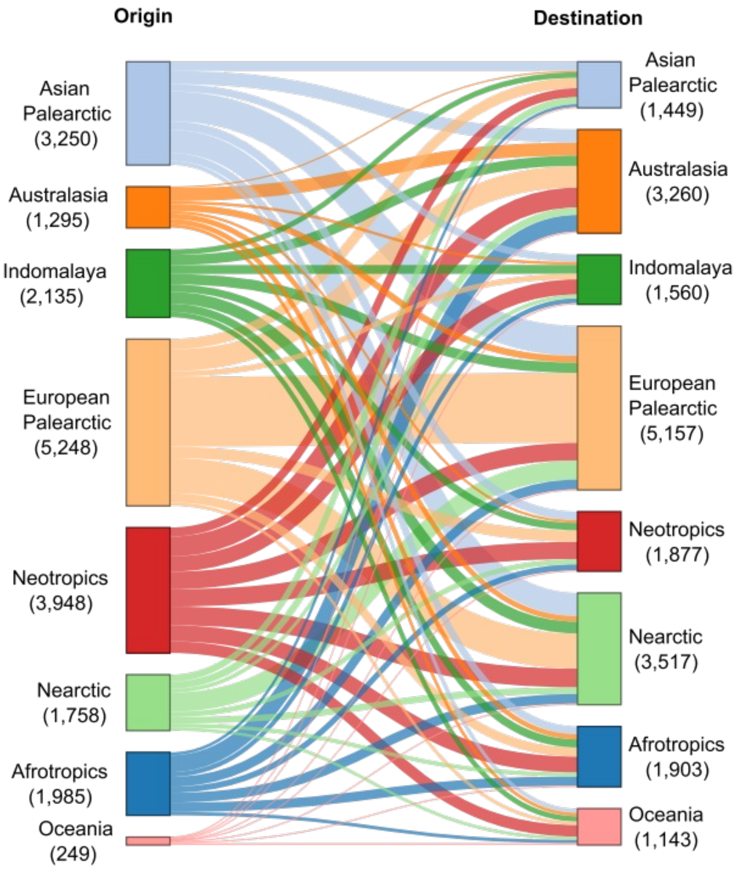
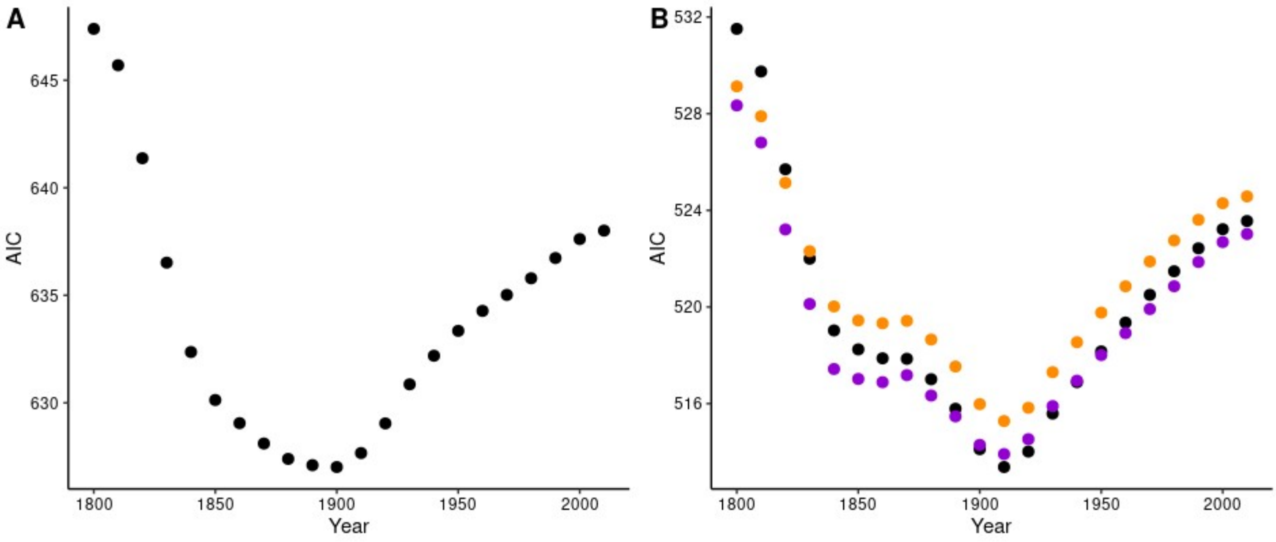
## Supplementary information



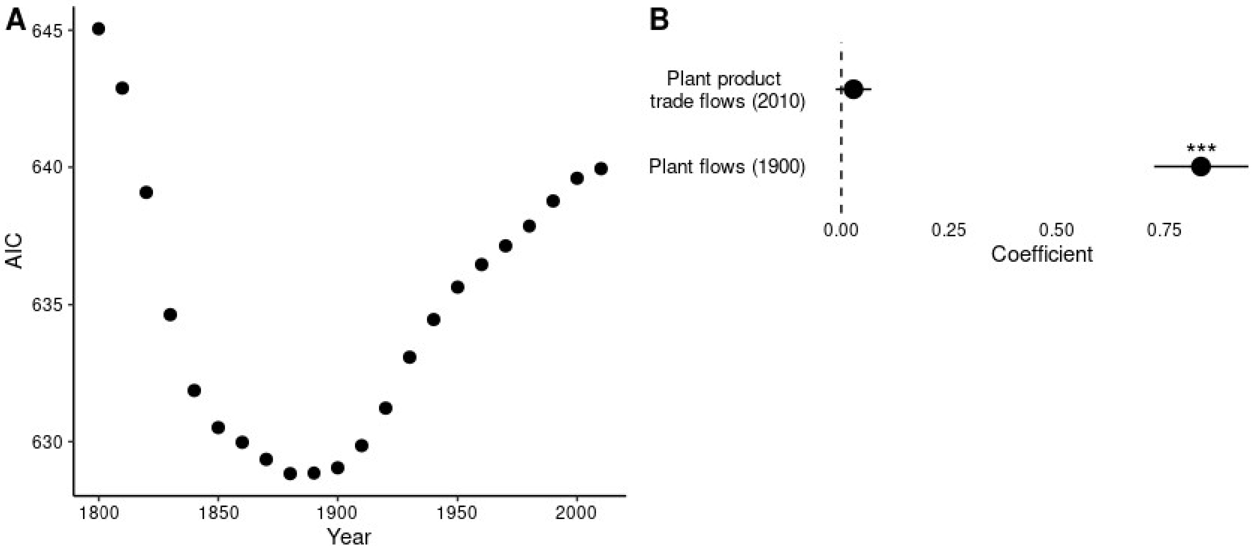
**Supplementary figure 1:** Correlation between insect flows (2010) and plant flows (1900) including the destination of the flow as random effect on the intercept.



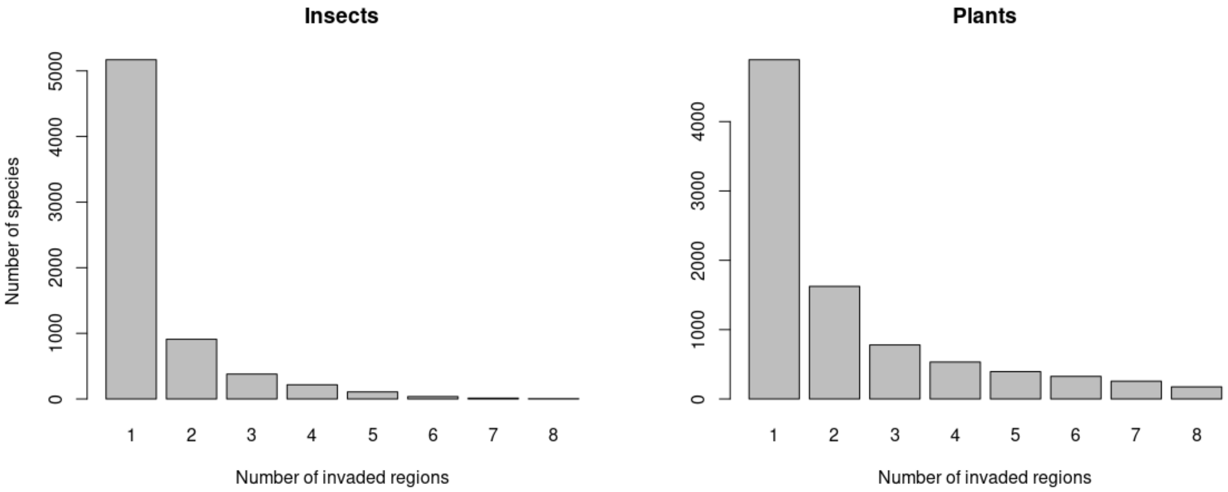
**Supplementary figure 2:** Observed flows of non-native plants through 2010



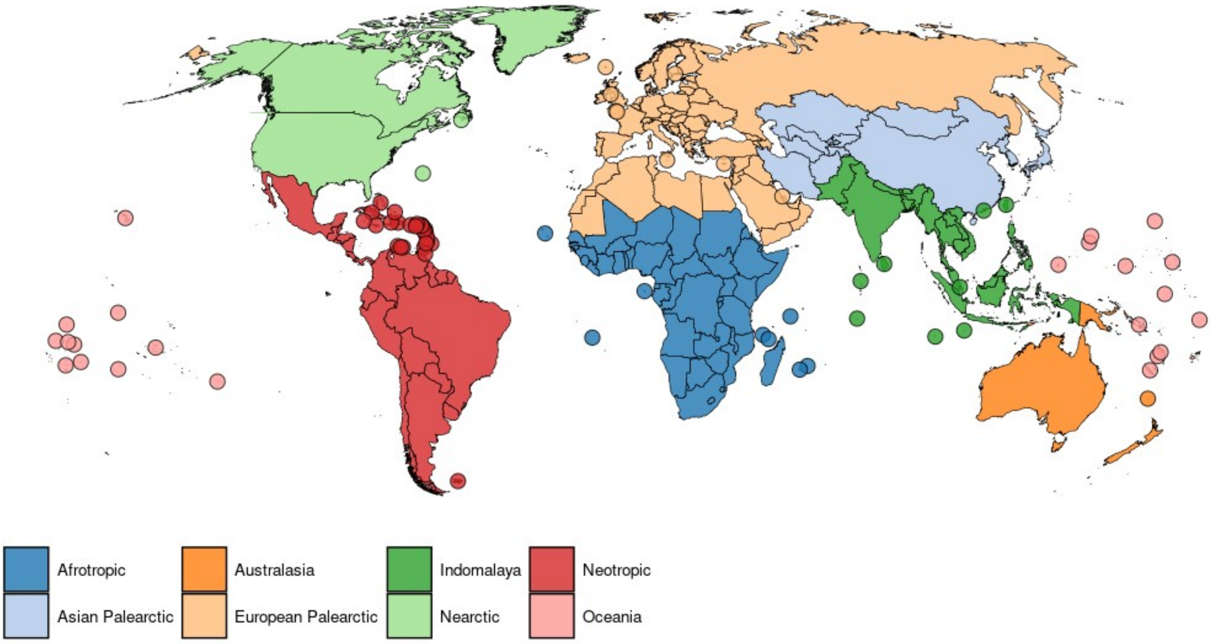
**Supplementary figure 3:** A) Fit of the GLMMs of current non-native insect flows between each region as a function of non-native plant flows (based on cumulative values up to the year shown on the x axis) and sampling effort as predictors. B) Fit of the GLMMs of current non-native insect flows between each region as a function of non-native plant flows (based on cumulative values up to the year shown on the x axis) as a predictor (black), and including general trade flows of 1900 (purple) and 2010 (orange) as a second predictor. To allow comparison between the three model groups, the number of flows in all the models was restricted to pairs of origin-destination regions for which trade flow data were available for both 1900 and 2010. (A, B) AIC values were averaged using a 30-year sliding window for visualisation.



**Supplementary figure 4:** A) Fit of the GLMMs of current non-native insect flows between each region as a function of non-native plant flows (based on cumulative values up to the year shown on the x axis) and plant product trade flows of 2010 as predictors. AIC values were averaged using a 30-year sliding window for visualisation. B) Estimates of plant product trade flows (2010) and non-native plant flows (1900) as predictors for current (2010) non-native insect flows in GLMM model. Explanatory variables were standardized to a mean of 0 and a variance of 1 to allow coefficient comparison.



**Supplementary figure 5:** Number of non-native insect and plant species recorded in one to eight biogeographic regions. 76% of the non-native insect species were recorded in only 1 region, 54% for the plants.



**Supplementary figure 6:** Biogeographic regions

## Supplementary materials and methods

Sampling effort proxy:

We used the number of native insect occurrences per square kilometer as a proxy for sampling effort for each biogeographic region. We extracted insect occurrences from GBIF (1). We removed the occurrences of non-native insect species to consider only native insect occurrences. As some areas are highly unsuitable for insects, they could bias our proxy for sampling effort as these areas contain very few insect occurrences, but not because of a lack of observation but rather because very few insect species live there. To address this bias, we excluded the highly unsuitable areas to compute the proxy for sampling effort. We used the Köppen-Geiger climate classification (2) at 0.5° resolution and excluded the areas falling in BWh (Arid, desert, hot), BWk (Arid, desert, cold), ET (Polar, tundra) and EF (Polar, frost) climate categories. For each region, sampling effort was then computed as the number of native insect occurrences divided by the size of the region, excluding the unsuitable part of it.

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# General discussion

## Changing dynamics of invasions over the past centuries

We showed in **chapter 1** that insect and plant invasions did not increase continuously over the past centuries, but fluctuated, following variations in global trade openness, which confirms findings from a previous study on ants (Bertelsmeier et al., 2017). A recent study also found that the rate of Hemiptera invasions in Hawaii, Japan, New Zealand and North America fluctuated since 1850 and seemed to follow the dynamics of the two waves of globalization (Liebhold et al., 2024). There were however important difference between world regions (Liebhold et al., 2024). Future studies should therefore investigate the dynamics of invasions at a finer spatial scale to understand how a region's geopolitical history and involvement in global exchanges influenced non-native species introduction rate over the past centuries. Further studies are also required to compare invasion dynamics between insect groups, but also with other accidentally introduced taxa.

We investigated in greater details the dynamics of insect invasions over the past centuries in **chapter 2**. We found that the spatial dynamics of ant invasions differed between the two waves of globalization. While ant invasions before 1960 were centered on countries belonging to colonial empires, the fall of colonial empires led to a more global spread of species in the recent decades with no more effect of former colonial ties. Some recent studies also investigated the effect of colonial empires on non-native species richness. Capinha et al. (2023) found no effect of European colonial empires on the spread of various taxonomic groups, including insects, between 1950 and 2019, which is consistent with our finding that colonial ties did not influence invasion dynamics in recent decades. This study, however, did not investigate the effect of empires prior to 1950 (Capinha et al., 2023).

Another study on invasions of vascular plants, insects, birds and mammals between 1880 and 2005 found no link between colonial ties and species spread for all taxa (Juozaitienė et al., 2023). This study used relation event modeling, which allows to investigate time-varying effect of variables, yet no effect of colonial ties was found even during the 19th and beginning of the 20th centuries. This study used data from the Alien Species First Records database (Seebens, 2023; Seebens et al., 2017), which combines first records for thousands of non-native species, many of which might not be very well studied, in particular for taxa like insects. Records for those species are therefore likely to be incomplete, particularly for ancient invasion events, unlike records in our study restricted to a few well-known ant species for which we have good spread data over time (**chapter 2**). This may explain why, contrary to our results, Juozaitienė et al. (2023) found no effect of colonial empires on insect invasions in the past centuries.

So far, the effect of colonial empires on insect invasions has only been shown for ants (**chapter 2**), further studies on other insect taxa are therefore required. As many insect taxa share similar pathway of introduction as ants, such as the transport of live plants (Fenn-Moltu et al., 2022; Liebhold et al., 2012), it is likely that they also benefited from global exchanges in colonial times to spread to new regions. Moreover, it was shown that European empires influenced the spread of plants (Lenzner et al., 2022; Yang et al., 2021), suggesting that it also shaped the spread of insects as there is a strong link between plant and insect invasions (**chapter 4, appendix 2**). For example, colonization has promoted the introduction of European plants in many regions (Lenzner et al., 2018). These plant introductions during colonial times may be responsible for the asymmetric flows of insects observed between Europe, North America and Australia, with Europe having sent more insect species to these regions than it has received from them (Isitt et al., 2024; **chapter 4**). Future research should therefore consider European colonization and associated plant introductions as potential drivers of observed insect flows between regions (Isitt et al., 2024).

Overall, our knowledge on the dynamics of insect invasions over the past centuries remains limited. In particular, the lack of comprehensive data on ancient invasions hinders our ability to study the early spread of insects since the rise of colonial empires. Improving datasets of non-native species first records is therefore necessary to explore insect dispersal over the past centuries.

## Future insect invasions

We found an important time lag between plant and insect invasions, as the best predictor of current insect flows was plant flows dating back to 1900 (**chapter 4**). A recent study investigating insect invasion rate over the past centuries found a comparable time lag of 80 years between plant and herbivore invasions (Mally et al., 2024). Future studies could investigate in greater details the lag between plant and insect invasions, as it likely to varies between different pairs of insect and host plant species as well as between regions.

This time lag between plant and insect invasions yields an important invasion debt, as some regions have received many non-native plants but have not yet observed the insects associated with them (**chapter 4**). This lag was particularly important in tropical Asia and Africa, suggesting that the rate of insect invasions is likely to increase in those regions in the near future. The ongoing spread of non-native plants in the wild, which is expected to accelerate in the future under climate change

(Seebens et al., 2015), and their widespread use in horticulture, forestry and agriculture, will likely continue to create new niches for non-native insects, further facilitating their spread. Moreover, the increasing frequency of bridgehead effect over time, due to the positive feedback between species transport and establishment (**chapter 3**; Bertelsmeier et al., 2018), will increase the movement of insect propagules, also contributing to the acceleration of non-native insect dispersal. The future increase in insect invasion rate may however be limited to herbivores, as invasion rates of non-herbivorous insects have stagnated since around 1900, possibly due to the depletion of source species pool, effects of prevention programs or changes in invasion pathways (Mally et al., 2024).

Climate change will also be an important factor of future invasions, particularly for ectothermic taxa like insects (**appendix 1**; Hulme, 2017). Warming temperature will allow the establishment of insect species in regions that were previously not suitable for them. Climate change will also reshape trade networks which will influence insect dispersal dynamics. For example, the loss of sea ice will open new shipping routes through the Arctic, modifying global trade flows (Bekkers et al., 2018). Arctic shipping routes will also reduce sailing distance and travel time, thereby increasing species survival during transport. Overall, our results indicate that, in the absence of effective mitigation measures, the rate of insect invasions is likely to keep increasing in the future (Seebens et al., 2021).

## Analyzing species invasion dynamics: challenges and future directions

The recently adopted Kunming-Montreal Global Biodiversity Framework of the Convention on Biological Diversity calls for a reduction of at least 50% of the rate of non-native species introductions by 2030 (McGeoch et al., 2023). This objective requires an accurate quantification of the rate of invasion, which is currently not the case (McGeoch et al., 2023). Studies generally use observed rate of non-native species first records as an approximation for invasion rate (Seebens et al., 2017). However, these observed trends of invasions are misleading due to temporal variations in sampling effort (**chapter 1**; Mangiante et al., 2018; McGeoch et al., 2023; Solow and Costello, 2004). It is urgent to address this widely underestimated problem in order to inform the Global Biodiversity Framework and decision-making on non-native species in the near future.

As data on sampling effort are not readily available, analytical methods have been developed to bridge the gaps in data availability and estimate underlying rates of introduction from discovery records. Solow and Costello (2004) described a statistical model of discovery records that disentangles the introduction and discovery processes and estimates observation probability, which is allowed to change over time.

Another possible approach is to include a proxy for sampling effort in the model, for example using the native species discovery rate (Belmaker et al., 2009; MacLachlan et al., 2021), native species occurrences from the Global Biodiversity Information Facility (GBIF.org, 2025; **chapter 1**), or number of publications on non-native species over time. A recent study compared different modeling approaches in their ability to estimate introduction rate based on discovery records (Buba et al., 2024). They found that, in scenarios where species detection probability is high (i.e., with an annual detection probability of more than 0.5), a naive model that fits a non-linear curve to observed first record data provides good estimates of introduction rate. However, in scenarios with imperfect detection (e.g., with species difficult to detect, such as insects, or in poorly sampled regions), disentangling the introduction and discovery processes improves estimates, in particular when a proxy for sampling effort is included in the model (Buba et al., 2024). But further evaluations of these models are required as, so far, their performance has only been measured based on scenarios assuming an exponentially increasing introduction rate (Buba et al., 2024), while real-life scenarios are more complex and might involve non-monotonic trend in introduction rate (e.g., **chapter 1**; Bertelsmeier et al., 2017; MacLachlan et al., 2021). Overall, when high species detection probability cannot be assumed, it is recommended to incorporate information on sampling effort to improve model estimates of introduction rate (Buba et al., 2024; **chapter 1**), highlighting the need to develop, collect and standardize such data on sampling effort (McGeoch et al., 2023). New modeling methods are also needed to better capture the complex dynamics of non-native species introduction and discovery rates in real-life scenarios.

A better sampling of non-native species and an increasing access to the most up-to-date data are also required to improve our knowledge on non-native species distribution, better understand the dynamics of invasions and facilitate their management (van Rees et al., 2022). Significant progress has been made to standardize and share data on non-native species distribution, such as the SInAS workflow (Seebens et al., 2020), the Global Invasive and Alien Traits And Records dataset (Saffer et al., 2024) or the Global Register of Introduced and Invasive Species (Pagad et al., 2022). But these data remain incomplete, particularly for certain taxonomic groups such as invertebrates, and highly biased towards certain regions (Roy et al., 2024). It is estimated that 20% of established Hemiptera species remain undiscovered in Eurasia, and around 40% in the Neotropics and the Afrotropics (MacLachlan et al., 2021). Similarly, the majority of non-native insect species intercepted by biosecurity services and arriving from South America and Africa are not yet recorded as introduced in those regions (Nahrung and Carnegie, 2021), suggesting that non-native species checklists are highly incomplete for these parts of the world.

Interception data also constitute important resources to investigate the accidental spread of species such as insects (**chapter 3**). They provide a proxy for propagule pressure which is otherwise not possible to measure for taxa transported accidentally (Turner et al., 2021), and they allow to identify bridgehead regions and assess the importance of secondary spread in species dispersal (**chapter 3**; Bertelsmeier et al., 2018; Worm et al., 2024). A challenge for invasion science is to make interception data more widely available (Ricciardi et al., 2021) as they are so far limited to certain regions (**appendix 3**). These data also contain biases that need to be accounted for before they can be used to predict invasions (Turner et al., 2024). For example, plant-feeding insects are generally overrepresented in interception data, likely because of greater search effort for these insect groups during inspections (Turner et al., 2024).

Ultimately, increasing data availability on non-native species spread and filling important knowledge gaps on invasions, in particular in developing countries, will be key to improve our understanding of invasion dynamics and inform preventive and management actions (Roy et al., 2024).

More precise knowledge on the drivers of invasions is also needed. For example, information on the precise type of commodity that serves as a pathway of introduction for a particular insect species is necessary to better understand invasion flows and identify potential source regions for future invasions (Ollier and Bertelsmeier, 2022). Integrating more precise socioeconomic predictors might improve models of non-native species richness, which currently often have limited predictive accuracy (Capinha et al., 2018).

**Chapter 4** also highlighted the important role of non-native plant flows in driving insect invasions (see also **appendix 2**). This suggests that future studies on the spread of non-native insects should include non-native plants in their analysis. Methods such as relational event models could for example be used to investigate the interdependence in spread between plants and herbivorous insects, and between herbivorous insects and their associated predators and parasitoids (Juozaitienė et al., 2023). These models can describe the temporal sequences of invasion events and deal with time-varying variables and time-varying effects, unlike classical modeling tools that usually simplify the dynamic structure or the complex interactions of drivers of invasions (Juozaitienė et al., 2023).

The relationship between invasions and their drivers can also be blurred by bridgehead effect which distorts our view of species spread (Bertelsmeier and Ollier, 2021). As secondary introduction are becoming more frequent over the years (**chapter 3**), accounting for bridgehead regions will become necessary to improve species spread models and understand how species move around the globe (Mwebaze et al., 2023).

Understanding the dynamics of invasions, and in particular the role of human-mediated dispersal, is key to better predict and prevent future invasions. Prevention remains the most cost-effective way for limiting the impact of biological invasions, compared with the resources needed to manage impacts once invasive species are established and widespread (Roy et al., 2024). Management of introduction pathways, such as effective import controls and enhanced border biosecurity and quarantine services, is an important step to reduce invasion rate in the future (Hulme, 2021; Roy et al., 2024). Our results also highlight that targeting plant imports and limiting the spread of undesired non-native plants would not only limit the impact of non-native plants themselves, but also reduce the number of non-native insect introductions and establishments (**chapter 4; appendix 2**).

When preventing introduction is not possible, early detection is necessary in order to enable rapid response to eradicate or contain populations of invasive species before they spread. National surveillance strategies are therefore required, for example by engaging the general public. Citizen science platforms are a valuable source of information for early detection of non-native species (González-Moreno et al., 2025). They have for example supported the early detection of the Asian brown marmorated stink bug, *Halyomorpha halys*, in Southern Europe (Maistrello et al., 2016) and New Zealand (Payne et al., 2023).

Limiting the rate of invasions in the future will also require more cooperation between countries. In particular, cooperative biosecurity strategies are needed to develop programs that are more efficient than those where countries act in isolation (Ricciardi et al., 2021). Certain countries have been identified as central hubs for non-native species before subsequent dispersal to other regions (**appendix 3**; Capinha et al., 2023). Cooperation among countries to prevent species from establishing in these bridgehead regions, or to control or eradicate species already established there, could have cascading effects on the spread network of non-native species, thus reducing biological invasions (Ricciardi et al., 2021). With the increasing frequency of secondary introductions (**chapter 3**), ensuring that species record and interception data are more widely and quickly available and shared between countries is necessary to prevent regions that have received an invasive species from serving as a source for subsequent introductions. Such data sharing would greatly improve biosecurity programs and reduce risks of future invasions (Ricciardi et al., 2021). The remarkable international sharing of spatiotemporal spread data during the COVID-19 pandemic should serve as an example for tracking other invasive organisms (Bertelsmeier and Ollier, 2020).

Overall, this thesis highlights the important role of globalization and human activities on the spread of non-native insects over the past centuries. Even though trade and transport have long been recognized as important drivers of biological invasions, most research has focused on the biological and ecological aspects of invasions, such as species or habitat characteristics influencing invasion success or impacts of non-native species on ecosystems (Vaz et al., 2017). Out of 9,192 scientific publications on biological invasions between 1950 and 2014, only 8% address human aspects, and the majority of these 8% deal with impacts and management of non-native species, not with the invasion process (Vaz et al., 2017). This thesis improves our understanding of the socio-economic drivers of the spread of non-native species, and highlights the need for more research on the human dimensions of biological invasions. This interdisciplinary approach is required to understand invasion dynamics (Vaz et al., 2017) as a purely biological theory of invasions cannot explain or predict the spread of non-native species (Kueffer, 2017).

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# Appendix 1

# Effects of climate change on insect distributions and invasions

# 15. Effects on distributions and biological invasions

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## 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).

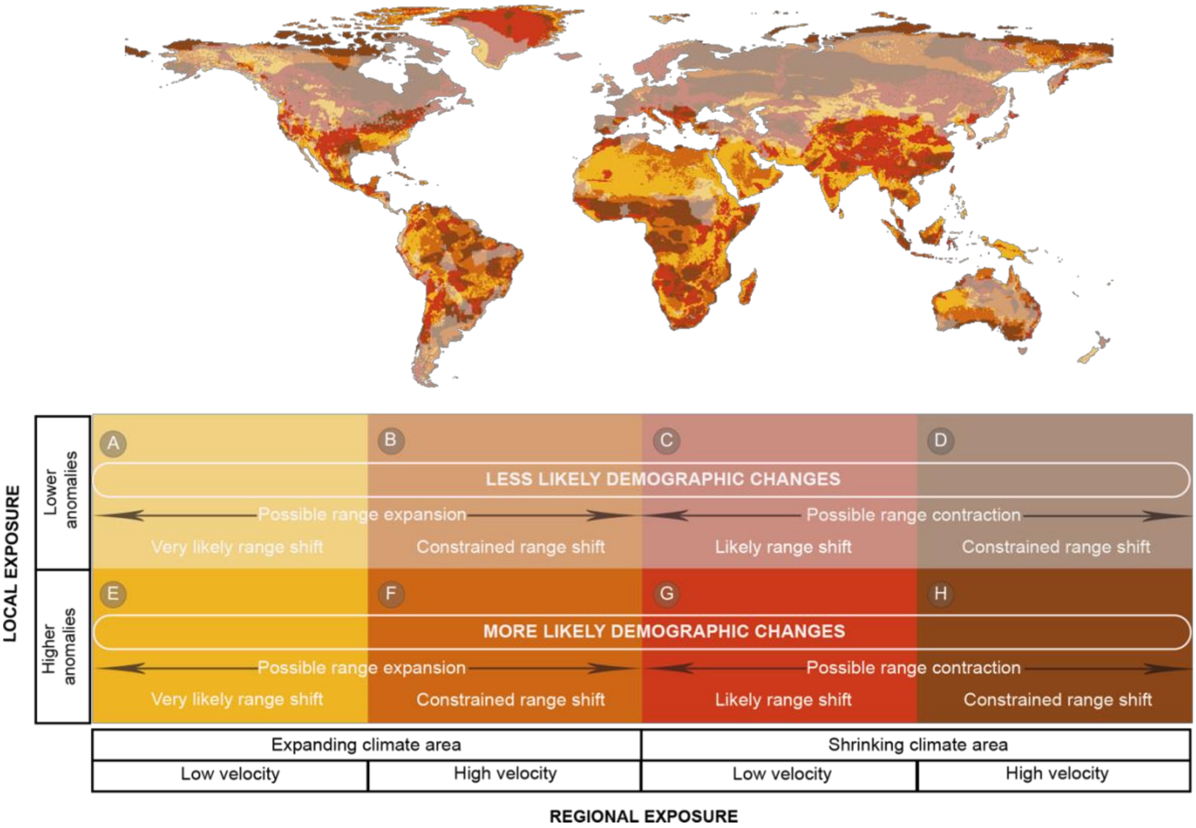

Figure 1. Spatial overlap of climate change metric and its effect on species range shift. The interplay of three metrics is displayed in this illustration adapted from Garcia et al. 2014 (see their paper for more details). Climatic metrics are displayed in black. One metric is at the local scale: the 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 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.

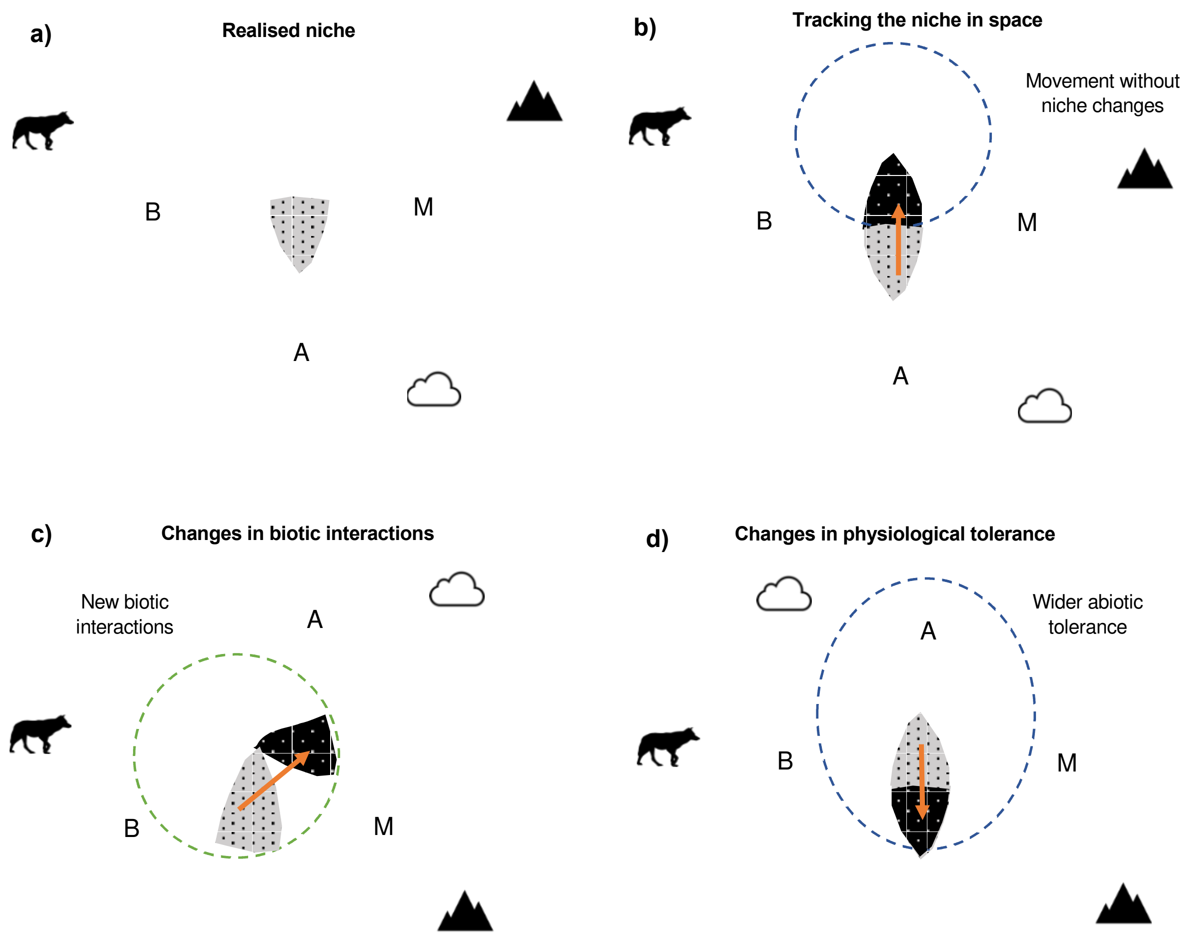

Figure 2. a) The 'BAM diagram' is a simplified framework for understanding species distributions. Three sets of factors determine where a species occurs: the abiotic niche (A) and biotic interactions (B), and the possibility to access the area (through species 'movement' (M)). The realized niche corresponds 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 adaptative 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 website[1] 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.

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[1] https://www.cadima.info/index.php

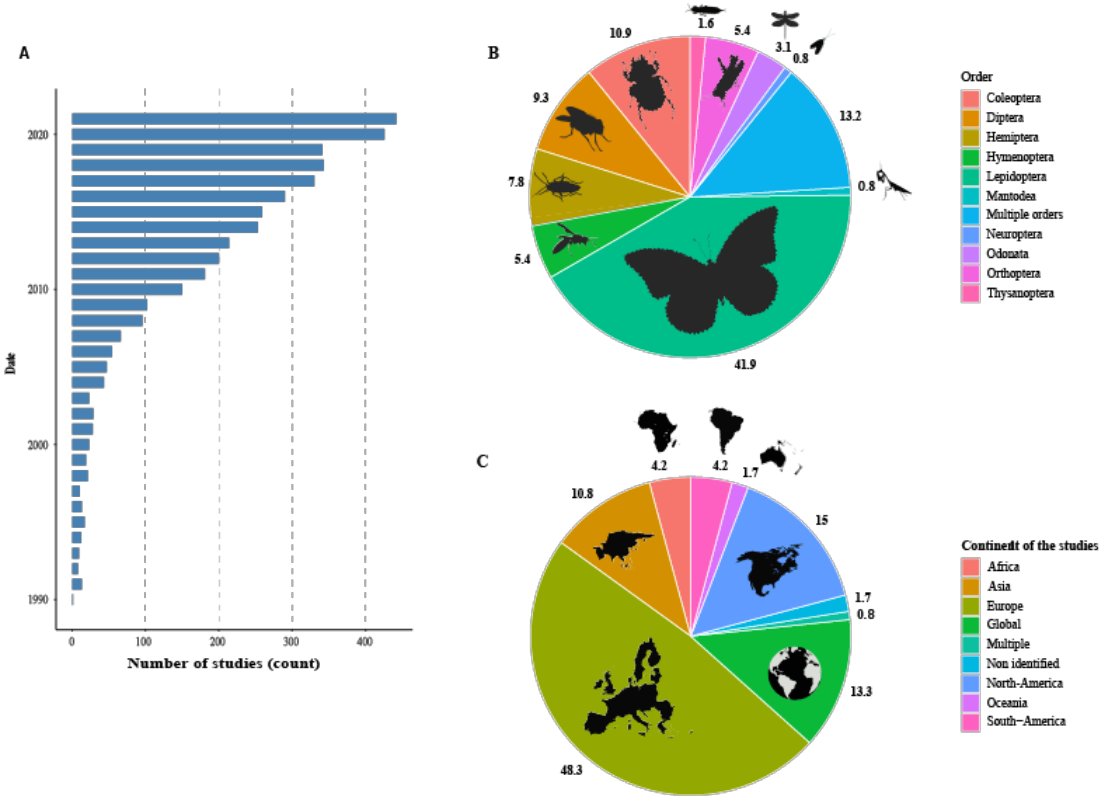

Figure 3. Trends in studies on insects' distribution responses to climate change from 1990 until present. a) General trends in publications over time (4195 studies), b) insect orders studied. Lepidoptera were 2.4 times overrepresented compared to the total number of species described (~160 000 species, 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).

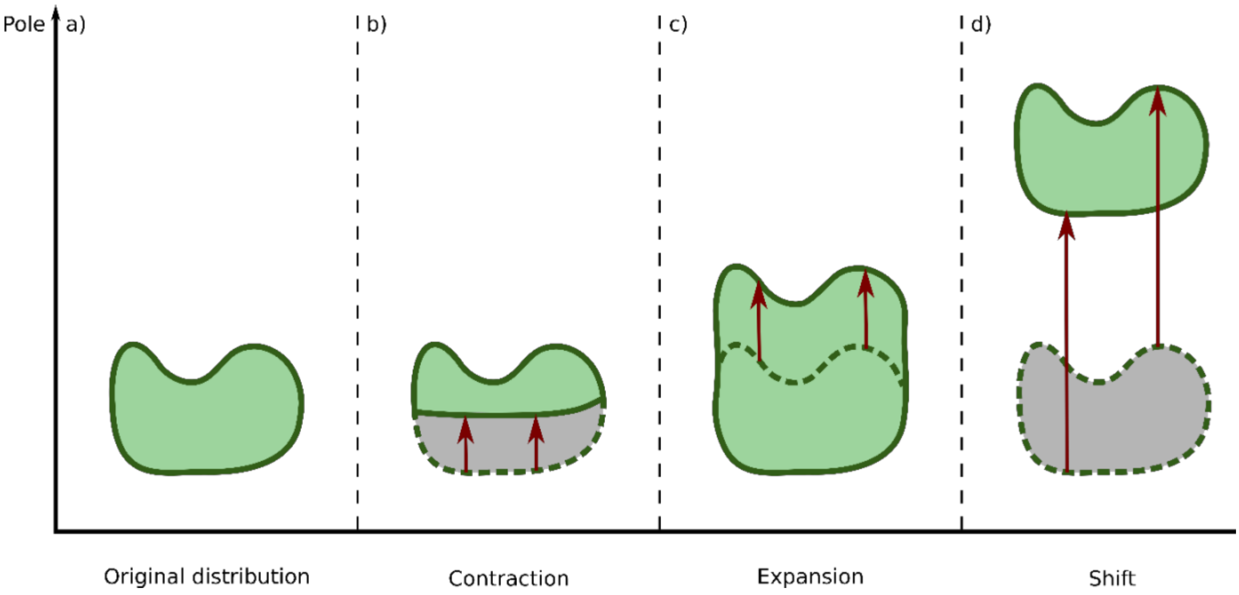

Figure 4. The main types of distribution changes and their consequences on range size. a) the original distribution area, b) a poleward contraction, c) an expansion of the original distribution, d) a complete poleward shift of the original distribution with an equal shift of both lower and upper limit. 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 metanalyses 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 experiment 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).

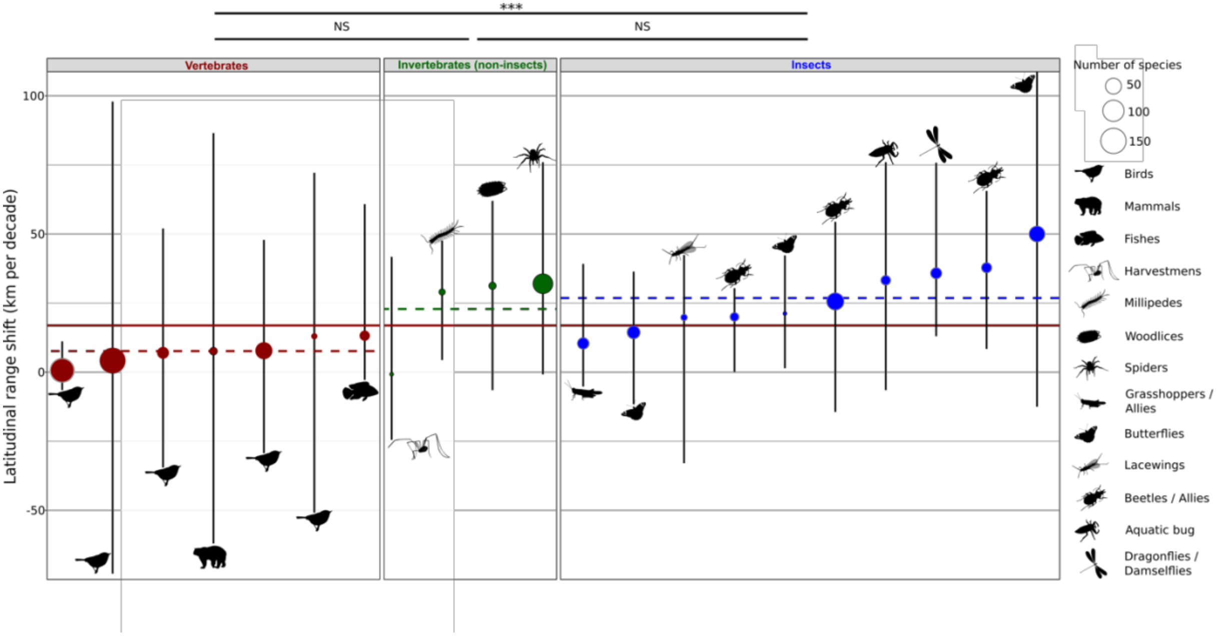

**Figure 5.** Latitudinal shift per decade for three main groups, based on data available from a previous meta-analysis (Chen *et al.* 2011). Each circle represents the median latitudinal shift per decade for a taxonomic group in a specific study region as described in the metanalysis. The error bars 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).

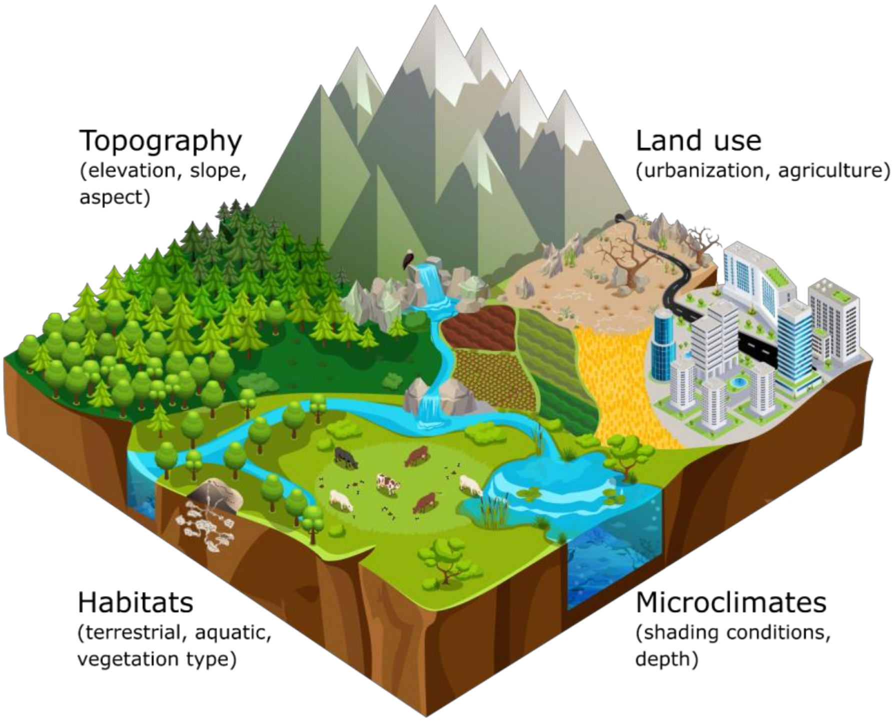

**Figure 6.** Landscapes are heterogenous. They vary in topography, comprise different types of habitats, and are subject to diverse anthropogenic modifications such as agriculture, urbanization, and pollutions. Therefore, within landscapes, environmental conditions can greatly vary over short distances 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 (Rödder *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 gobal 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).

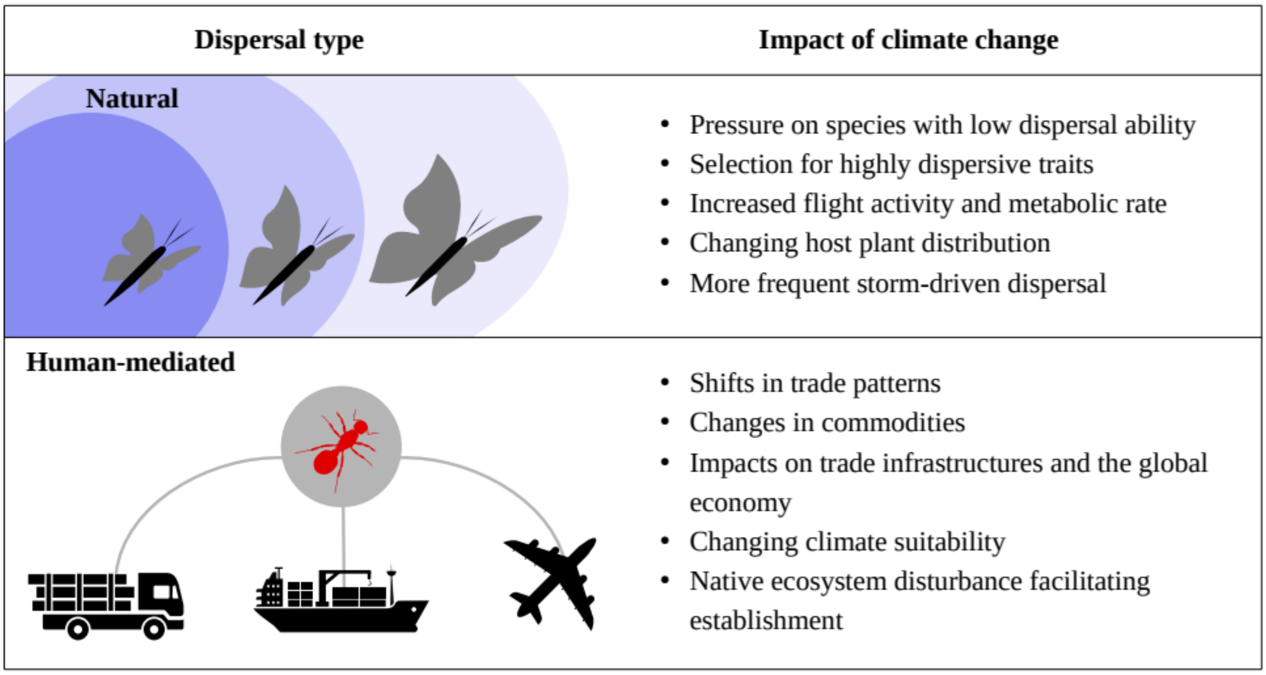

Figure 7. Impact of climate change on insect natural and human-mediated dispersal

## 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 (CTmax-CTmin), and they are expected 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 metanalysis 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 (-).

| | **Response** | |
|---|---|---|
| **Type of interaction** | 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; Vilcinskas 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).

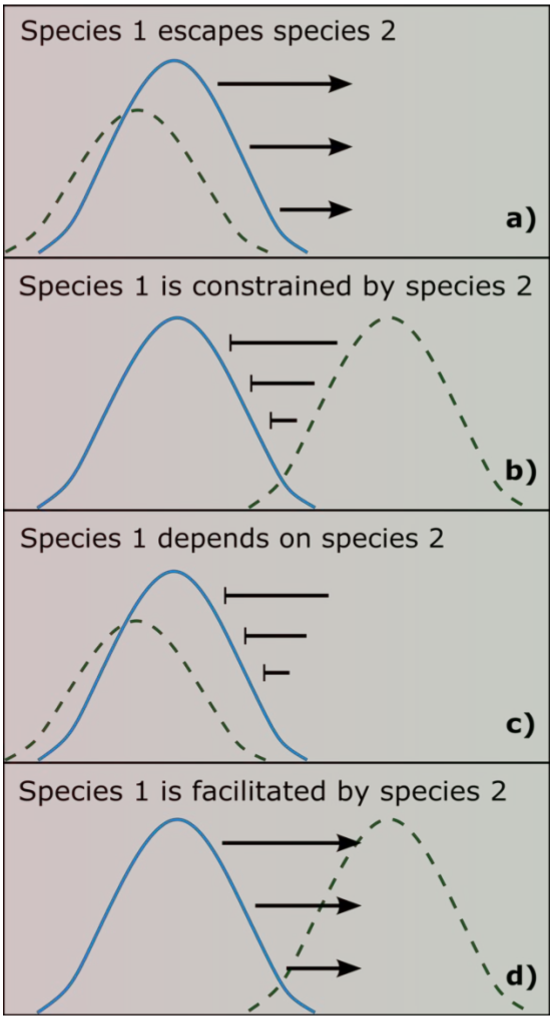

Figure 8: Interactions determine species' climate-tracking ability, impacting the distributions of focal species (blue line) and their interaction partners (dashed green line). The gradient indicates changing climate and habitat suitability. a) species track climate change through enemy release, b) species 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 morality 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 decemilineata*) 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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# Appendix 2

# Global proliferation of nonnative plants is a major driver of insect invasions

OXFORD

*BioScience*, 2024, **74**, 770–781
https://doi.org/10.1093/biosci/biae088
Advance access publication date: 18 October 2024
**Overview Article**

# Global proliferation of nonnative plants is a major driver of insect invasions

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## Abstract

Invasions by nonnative insect species can massively disrupt ecological processes, often leading to serious economic impacts. Previous work has identified propagule pressure as important driver of the trend of increasing numbers of insect invasions worldwide. In the present article, we propose an alternative hypothesis—that insect invasions are being driven by the proliferation of nonnative plants, which create niches for insect specialists and facilitate their establishment outside their native ranges where their hosts are planted or are invasive. We synthesize mechanisms by which plant invasions facilitate insect invasions, macroecological patterns supporting the tight link between plant and insect invasions, and case studies of plant invasions having facilitated subsequent insect establishment. This body of evidence indicates that plant invasions are a major driver of insect invasions. Consequently, the benefits of limiting the spread of nonnative plants include averting the proliferation of nonnative insects and their spillover onto native plant species.

**Keywords:** human-mediated dispersal, facilitation, enemy release, introduction pathways, empty niche

Insects make up the majority of animal species, having colonized every major biome with the exception of most marine habitats. Insects also make up the majority of nonnative animal species and insect invasions are ubiquitous in all world regions (Seebens et al. 2017, Liebhold et al. 2018). Over the last 200 years, rates of insect invasions have increased worldwide (Roques et al. 2016, Bertelsmeier et al. 2017, Seebens et al. 2017), causing a wide range of ecological impacts, primarily through their feeding on plants but also by outcompeting native insect species, disrupting insect–plant mutualisms, altering pollination services and vectoring animal and plant diseases (Traveset and Richardson 2006, Kenis et al. 2009, Boyd et al. 2013, Hill et al. 2016). The socioeconomic consequences of these impacts on agriculture, human health and ecosystem services are manifold (Lounibos 2002, Aukema et al. 2010, Paini et al. 2016). However, despite their obvious importance as invaders, insects have received disproportionally less attention from invasion biologists than other taxonomic groups, especially plants (Pyšek et al. 2008, Edney-Browne et al. 2018). This may be because insects are typically small and only noticeable during part of the year. By contrast, plant invasions are often more visible, which draws more attention to them.

The number of insect species detected during import inspections vastly exceed that of nonnative species recorded as established (Turner et al. 2021), indicating that most insects transported to new regions fail to establish or have not yet established. To improve strategies for minimizing future insect invasions, it is crucial to develop a comprehensive understanding of the factors driving current invasion trends. Propagule pressure, associated with international trade and human travel, has been implicated as an important driver of insect invasions (Bertelsmeier et al. 2017, Brockerhoff and Liebhold 2017, Hulme 2021, Ollier and Bertelsmeier 2022, Fenn-Moltu et al. 2023, Liu et al. 2023). High propagule pressure can come from either many introduction events or many individuals being introduced in a single introduction event. The reasons that high propagule pressure might increase establishment success include increased genetic diversity and greater resistance to stochastic or density-dependent effects (e.g., Allee effects; Lockwood et al. 2005, Simberloff 2009). Most efforts to reduce problems associated with insect invasions focus on reducing propagule pressure (i.e., preventing the accidental transport of insects in trade and travel; Hulme 2013, Nahrung et al. 2023). However, we argue in the present article that considerable evidence points toward the establishment of nonnative plants as a major driver of the establishment of nonnative insect species—in particular, specialist herbivores (Liebhold et al. 2018, Bonnamour et al. 2023). Although propagule pressure is a necessary ingredient for any invasion, the increasing dominance of nonnative plants explains spatial variation in the number of historical insect invasions (Liebhold et al. 2018, Bonnamour et al. 2023) and therefore appears to be a major driver of insect invasions.

The establishment of nonnative plants may be a necessary precondition for the subsequent spread of nonnative insects because insect herbivores and plants have a long shared coevolutionary history that has spawned evolutionary radiations and parallel trends in diversification (Zeng et al. 2014). Because herbivores may, in turn, have coevolved specialist predators or

**Received:** February 26, 2024. **Revised:** July 31, 2024. **Accepted:** August 20, 2024

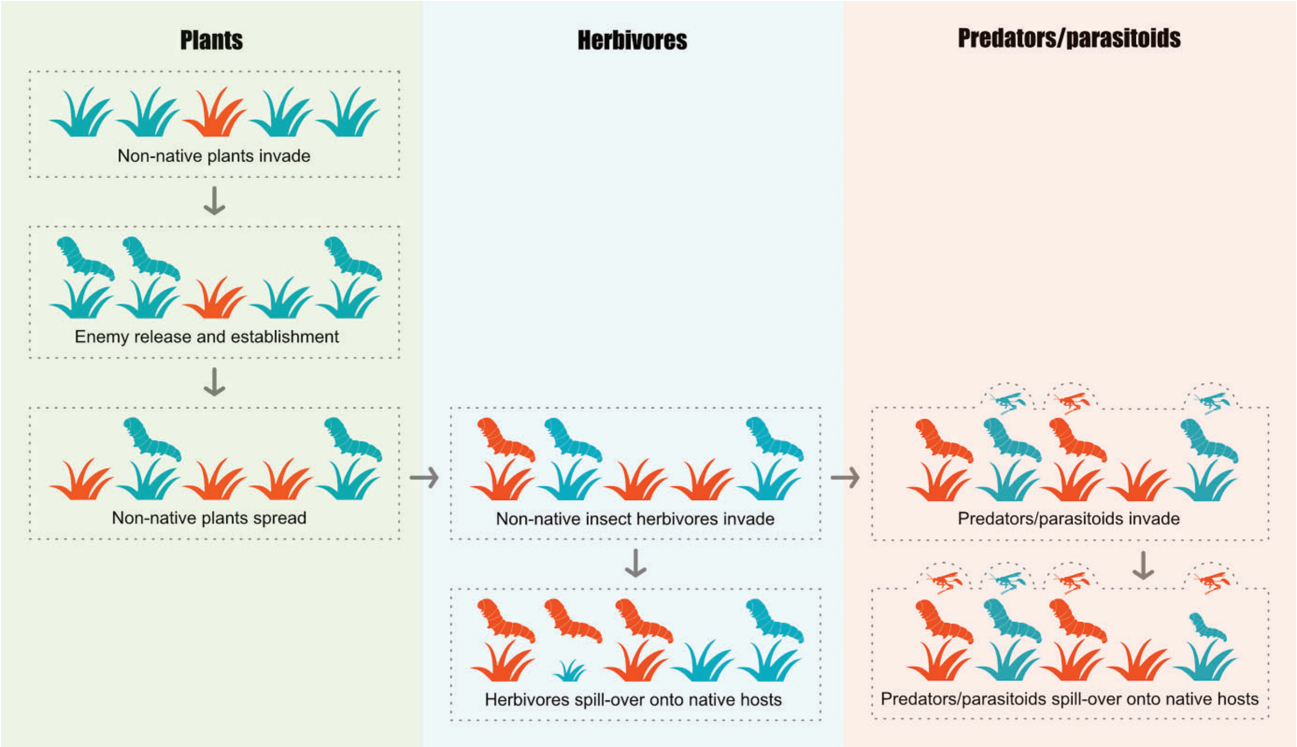

**Figure 1.** Mechanisms of nonnative plants facilitating the establishment of nonnative insect herbivores and higher trophic levels such as predators and parasites. Nonnative species are shown in red and native species in blue.

parasites, an invasion by a plant can open up opportunities for establishment not only for herbivores directly using it as a resource but also subsequently by species of higher trophic levels such as parasitoids (figure 1; Weber et al. 2021). Nonnative plant species are spreading extensively in terrestrial and aquatic ecosystems around the world (Pyšek et al. 2020), facilitated by human-caused disturbance of natural ecosystems (Chytrý et al. 2008, Sánchez-Ortiz et al. 2020, Liu et al. 2023). When insects are transported to novel regions, they no longer face a landscape devoid of their preferred host plants but instead are reunited with hosts from their native range, which allows them to establish, thrive and spread (Gougherty and Davies 2022). Elevated diversity of nonnative plant species creates more ecological niches for arriving insect herbivores (Guo et al. 2019b, Ward et al. 2022), which, in turn, provides new niches for insect predators and parasitoids (figure 1; Wilson et al. 2013). In that way, plant invasions may have a catalytic effect on new invasions of diverse types of insects and the species relying on them. This concept of invasions by one or more species facilitating the invasion of another species has been termed *invasional meltdown* (Simberloff and von Holle 1999, Simberloff 2006, Braga et al. 2018).

## Mechanisms: How plant invasions favor insect invasions

The exchange of plants became a truly global phenomenon since the end of the fifteenth century (di Castri 1989, van Kleunen et al. 2015). European explorers and plant hunters collected plants elsewhere and introduced them to Europe and also to newly settled areas to provide food for humans and animals and for medicinal and aesthetic purposes (di Castri 1989, Mack and Lonsdale 2001, Lenzner et al. 2022). Since then, nonnative plants have become increasingly dominant in the world's ecosystems (Stohlgren et al. 2011, Pyšek et al. 2017), following the establishment of self-sustaining populations that recruit from both escapes from cultivation and accidental introductions (Lambdon et al. 2008, Lehan et al. 2013, Saul et al. 2017). Today, more than 13,000 plant species are established outside of their native ranges (van Kleunen et al. 2015), leading globally to a decline in species diversity in plant communities (Pyšek et al. 2012) and strong biotic homogenization (Yang et al. 2021), a pattern that is also observed in insects (Aulus et al. 2024). The numbers of species that successfully naturalize in the new regions are still increasing (Seebens et al. 2017, Bonnamour et al. 2021) and will likely keep increasing in the future (Seebens et al. 2015).

Agriculture probably represents humanity's largest transformation of the world's flora, with 32% of the global land area devoted to agricultural use (Ellis et al. 2010); most agricultural crops are nonnative in most areas where they are planted (Young 2016) and they create ecological niches for insects that specialize on them (Paini et al. 2016). Likewise, forest plantations of nonnative tree species also provide new ecological niches for nonnative insect species in world regions where these insects could previously not exist (Wingfield et al. 2015). Planted forests (including plantations), many of which are using nonnative trees (Brockerhoff et al. 2008), now cover about 294 million hectares (ha), representing 7% of the world's total forest area (FAO 2020). But they are continuously expanding and likely to reach 20% by 2100 (Brockerhoff et al. 2013, Payn et al. 2015). For example, nonnative trees in the genera *Acacia, Eucalyptus* and *Pinus* are extensively planted in forestry operations throughout much of the southern hemisphere. Plantations of nonnative *Pinus radiata* in New Zealand, Australia

South Africa, and Chile exceed 4 million ha (Brockerhoff et al. 2023), and nonnative plantations of *Eucalyptus* species cover more than 20 million ha, with the largest area in China, Brazil, and India (Wingfield et al. 2015). Australian *Acacia* species have been planted in many parts of the world to support commercial forestry and for many other purposes (Richardson et al. 2023). In most parts of the world, widespread plantings and invasions of *Acacia* species are more recent than those of eucalypts and pines; insect invasions and tree-health problems associated with nonnative *Acacia* species are therefore relatively few compared with those in eucalypts and pines (Hurley et al. 2023). Nonnative plants in arboreta and urban settings also provide ecological niches that facilitate invasions of insects from the native ranges of these plants. During the eighteenth and nineteenth centuries, collecting live "exotic" plants became very popular, and important botanical institutions were created, such as the Royal Botanical Gardens, Kew, in the United Kingdom, and the Leiden Hortus Botanicus, in the Netherlands (Mack and Lonsdale 2001, van Kleunen et al. 2018). More than 160,000 vascular plant species are now grown in botanical gardens around the world, representing almost 50% of the global known vascular flora (van Kleunen et al. 2018). Some of the species in botanic gardens are native where they are grown, but a large fraction is nonnative. Therefore, arboreta provide a virtual smorgasbord of host plants for arriving nonnative insect species and there are several records of insects and plant pathogens that have established there (Wondafrash et al. 2021).

In addition, a large fraction of plantings in urban landscapes is dominated by nonnative plants. For example, in UK gardens, about 70% of plants are nonnative (Loram et al. 2008). Urban areas are also well connected to introduction pathways as most imports arrive in urban areas. So, the combination of high arrival rates and facilitation of establishment by copious numbers of nonnative plants leads to urban areas being the site of most insect invasions (Branco et al. 2019, Ward et al. 2019). It has been argued that urban plantings are the first places where for nonnative insect species can be detected because they are often the first point of contact for arriving species (Branco et al. 2015, Paap et al. 2017). However, additional populations of the host plant may be located at great distances from those arrival points. Therefore, regional transport routes are a key factor determining further spread of nonnative insects (Gippet et al. 2019). Indeed, many invasive plant species are now so well established and cover large areas that they can provide stepping stones for a newly arriving insect species that can move rapidly over great distances. For example, the nonnative pine bark beetle, *Hylurgus ligniperda* has invaded much of the southern hemisphere (i.e., Australia, New Zealand, South Africa, and southern South America) and spread quickly, using planted pines as stepping stones (Brockerhoff et al. 2006, Faccoli et al. 2020). Overall, nonnative trees are widespread across urban areas and are likely to provide increased host availability compared with surrounding forests (e.g., Augustinus et al. 2024).

Even protected areas, including those located at great distances from human-dominated ecosystems and seemingly isolated from the major pathways of plant introductions, are increasingly affected by nonnative plant invasions (Foxcroft et al. 2013). So far, however, less than 3% of protected areas are invaded by nonnative invertebrates, perhaps because the low levels of human activity provide few opportunities for introduction (Liu et al. 2020). Alternatively, there may be substantial time lags between the establishment of plants in these areas and the subsequent spread of insects.

## Nonnative insects are continuously arriving

Nonnative insects are continuously moving over long distances, mainly through human transport but, in some cases, also via natural dispersal. Some insect species are able to perform natural long-distance dispersal flights and can thereby spread to new regions and across physical barriers (Chapman et al. 2015). Extreme climatic events such as storms and hurricanes also can cause long-distance dispersal of insects. For instance, there is evidence that several species of insects have dispersed from Australia to New Zealand across open ocean by suitable air currents (Close et al. 1978). Although it is likely that many different species of insect have been translocated between continents over the last centuries via wind, birds or marine rafting (Holzapfel and Harrell 1968), most such translocations have not resulted in new invasions because of a lack of hosts. Insects are now mainly introduced through international trade and transport (Gippet et al. 2019). In particular, the worldwide movement of plants can directly promote insect invasions by providing pathways by which insects can travel long distances. The global trade of live plants is well known as the historically dominant pathway for insect introductions (Kenis et al. 2007, Smith et al. 2007, Liebhold et al. 2012, Meurisse et al. 2019). These natural and human-meditated long-distance dispersal events occur continuously, but many of them do not lead to insect establishment, probably most importantly because suitable host plants are absent or scarce in the introduced range. Indeed, host plant availability is a major factor determining the distribution and spread of nonnative insects (Zalucki and Clarke 2004, Dang et al. 2021). This will however depend on the host specificity of individual insect species; the availability of hosts from the native range will be more significant for specialists, whereas the establishment of generalists is less likely to be facilitated by nonnative plants.

## Filling the vacuum of insect diversity on introduced host plants

In their native ranges, most plants are associated with a large number of more or less specialized herbivorous and other insects (Strong et al. 1984), while they are in their nonnative ranges, they are often, at least initially, exploited by fewer insects recruited from the native insect fauna (Goßner et al. 2009, Pyšek et al. 2011, Branco et al. 2015). This leads to enemy release, especially when there are no closely related (e.g., congeneric) native plants in the invaded region (Procheş et al. 2008, Carrillo-Gavilán et al. 2012, Branco et al. 2015). This is because most herbivorous insect species are specialists (Forister et al. 2015). However, nonnative plants offer niches that facilitate the establishment of insects outside their native ranges where their hosts are planted and, over time, specialists from the native range can catch up with their host plants (figure 1; Hawkes 2007, Brockerhoff and Liebhold 2017). When no closely related native plants are present, accumulating specific natural enemies in the new range takes time; it has been shown that for pathogens, this process happens on a scale of centuries (Mitchell et al. 2010). Similarly, nonnative plants have been shown to benefit from release from herbivore enemies most during early invasion stages, but this release is diminished 50–200 years after their invasion (Hawkes 2007). The diminished herbivore richness may result in high rates of growth and reproduction for nonnative plants that substantially exceed rates occurring in their native range through enemy release (Keane and Crawley 2002). Although the universality of this process in nonnative plants has been questioned (Schultheis et al. 2015, Brandenburger et al. 2020), recent analyses indicate its and common occurrence (Xu et al. 2021). The spread of nonnative plants leads initially to a “vacuum” of insect diversity (specialist herbivores that are present in the native but absent in the introduced range). Over time, this vacuum is filled as specialist herbivores feeding on these nonnative plants can establish, which, in turn, results in a diminution of the benefits of enemy release with time since the introduction of the host plant (Hawkes 2007, Chen 2016).

For example, early *Eucalyptus* plantations benefited from a largely herbivore-free environment in their nonnative ranges, but the rate of spread of nonnative pests of *Eucalyptus* has increased nearly fivefold since the 1980s (Hurley et al. 2016). Similarly, the spread of black locust (*Robinia pseudoacacia*), a tree species that has invaded every temperate continent, has led to a parallel, but delayed, spread of insect herbivores that feed on it (Medzihorský et al. 2023). The reunification of nonnative plants with herbivore species accidentally introduced from their native ranges can result in a pronounced decrease in the benefits of enemy release experienced by these plants. Shaw and colleagues (2018) show that prior to 2010, all introductions of natural enemies affecting weeds in the European Union have been unintentional, but several of these species have substantially reduced the abundance of their hosts.

Once they have established, nonnative herbivores are sometimes able to expand their host range beyond their nonnative host to include native plant communities, sometimes with detrimental consequences to those communities (White and Whitham 2000, Gougherty and Davies 2021). This spillover effect may occur when insects reach high densities on their preferred hosts and then begin exploiting less preferred neighboring plants (White and Whitham 2000), or they simply may be able to feed on native plants that are phylogenetically related to their nonnative hosts (Gougherty and Davies 2021). For instance, the North American chrysanthemum lace bug (*Corythucha marmorata*), which was unintentionally introduced to Japan, was shown to feed on native Asteraceae that grow next to its preferred nonnative host (*Solidago altissima*; Sakata and Craig 2021) but also on less related plants in the Convolvulaceae and Solanaceae families (Rizkawati et al. 2023). In another example, the invasion of North America by the spotted lanternfly (*Lycorma delicatula*) has been facilitated by the ubiquity of its preferred host, the nonnative tree of heaven (*Ailanthus altissima*), but once established, this sap-feeding insect of moderate host specificity can also feed on and damage native trees such as black walnut (*Juglans nigra*) and cultivated crop plants such as grape (*Vitis vinifera*; Murman et al. 2020). The spillover may occur after some initial time lag following the establishment of the nonnative insect. However, typical time lags are so far unknown.

Nonnative plants can also facilitate invasions of nonherbivorous insects, such as pollinators and ants. Nonnative pollinators tend to visit more nonnative than indigenous plants, suggesting that nonnative plants might act as stepping stones facilitating pollinator invasions (Morales and Aizen 2002, Fontúrbel et al. 2023). Furthermore, the widespread presence of nonnative plants can facilitate invasions of specialist pollinators. For example, the cultivation of squash (*Cucurbita* spp.) throughout North America has enabled the invasion of the pollen specialist *Peponapis pruinosa* from the native range of squash in southern Mexico (López-Uribe et al. 2016). Nonnative herbivorous insects can also facilitate the spread of other insects that have mutualistic relationships with them. For instance, the abundance of the red imported fire ant, *Solenopsis invicta,* in North America increases with the abundance of the nonnative honeydew-producing mealybug *Antonina graminis* (Helms et al. 2011). The abundance of this mealybug is positively affected by the abundance of the nonnative host grass *Cynodon dactylon*. Therefore, the abundance of the nonnative plant indirectly facilitates the fire ant invasion.

A substantial fraction of insect species worldwide are predators and parasitoids, although the true richness of parasitoids, especially in the understudied Hymenoptera, is probably at least twice the number of described species (e.g., Dolphin and Quicke 2001). Similar to the way plant invasions can create niches for herbivorous insects and facilitate their invasion, invasions of herbivorous insects create niches for insects at higher trophic levels (predators and parasitoids) and thereby facilitate their invasions. The unintentional introduction of parasitoids and predators of insect pests is a phenomenon recently referred to as “accidental biocontrol,” and several studies show that this phenomenon is common worldwide (Weber et al. 2017, 2021). It is estimated that 35% of parasitic Hymenoptera in the United States and 32% of arthropod predators and parasitoids in Europe were introduced accidentally (Weber et al. 2017). Similarly, Charles (1998) reported that 79% of parasitoids attacking nonnative fruit crop pests in New Zealand arrived accidentally. In most cases, it remains unknown if these species entered with their insect hosts or were hitchhikers in trade and human travel. However, it is clear that for many species, establishment would not have been possible without the presence of hosts from their native range. In the Mediterranean region, several specific parasitoids of nonnative eucalypt pests are thought to have been accidentally introduced after their host (Kenis et al. 2017). For example, the parasitoid *Psyllaephagus bliteus* was first observed in Portugal in 2011, 4 years after the first record of its nonnative host, *Glycaspis brimblecombei*, that feeds on eucalypts (Boavida et al. 2016).

Much like invasions of insect herbivores, accidental invasions of parasitoids facilitated by invasions of their hosts can spill over onto other hosts, adversely affecting native fauna (Mason et al. 2017). Teulon and colleagues (2008) note that a very small number (approximately 15) of aphids are native to New Zealand and these are mostly rare; however, they are being adversely affected by accidentally introduced aphid parasitoids. More than 110 species of nonnative aphids have invaded New Zealand (Brockerhoff and Liebhold 2017) and, apparently, have facilitated invasions by at least 10 species of nonnative aphid parasitoids, some of which have been found to spillover onto native aphid hosts (Teulon et al. 2008). Together, these pieces of evidence suggest that the establishment of host plants is a crucial prerequisite to the subsequent establishment of insects.

## Macroecological patterns: Empirical evidence for the link between plant and insect invasions

Analysis of geographical variation in the numbers of naturalized or invasive species can be used to identify dominant drivers of invasions (Pyšek et al. 2010, Dawson et al. 2017, Essl et al. 2019). In a global study, Liebhold and colleagues (2018) analyzed variation in nonnative insect richness among 44 land areas, ranging from small oceanic islands to entire continents. Using structural equation modelling, they found that the most important determinants of nonnative insect richness are native and nonnative plant richness. Several studies report that variables related to human population size and economic activity explain variation in numbers of naturalized plant species, presumably because they are correlates of plant propagule pressure (Pyšek

Wohlwend et al. 2021). Similar measures of human activity have also been reported to explain variation in nonnative insect species numbers (Lantschner et al. 2020, Trombik et al. 2023), but these correlations may arise either directly as a result of associations with propagule pressure or indirectly as a result of their impacts on plant invasions that subsequently facilitate insect invasions.

Recent studies indicate that there may be a substantial temporal lag in the link between plant invasions and insect invasions. Bonnamour and colleagues (2023) analyzed the association between current insect invasions and historic plant invasions among biogeographic regions; they found that recent detections of insect invasions (i.e., prior to 2010) are well explained by cumulative plant invasions prior to 1900. In fact, these historical plant invasions were a better predictor of current insect invasions than more recent plant invasions (Bonnamour et al. 2023). Global flows of invasive plants also explained much more of the variation in global flows of invasive insect than did trade between regions. The long time lag between plant and insect invasions is probably attributable to the combined effects of several processes. First, following initial plant naturalization, it takes time for a given species to spread and become abundant within the region where it first arrived (e.g., Gassó et al. 2010). Second, the reporting lag for insect invasions may be quite long; for example, Maclachlan and colleagues (2021) estimated an approximately 80-year median lag between the establishment and discovery of invasions by Hemiptera in the United States. One implication of the long lag between plant invasions and discoveries of insect invasions is that there is likely a relatively large invasion debt for insects worldwide. This means that there may already be numerous insects at early stages of establishment, but they might still be so rare and cryptic that many of them will not be detected for many years or decades.

Potentially, plant diversity can have both positive and negative effects on the population growth and invasion success of herbivorous insects. According to the resource concentration hypothesis or facilitation effect, higher densities of host plants facilitate population growth by minimizing dispersal loss (Root 1973, Stephens and Myers 2012). In a similar fashion, the presence of large numbers of nonhost plants may depress insect herbivore population growth, a phenomenon termed *the dilution effect* (Jactel and Brockerhoff 2007). Guo and colleagues (2019a) analyzed variation in numbers of tree-feeding insect pests per county across the United States and found a hump-shaped relationship between nonnative forest insect species richness and tree species richness. On further dissection of this relationship, they determined that it likely arose from the combination of a positive effect of host tree richness on nonnative insect richness (as a result of the facilitation effect) and a negative effect of nonhost richness (as a result of the dilution effect). In a subsequent analysis of the same data, Ward and colleagues (2022) found evidence of a host tree facilitation effect on the establishment of some nonnative tree-feeding insects (especially sap-feeding insects), a dilution effect by which the presence of nonhosts inhibited establishment of other insect species and several species that did not exhibit either a facilitation effect or dilution effect. However, taken together, these studies provide evidence that the diversity of plants, both nonnative and native, can promote insect invasions.

A common observation in macroecological analyses of invasions is an association of native and nonnative species richness. This pattern is opposite the expectation of the biotic resistance hypothesis, originally posited by Elton (1958), which predicts that systems with high species diversity are more resistant to invasion because of a higher proportion of niches already being filled. In plants, the evidence is mixed: In some cases, nonnative plant richness is negatively related to native plant diversity (Tilman 1997, Naeem et al. 2000), but in other studies, it is a positive relationship (Stohlgren et al. 2003, Pyšek et al. 2017). This discrepancy is mostly because of the spatial scale of observation and can be explained by covarying external factors; at the large scale, the same abiotic conditions that promote a high diversity of native species (climate, substrate, habitat heterogeneity, etc.) also support a high diversity of nonnative floras (Shea and Chesson 2002). Fridley and colleagues (2007) termed this phenomenon the *invasion paradox*, because the biotic resistance is mostly observed at small spatial scales but is reversed at larger scales (see also Rossignaud et al. 2022). The association between native and nonnative species richness has also been explored in insects at a macroecological scale. In a study of geographical variation in arthropod richness across the Azorean archipelago, Borges and colleagues (2006) found that nonnative arthropod species richness was strongly correlated with native arthropod species richness. A similar correlation was found in the global macroecological study on insects by Liebhold and colleagues (2018). These positive correlations between the numbers of native and nonnative insect species may result from there being generally more ecological niches in some regions that support more native and nonnative insect species. Alternatively, in some regions, there may be factors (e.g., climate, soils, land area) that promote plant diversity (native and nonnative), and this, in turn, promotes both native and nonnative insect diversity, thereby causing the correlation. Overall, these macroecological studies have revealed evidence that temporal dynamics and spatial patterns of plant and insect invasions are tightly linked.

## Case studies

Many widely abundant nonnative plant species have associated specialist insects that invaded from the nonnative plant's native range and were reunited with the plant in its nonnative range. Surprisingly, however, research that tests explicitly whether the establishment of a certain host plant was a necessary precondition for the establishment of a specific insect species and subsequent spillover to native plant species is scarce. In the present article, we will focus on well described examples that illustrate the fundamental role that plant invasions play in facilitating insect invasions (table 1).

Tree of heaven, *A. altissima,* is native to east Asia but is one of the most widespread nonnative woody plants in virtually every part of the temperate world. This species spreads very fast, easily colonizes disturbed areas, and exhibits remarkable growth (Kowarik and Säumel 2007). Over time, several herbivores associated with it in its native range are catching up and invading portions of its invaded range (Ding et al. 2006). Examples include the spotted lanternfly (*L. delicatula*), the brown marmorated stink bug (*Halyomorpha halys*), and the ailanthus silk moth (*Samia cynthia*). The ailanthus silk moth was introduced to several world regions for purposes of silk production but escaped cultivation and continued to spread via natural dispersal into areas where *A. altissima* is abundant (Frank 1986). Both the spotted lanternfly and the brown marmorated stinkbug most likely invaded new regions as hitchhikers in cargo and are considered nuisance pests because they frequently reach very high densities near human settlements (Leskey and Nielsen 2018, Urban and Leach 2023). Furthermore, although both species prefer *A. altissima* as a host, both also feed opportunistically on economically important forest and crop plants (e.g., *Acer*, *Prunus*, *Vitis*) causing economic impacts in those sectors, providing an example of the spillover e

**Table 1.** Examples of insect herbivore species whose invasion was facilitated by plants from the same native range.

| Nonnative plant | Origin | Insect | Invaded range | Spillover onto native hosts? | Likely pathway | References |
|---|---|---|---|---|---|---|
| *Ailanthus altissima* (tree of heaven) | East Asia | *Lycorma delicatula* (spotted lanternfly) | North America | Yes, *Vitis*, *Acer*, *Malus*, *Populus*, *Salix* | Plants | Urban and Leach 2023 |
| *Ailanthus altissima* (tree of heaven) | East Asia | *Samia cynthia* (ailanthus silkmoth) | North America, South America, Europe, Australasia | Yes, *Ricinus* (castor bean) and other plants | Intentional introduction | Baker 1985, Frank 1986 |
| *Asclepias* spp. | North America | *Danaus plexippus* (monarch butterfly) | Oceania, Australasia, Europe | No | Wind dispersal, hitchhiking | Zalucki and Clarke 2004, Pierce et al. 2014 |
| *Cucurbita pepo* (squash) | Central and Southern Mexico | *Peponapis pruinosa* (squash bee) | Conterminous United States | No | Wind | López-Uribe et al. 2016 |
| *Eucalyptus* spp. | Australasia | 43 species | Europe, North America, Africa, South America | No | multiple | Hurley et al. 2016 |
| *Gossypium* spp. (cotton) | Neotropics | *Anthonomus grandis* (boll weevil) | Conterminous United States, South America | Yes, *Anthonomus grandis* (boll weevil) | Wind | Kim and Sappington 2006, Sánchez-Reyes et al. 2022 |
| *Picea abies* (Norway spruce) | Europe | *Ips typographus*, *Dendroctonus micans* | Continental Europe and United Kingdom | No | Wood | Mayer et al. 2015 |
| *Pinus radiata*, other *Pinus* spp. | Europe and North America | Numerous species of insects | Southern hemisphere | No | Wood, plants | Brockerhoff et al. 2023 |
| *Pueraria* spp. (kudzu) | East Asia | *Megacopta cribraria* (kudzu bug) | North America, Indomalaya | Yes, *Glycine max* (soybean) and other species | Plants | Ruberson et al. 2013 |
| *Robinia pseudoacacia* (black locust) | Eastern North America | 8 species | Europe, North America, Australasia | Yes | Plants | Medzihorský et al. 2023 |
| Diverse trees and shrubs | South America, Europe, Asia, Australia, Indomalaya | 46 species of Psylloidea (Hemiptera) | North America | Maybe | Wood, plants | Horton et al. 2021 |

*H. halys* has facilitated the invasion of at least one insect parasitoid species, *Trissolcus japonicus*. Starting in 2007, this species was being considered for release as a biological control agent targeting *H. halys* populations in North America, but in 2014, it was discovered that the parasitoid species had already invaded accidentally (Talamas et al. 2015). Nonnative populations were also recently discovered in Europe, having also arrived accidentally and established, apparently because of the widespread abundance of its host *H. halys* (Stahl et al. 2019).

Another example of an insect invasion that has been facilitated by the invasion of its host is provided by the monarch butterfly, *Danaus plexippus*. In its native North American range, it is an iconic species known for its annual long-range migrations to and from overwintering locations. However, over the last 100 years, the species has established nonnative populations across the Caribbean, Pacific islands, Australasia, Atlantic islands, and the southern Iberian Peninsula (Nail et al. 2019). Zalucki and Clarke (2004) speculate that invading populations arrived through some combination of hitchhiking with cargo and windborne dispersal. However, in these nonnative regions, its hosts (milkweeds in the subfamily Asclepiadoideae) are not native but are widely abundant as nonnative weeds or ornamental plants. Therefore, the worldwide spread of Asclepiadoideae through introductions, naturalization and invasion has paved the way for the global spread of monarchs.

The genus *Pinus* (pines) is one of the most abundant and diverse woody plant genera in the northern hemisphere. Although pines are not native to the southern hemisphere (except *Pinus merkusii*, which just crosses the equator in Indonesia), they are widespread and highly abundant there because of large-scale plantings for production forestry (Sedjo 1999) and because of the invasiveness many pine species exhibit in certain habitats (Richardson et al. 1994). The success of both planted and invasive pines can be attributed, in part, to their escape from their natural antagonists, mainly insects and plant pathogens, that are present in their native ranges and may limit their growth and reproduction (Richardson et al. 2007). However, numerous species of insect herbivores and plant pathogens that use pines as their main or only host have been accidentally transported to the southern hemisphere where, over time, many have found host pines and successfully established (Burgess and Wingfield 2001, Wingfield et al. 2006, Brockerhoff et al. 2023). The first prominent pine insect to invade the southern hemisphere was the European woodwasp, *Sirex noctilio*. Establishments were detected first in New Zealand around 1900 and subsequently in all southern hemisphere regions with pine plantations: Australia, South Africa, and South America (Slippers et al. 2015), where it is often considered one of the most important pests of pines. Other well-known illustrative cases include the North American pine bark beetle *Ips grandicollis* and the European pine shoot moth, *Rhyacionia buoliana*, which invaded Australia and Chile, respectively (Neumann 1987, Toro and Gessel 1999). All these invasions can be attributed mainly to the widespread presence of pines, their main or only host plants. Interestingly, these and many other pine insects are far more abundant and much more damaging in the invaded southern hemisphere regions than in their native ranges (where they are considered minor pests). This can be attributed to the combination of highly susceptible plants and the lack of specialized natural enemies of these insects. Many other potentially damaging insect species in the native range of pines have not yet invaded the southern hemisphere but hold potential for invasion, potentially diminishing the benefits of enemy release currently experienced by nonnative pines and decreasing the productivity of pines in forestry (Lantschner et al. 2017, Brockerhoff et al. 2023).

A final example is provided by potatoes (*Solanum tuberosum*), which are one of the globally most important staple foods and are grown on all continents (Singh and Kaur 2016). The ancestors of the main potato varieties originate from western South America, but other related wild potato species occur as far north as the southern United States (Ames and Spooner 2008, Singh and Kaur 2016). From the sixteenth century, potatoes were introduced to Europe and, subsequently, most of the rest of the world (Ames and Spooner 2008, Sauer 2017). The Colorado potato beetle (CPB), *Leptinotarsa decemlineata*, is considered the most important defoliator of potatoes and one of the most important potato pests in the northern hemisphere; infestations can lead to complete defoliation and crop loss (Hare 1990). CPB is endemic to North America, and the pest populations of CPB originate from the southern Plains of the United States (Hare 1990, Izzo et al. 2018). There, it made a host shift from native Solanaceae to cultivated potatoes around the mid-1800s (Hare 1990). Despite considerable efforts to prevent its introduction to Europe, it became established in the early 1900s and spread quickly through much of Europe and all the way to northeast Asia. Because potatoes are the main host of pest populations of CPB, the large-scale cultivation of potatoes in their nonnative range in Europe and Asia clearly facilitated its invasions, and the cultivation of potatoes in North America enabled the expansion of CPB's host range to potatoes in the first place.

## Conclusions

The evidence compiled in the present article supports our hypothesis that plant invasions are a crucial determinant of insect invasions. The close associations that many plants and insects form have evolved over millions of years. Consequently, the availability of host plants is a fundamental factor limiting the establishment success of nonnative insects. Plant invasions facilitate insect invasions directly by providing ecological niches for arriving insect herbivores, and indirectly by favoring the establishment of insect predators and parasitoids. Macroecological analyses support the hypothesis that nonnative plant richness is a major determinant of nonnative insect richness. Global flows of historical plant invasions are closely associated with flows of insect invasions a century later (Bonnamour et al. 2023); the existence of this century-long lag can be explained by the time required for nonnative plants to become widespread before functioning as stepping stones for subsequent insect invasions. Although there is macroecological evidence for such broad associations between nonnative plants and insects, more research is needed to document the invasions of specific pairs of plants and insects more generally and to test for time lags between the establishment of the host plant and the insect species and subsequent spillover to native plant species.

Overall, our synthesis provides evidence for mechanisms and global patterns supporting the links between plant and insect invasions. Variation in numbers of insect invasions worldwide are much more closely related to variation in numbers of plant invasions than they are to proxies of propagule pressure (Liebhold et al. 2018, Bonnamour et al. 2023). Although propagule pressure is a necessary ingredient of any invasion, rates of insect invasions are instead much more strongly limited by the availability of plants. Current biosecurity practices mainly focus on prevention of new arrivals of insects, but limiting the accidental spread of nonnative plants is also important for limiting insect invasions in the future. In this way, controlling the spread of undesired nonnative plant species would not only be beneficial because it mitigates the impacts of the plant species themselves, it woulc
spillover of associated nonnative insects to native p

Although nonnative crops may host nonnative insects, limiting their spread is not an option because of the benefits that they provide to humanity.

## Acknowledgments

CB and AB were supported by the Swiss National Science Foundation (through grant no. 310030_192619) and by the SEFRI-funded ERC starting grant SPREAD (contract no. MB22.00086). AML acknowledges support by the USDA Forest Service and grant no. EVA4.0, no. CZ.02.1.01/0.0/0.0/16_019/0000803 financed by Czech Operational Programme Science, Research, and Education. PP was supported by EXPRO grant no. 19–28807X (Czech Science Foundation) and long-term research development project no. RVO 67985939 (Czech Academy of Sciences). DMR acknowledges support from Mobility 2020 project no. CZ.02.2.69/0.0/0.0/18_053/0017850 (Ministry of Education, Youth and Sports of the Czech Republic), long-term research development project RVO 67985939 (Czech Academy of Sciences) and the DSI-NRF Centre of Excellence for Invasion Biology. EGB acknowledges support from the Swiss Federal Research Institute WSL. JS was supported by grant no. NAZV QK22020019 and from the Ministry of Agriculture of the Czech Republic (RO0423).

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**Received:** February 26, 2024. **Revised:** July 31, 2024. **Accepted:** August 20, 2024

# Appendix 3

# Temporal dynamics and global flows of insect invasions in an era of globalization

nature reviews biodiversity

https://doi.org/10.1038/s44358-025-00016-1

Review article

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# Temporal dynamics and global flows of insect invasions in an era of globalization

**Cleo Bertelsmeier**[1], **Aymeric Bonnamour**[1], **Jeff R. Garnas**[2], **Tongyi Liu**[1], **Rosaëlle Perreault**[1] & **Sébastien Ollier**[1,3]

## Abstract

Human-mediated transport has led to the establishment of more than 6,700 non-native insect species with wide-ranging effects on ecosystems, economies and human health. Understanding how different aspects of globalization affect the spread of non-native insects is crucial to reducing their effects. In this Review, we explore current and historical patterns, drivers and dynamics of global insect invasions facilitated by humans since prehistory. Multiple aspects of the history of globalization have influenced invasion dynamics, including the spread of agricultural practices in the Neolithic period, the advent of early empires and their trade routes, colonization, geopolitical events, wars and economic crises. Technological innovations such as steam ships, containerization and the internet have further accelerated global insect invasions. Spatial invasion patterns are characterized by frequent secondary spread via bridgehead populations, asymmetric intercontinental species flows originating disproportionally from Europe, and biotic homogenization of communities. Insect invasions are predicted to increase dramatically and their dynamics will shift, especially with the opening of trade routes and introduction pathways. Inspection at ports of entry and early detection systems are crucial to inform mitigation efforts. Future interdisciplinary collaborations will integrate knowledge from diverse and emerging data sources and technologies, advancing our understanding of insect invasion biology.

## Sections

Introduction

Temporal dynamics since prehistory

Spatial patterns of insect invasions

Future invasions

Possible mitigation

Summary and future directions

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## Introduction

Ongoing human-mediated movements of insects around the world have led to the establishment of more than 6,700 insect species outside their native ranges, and this number is expected to increase dramatically over the coming years[1,2]. Non-native species of insects outnumber all other non-native animal species[3,4]. They have a wide range of ecological effects, such as outcompeting and displacing native species, disrupting food webs, affecting nutrient cycling and changing vegetation structure[5–8]. Non-native insects are infamous as forest pests, including species such as the spongy moth (*Lymantria dispar*), which causes widespread defoliation, and the emerald ash borer (*Agrilus planipennis*), which has killed tens of millions of ash trees[5]. More than 1,300 species of non-native insects are considered major threats to agriculture[9]. A prominent example is the Mediterranean fruit fly (*Ceratitis capitata*), which is native to sub-Saharan Africa and a major pest of various fruit crops in several world regions including Europe, Asia, Central and South America, causing harvest losses of up to 100% (ref. 5). Furthermore, non-native insects are well known vectors of many human and animal diseases[10]. The tiger mosquito (*Aedes albopictus*), which is spreading rapidly throughout Europe, is a vector of 22 arboviruses, including the dengue, chikungunya and yellow fever viruses[10]. Economic costs associated with insect invasions are estimated to total US $70 billion annually, with health costs amounting to US $6.9 billion[11]. Despite their importance as invaders, non-native insects have received disproportionally less attention by invasion biologists compared with non-native organisms in other taxonomic groups, especially plants[12].

Humanity's dominance, propensity to expand, to trade and to domesticate a wide variety of plant and animal species has dramatically influenced the history of human-mediated dispersal for thousands of years[13]. Despite this long history, most research on invasion dynamics has focused on modern post-1950 globalization of trade and travel and considers globalization to be a steadily rising phenomenon responsible for the steep acceleration of global species introductions[14–16]. However, some species introductions can be traced back to the earliest human migrations and the spread of agriculture, which occurred over 10,000 years ago[13]. Furthermore, the magnitude of global exchanges has not increased steadily but has fluctuated over time – decreasing during times of economic crises, for example[17]. Large-scale geopolitical events, such as the rise and fall of European colonialism, have affected the global movements of commodities and people. In addition, technological innovations have also influenced the nature of species spread. For example, the containerization of products greatly increased both the speed and efficiency of product transport, but also enhanced the survival of stowaway species[1]. The ease of access to the internet in the twenty-first century has enabled online trading, including the trade of exotic pets, which has the potential to become a major pathway for non-native species introduction and spread[18,19].

We need to understand how different aspects of global trade affect the spread of non-native insects, and biological theory alone cannot explain where, when and how species invade[20]. The field of invasion biology has made great progress in better understanding the roles of habitat or species characteristics that affect invasion success[21–25] but less attention has been given to human-mediated dispersal[26]. There is an urgent need to investigate human-mediated spread of species globally[27]. However, a broad-scale synthesis of temporal dynamics and spatial patterns of insect invasions in the light of ongoing globalization is still lacking.

In this Review, we synthesize research on the effects of globalization on temporal dynamics and spatial patterns of insect invasions and highlight research priorities in these areas. We summarize predictions for future invasions and explore possible options for the mitigation of further invasions (Fig. 1). We conclude that non-native insect introduction routes are often complex, resulting in a high frequency of secondary introductions from trade or transport hubs found in interceptions at ports of entry. Global intercontinental flows of insects disproportionately originate from the European Palaearctic, whereas the Afrotropics, Neotropics and Indomalaya have incurred large invasion debts as recipient regions. We find that

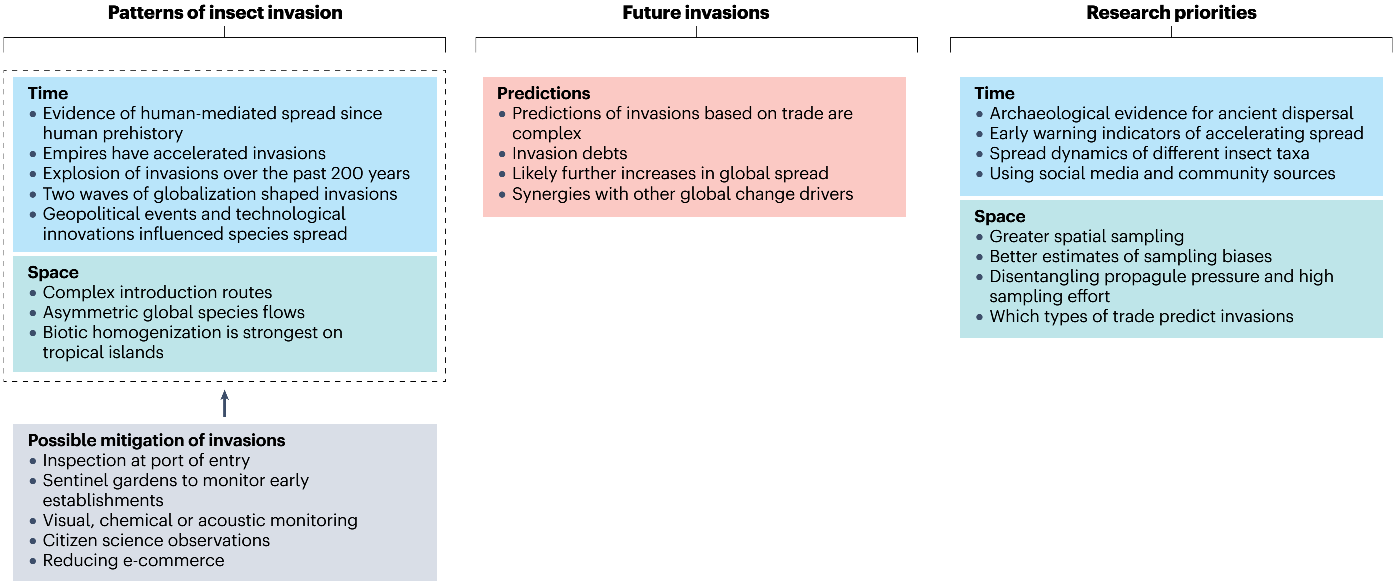


**Fig. 1 | The globalization of insect dispersal.** Synthesis of the key points of this Review, summarizing how globalization of trade and transport affects patterns of global insect invasions over time and space. Mitigation strategies and future research priorities to develop a better understanding of global insect invasions are indicated. Interdisciplinary collaboration is crucial to research in the invasion science field and will influence future research priorities.

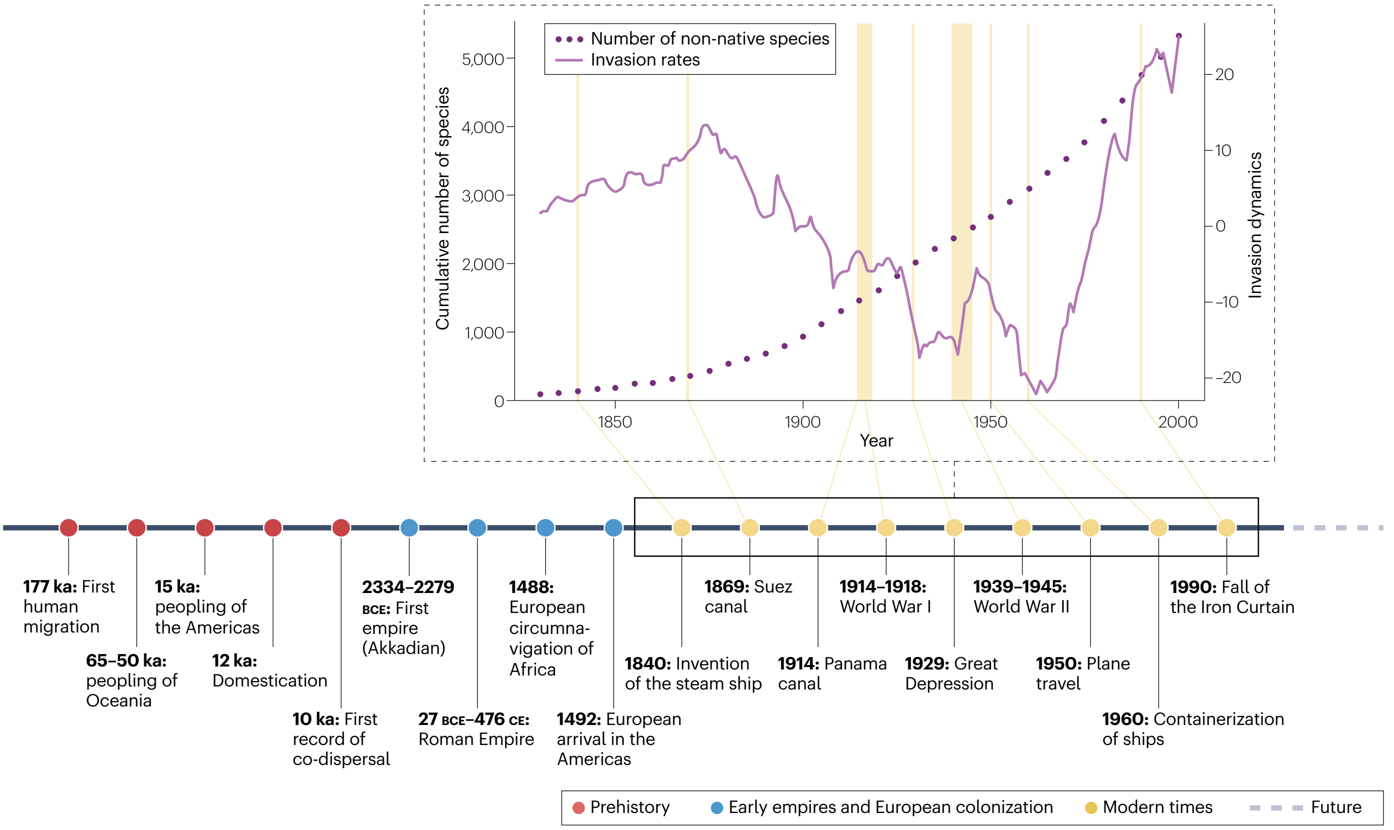


**Fig. 2 | Timeline of events increasing global insect dispersal.** Multiple facets of the history of human globalization (timeline) have influenced invasion dynamics (purple dotted line) and resulted in the accumulation of non-native species over time (purple solid line). The total number of established non-native insect species is based on the FirstRecord database (https://dataportal.senckenberg.de/dataset/global-alien-species-first-record-database) as of July 2024 (ref. 4). Global insect invasion rates account for variations in sampling effort over time based on a null model of insect invasion dynamics[52].

insect invasions have led to biotic homogenization of communities, particularly on tropical islands, and the erosion of biogeographic boundaries. Moreover, we expect invasions to increase further and their dynamics to shift, especially with the opening of trade routes and introduction pathways.

## Temporal dynamics since prehistory

Insect invasions have a long history, which started when humans began to migrate and intensified with the advent of agriculture and with increased modes of transportation. However, the spread of non-native species greatly accelerated after the Industrial Revolution, when globalized trade and travel became faster and more efficient. This general acceleration of invasions is, however, punctuated by specific geopolitical events.

### Neolithic humans facilitated insect dispersal

Insects have been living in close association with humans since human prehistory[28] and have been dispersed through human movement possibly since the first human migrations out of Africa, as early as 177 thousand years ago (ka)[29,30]. The earliest archaeological evidence of human-mediated dispersal of insects can be dated to 10 ka (ref. 28) (Fig. 2). Humans eventually colonized every continent, reaching Oceania between 65 ka and 50 ka (refs. 31,32) and the Americas around 15 ka (ref. 33). Owing to the rarity of insect fossil preservation from that time and the lack of dedicated research[34], records of insect dispersal pre-dating agriculture are scarce[35]. Plant and animal domestication has been dated to the mid-Neolithic period (around 12 ka), leading to the spread of early farming and a substantial increase in human populations driven by increased resource availability[36]. Several plant and animal species were intentionally introduced to new regions for agricultural purposes as humans continued to expand their range[36], in the process accidentally dispersing insects associated with crops[37], livestock[30] and pets[38].

Surplus resources as a result of improving agricultural technologies amplified the need for long-term food storage, creating ecological niches that facilitated the movement and establishment of insect pests such as the grain weevil (*Sitophilus granarius*), which could have caused considerable losses of harvested grain[35]. Being flightless, and therefore having limited dispersal capacity, the synchronous appearance of grain weevils across scattered archaeological sites can be interpreted as evidence of the early spread of a pest in an emerging agricultural context[35]. Evidence of insect feeding activity in unexpected locations, such as outside their historical ranges, can sometimes be interpreted as evidence of unintentional trade-linked introduction; for example, the detection of a storage-associated weevil (*Rhyzopertha dominica*) in Santorini, Greece[35].

### The advent of early long-distance trade routes

The advent of Bronze Age (about 3000 BCE) and Iron Age (1200 BCE) ancient empires[39] and their trade routes, such as the Silk Roads in Eurasia (around 138 BCE to 1453 CE) expanded human movement and long-distance trade. Genetic analyses indicate that this expansion led to global introduction of non-native insects, mostly through intentional dispersal of domesticated hosts[40,41]. Complementing archaeological evidence with genetic analyses can help to retrace historical insect movements[42]. Trading of peaches in Eurasia along the Silk Roads seems to have shaped the current distribution of the mealy peach aphid (*Hyalopterus arundiniformis*)[40]. Similarly, the small cabbage white butterfly (*Pieris rapae*) was dispersed along the Silk Roads[43]. It is likely that many other species yet to be studied were similarly dispersed. Alongside the increased trading facilitated by the Eurasian Silk Roads, the Islamic Umayyad and Abbasid caliphates also intensified commercial and military activities, thereby probably contributing to the accidental dispersal of several insect species[44]. Population genomic data suggest that the German cockroach (*Blattella germanica*) originates from Asia, where its closest ancestor lives in close association with human settlements. It has been estimated that this species spread westwards to the Middle East around 1,200 years ago along these early Islamic trade routes[44].

Species introduced in such historic periods can now be mistaken for native species, because they have become an integral part of ecosystems and human economies and culture, as is the case for the cochineal (a scale insect)[45] and the Chinese oak silkworm (*Antheraea pernyi*)[46]. Debate exists as to whether these long-naturalized species should be considered native or non-native[47], with implications for restoration and management priorities.

### Colonization promoted invasions

Exploration and colonization by European empires between the fifteenth and nineteenth centuries marked the beginning of modern globalization. The advent of modern colonialism has been a major driver of the increase in biological invasions that transformed patterns of species movement from sporadic introductions within continents to frequent, repeated and intentional introductions from one continent to another[48]. Colonists brought crops and livestock with them and transported weeds and insects as stowaways on imperial ships[48]. The global distribution of non-native plants still bears signatures of European colonialism, in that the compositional similarity of the floras is higher than expected in regions that once were occupied by the same empire[49]. However, the effect of European colonialism on non-native insect distributions still requires careful investigation. In former European colonies, most non-native insects that have established so far have originated from Europe. For example, in Canada and Chile, 41% and 50% of non-native insects are of Palaearctic origin[50,51].

### Rising invasions over the past 200 years

The past two hundred years have seen a phenomenal increase in new records of non-native species[4], which have occurred in two main waves[52]: 1850–1914, and 1960 to the present day. These waves correspond to two historical periods of globalization characterized by abundant open trade and separated by a long period with a global recession and two world wars[52].

The 1840s marked the beginning of major technological advances leading to an unprecedented expansion of global trade. The invention of the steam ship (around the 1840s) and the use of containers on trading ships (around the 1960s) enabled faster and more efficient transport, while also facilitating introductions of non-native insect species[53]. In particular, refrigerated containers and wood-based packaging materials both provide excellent conditions for insect survival[54]. Owing to these new technologies, a single container could cover 75,762 km in one shipping trip (421 days)[53]. As well as posing ecological problems, these global insect introductions posed a risk to human health by transporting disease vectors[55].

The advent of affordable freight and travel starting around the 1950s also contributed to the observed increase in insect invasions. Air transportation facilitated international tourism and the trade of certain insect-associated commodities, including freshly cut flowers[53,56]. Horticultural and ornamental plant trade has been identified as one of the main pathways for non-native insect introductions[57–59]. The transport of plants, and with them plant-feeding insects, is probably the reason why non-native herbivorous insects are over-represented compared to fauna, as well as why their relative proportion among non-native insects is continuing to increase whereas that of other trophic groups such as predators and detritivores is experiencing decline[60].

In addition to shifting introduction pathways, new infrastructure for trade and transport can accelerate invasions. For example, the construction of the Suez canal (1869) and the Panama canal (1914) led to a major increase in marine biological invasions[61,62]. Although the analytical focus so far has been on marine invasions when considering the effect of these pathways, ships moving via these new routes almost certainly transported many insects and other stowaway organisms. By extension, China's investment in new ports and infrastructure (such as the Belt and Road Initiative[63]) and the opening of trade routes due to climate change (including the Arctic trade route[64]) are highly likely to facilitate new invasions.

Since the 1800s, at least 6,700 non-native insect species have been recorded as established worldwide[1], although this is likely to be an underestimate and actual numbers are estimated to exceed 10,000 species[65]. Global biological invasions do not currently show signs of slowing down[4] and are even accelerating in Europe[66]. Despite growing accessibility to big data through initiatives such as the Global Biodiversity Information Facility (GBIF), global trends in the post-2000s in insect invasions remain largely unknown.

### Geopolitical events influence introductions

Invasion rates are rising globally, but on a regional scale these rates can be variable. Geopolitical events can both facilitate and disrupt the movement of species through direct introductions or by affecting international trade openness. For example, the fall of the Iron Curtain in 1989 and the dissolution of the Soviet Union have been implicated in the massive spike recorded in insect invasions throughout Europe[66]. Conversely, the Cuban Revolution decreased plant introductions in Cuba compared with other Caribbean islands, by reducing tourism and international trade[67]. In China, the expansion of commercial activities and tourism has been linked to the accelerating spread of non-native insect species[68].

Armed conflicts can reduce biological invasions because of decreased international trade flows, but wars can also favour biological invasions[69]. For example, insects were accidentally introduced to the Americas and Europe as contaminants in wartime supplies[69]. Non-native species were also intentionally introduced through agroterrorism regimes in World War II and the Cold War, such as the fungus *Aspergillus* that can disrupt harvest yields[69]. The French and German governments also had breeding programmes for at least 15 insect species with capacity to inflict agricultural damage. Furthermore, arme accelerate biological invasions through habitat disturbance, thereby leading to more opportunities for invasions and spread[69].

## Spatial patterns of insect invasions

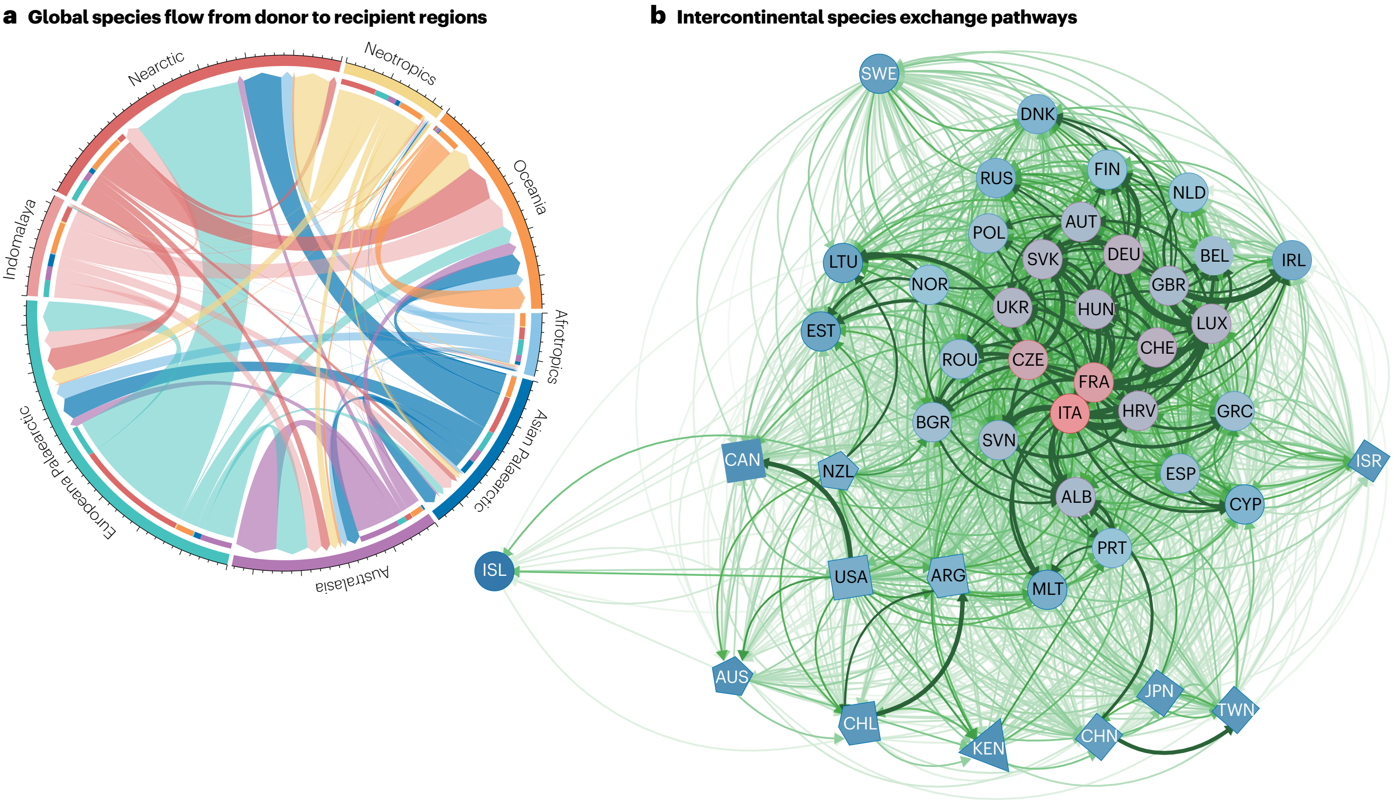
Non-native species are not homogeneously distributed across the world and intercontinental species flows are asymmetric between donor and recipient regions, resulting from unequal globalized trade routes and complex introduction pathways. As a result of these global exchanges of non-native species, assemblages are homogenizing, particularly on islands.

### Complex introduction routes

Introduction routes of non-native insects frequently include recurrent jump dispersal, multiple introductions from the native range, admixture and sometimes back-introductions into native ranges[42,70], and often include bridgehead effects[71]. Secondary introductions across multiple insect species can originate from non-native populations rather than the native ranges. Evidence for this process comes from interceptions at ports or airports, originating from the invaded range of the species rather than from their native range. For example, the proportion of secondary interceptions of ants in the USA and New Zealand that came from invaded regions was 75.7% and 87.8%, respectively[72], whereas the proportion of secondary interceptions of ants was 36% in the Taiwan region[73]. Similarly, among interceptions of non-native termites in the USA, 46% were secondary interceptions[74]. Border interception data indicate that secondary spread is a key feature of the establishment and distribution of non-native species. A potential mechanism to explain the success of the bridgehead effect is the evolution of enhanced invasiveness (that is selection for traits increasing spread) in the bridgehead populations[71]. However, there is only limited evidence that the success of a bridgehead population is due to adaptive evolution in the non-native population leading to greater invasiveness[75]. Another possibility is that the bridgehead populations were established in well connected trade or transport hubs, thereby facilitating secondary spread. However, the location of these hubs could change as global trade networks change according to altered commodity demand or geopolitical events.

### Global species flows and distributions

Pairwise species flows from donor to recipient regions for non-native insects have been established for general insect assemblages[2,76,77], for ants[78,79] and for beetles[80]. These associations indicate that intercontinental exchange among regions exhibits invasion asymmetry[77], with some donor regions being over-represented relative to others. For example, the European Palaearctic has been an important exporter of non-native insect species[2,81] (Fig. 3a). The greatest flow was from the European Palaearctic to the Nearctic[81,82], but flow in the opposite direction from the Nearctic to the European Palaearctic was much smaller[76].



**a** Global species flow from donor to recipient regions

**b** Intercontinental species exchange pathways

**Fig. 3 | Intercontinental species flow of non-native insects. a**, Global species flow from donor to recipient biogeographical regions. **b**, Spatial network of species exchange pathways. Countries or regions are shown as nodes (shapes correspond to different continents), with their labels corresponding to the ISO 3166-1 alpha-3 codes. Intercontinental species exchanges are asymmetrical, and well-connected trade and transport hub regions have a central role in the networks of global insect spread (the pinker the colour, the more central a node is in the network (the more species it shares with other countries)). Data for panel **a** are from ref. 2. Panel **b** reprinted from ref. 85, CC BY 4.0 (https://creativecommons.org/licenses/by/4.0/).

However, such global flows reflect the complex patterns of supply and demand, which are not static; for example, trade patterns shifting towards the Southern Hemisphere, or the development of countries or regions into global superpowers. These changing global balances among trading partners reorganize the global trade network[83], inevitably changing invasion asymmetries, and potentially overshadowing Europe as a species donor.

Importantly, species flows between donor and recipient regions can misrepresent true introduction routes, which frequently include multiple sequential introductions via bridgehead populations. Accordingly, these interpretations of global species flow might be distorted by the bridgehead effect, as demonstrated by the secondary interceptions of ant species flows to the USA[78]. To account for complex species flows, researchers are now dedicating more attention to understanding the role of networks in the spread of non-native species[84]. Using first recordings of 3,702 non-native insects and a sequential pattern mining approach, a hierarchical spread has been identified, with Italy and France acting as central hubs for insects before onward dispersal (Fig. 3b). Targeting countries identified as central hubs for improved biosecurity measures could have cascading effects on the spread network of non-native species, thus reducing biological invasions[85].

The species richness of non-native insects is largely unequal among countries and regions, with some, such as Europe, North America, Australia or New Zealand, being more invaded than others over the past centuries. Similarly, increases in invasions to South America, China and tropical Asia have been identified in the twentieth century (Fig. 4). This disparity is in part a consequence of asymmetric species flows from donor to recipient regions.

## Drivers of global species flow and distribution

The asymmetry of species flows between donor and recipient regions is due to several key drivers that seem to vary in important ways. Propagule pressure has been considered the principal driver of non-native species establishment[86], yet there is mixed evidence for international trade (a proxy for propagule pressure) as a driver of global insect flows. For example, cumulative trade was the most important factor in explaining bark beetle (Scolytinae) species flows among six biogeographic regions (the Nearctic, the Neotropics, the Palaearctic, Indomalaya, the Afrotropics and the Austro-Pacific)[80]. However, when all the insects of three world regions (Europe, North America and Australasia) are considered, neither import value nor species source pools influence global flows, indicating that historical plant introductions might be more important[76].

Differences in the species pool size of the donor region could influence species flows. In bark beetles, historical movement of non-native species might have depleted the availability of new species source pools in the native range[86], which can slow the accumulation of emergent non-native species in the future[87]. However, the depletion of source pools of candidate species that might be introduced in the future seems to be much slower in insects than in other taxa (including other invertebrates, birds, mammals, vascular plants and fishes)[87].

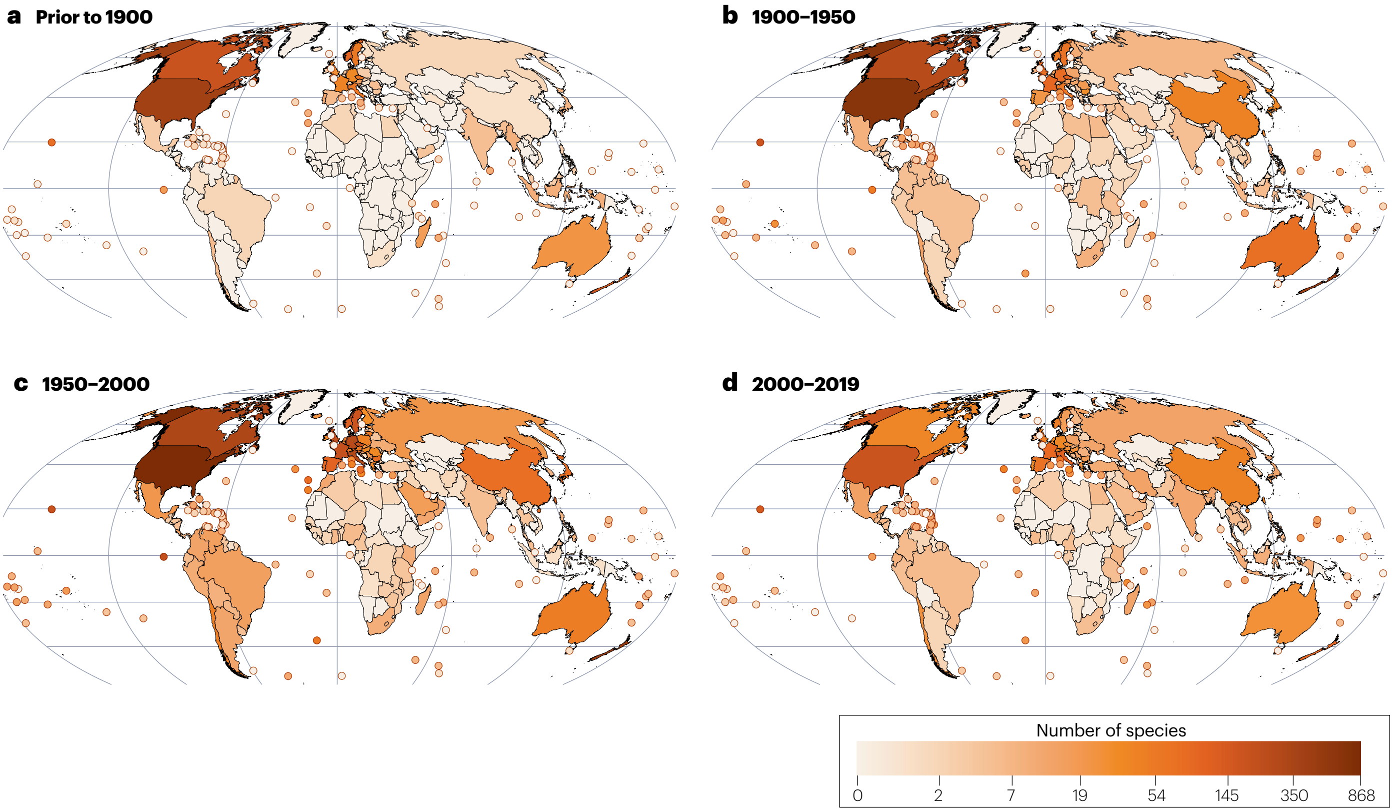


**Fig. 4 | Number of non-native insect establishments per region over time.** **a**–**d**, The cumulative number of established species for the years prior to 1900 (**a**), between 1900 and 1950 (**b**), between 1950 and 2000 (**c**) and between 2000 and 2019 (**d**). Hotspots of insect establishment before 1900 include North America, Europe, Australia and New Zealand, mainland China and Japan since the 1900s, and several South American regions and tropical Asia after 1950. Data for all panels are from ref. 4.

Another driver influencing species flow is the environmental conditions in the destination region, which help to determine the success of species establishment. Climatic similarity between native and non-native areas has been identified as a key factor determining the size of species flows within a global insect sample[88], because climatic conditions strongly influence the capacity of a species to survive and reproduce in a given area.

Non-native plant diversity also shapes global patterns of insect invasions, and this relationship has persisted through time[89,90]. The flow of insects in the modern day is well predicted by plant flows from more than a hundred years ago (until 1900), which is a more substantial predictor than general trade flows[2]. The establishment of non-native plants creates the necessary pre-conditions for the invasion of many insect species that reassociate with their host plants from their native range[90].

Finally, given that biological invasions involve multiple stages, including transport, introduction and establishment[91,92], the dominant mechanisms at different stages might vary. By making this assumption and mapping the insect global flows at the transport and establishment stage of the invasion process, transport flows have been shown to correlate with the economic status and global purchasing power of recipient countries, whereas the flows of established insects are also influenced by the biogeography of recipient regions[78].

The spatial patterns of non-native insect species richness at a global scale cannot be explained by differences in country or region size or climate, but instead are largely driven by socio-economic factors. Non-native insect species richness is greater in countries or regions with high gross domestic product (GDP)[93–95], high national wealth and population density[96], or with a high KOF index of globalization[93], than in those with lower metrics. The KOF index is a composite index measuring the global connectivity of a country in terms of economic and information flows, cultural proximity, social contact and political engagement, and it therefore integrates various dimensions of globalization[97]. Global trade and transport are known to facilitate insect invasions by increasing propagule pressure[77,92] and are therefore important determinants of non-native insect distributions[98]. In particular, countries that were more connected through trade networks for multiple commodities tend to receive more non-native insects than those highly connected for fewer commodities[98]. In addition to socio-economic activities shaping the global movement of non-native insects, the presence of non-native plants is another factor that is important in determining the probability of establishment[90]. At large spatial scales, non-native insect species richness is driven by both native and non-native plant species richness[89]. Thus, although propagule pressure is widely recognized as an important driver of insect invasions, the availability of suitable host plants is also a major determinant of non-native insect distributions[90].

### Homogenization of species assemblages

Owing to the global spread of non-native species, insect communities worldwide tend to become increasingly homogenized. This pattern has been particularly pronounced and is well studied in ants, whose assemblages are becoming increasingly more similar across different regions, especially on tropical islands[99]. Before the spread of non-native ants, species assemblages that were geographically closer were typically more similar[99]. However, the decline of similarity with increasing geographic distance is weakened with the global spread of non-native ants[99]. Consequently, the boundaries of historic bioregions, which are characterized by sudden changes in community turnover resulting from millions of years of evolution and natural dispersal limits, are eroding because of insect invasions[99]. Global biotic homogenization has also been found in plants[100] and terrestrial gastropods[101], but a global analysis for other insect groups is still lacking. On a more regional scale, biotic homogenization has been observed in insect communities of the Southern Ocean Islands, resulting from the establishment of non-native species[102].

The homogenization of landscapes, and in particular cultivated plants, might also favour the homogenization of herbivorous insect communities feeding on them. Forestry and agriculture rely on a small pool of species that are cultivated globally, vastly increasing the opportunity for the homogenization of insect pests among regions[103]. However, these observations are limited to a small subset of insect biodiversity. Further research is required to measure the effect of host plant homogenization on the similarity of insect communities.

Homogenization can also occur at a finer spatial scale. In coastal California, the Argentine ant (*Linepithema humile*) homogenizes ant communities by displacing native ant species that forage above ground[104]. Similarly, ant communities invaded by the fire ant (*Solenopsis invicta*) show greater trait redundancy, resulting in functional homogenization at the landscape scale[105]. Urbanization can also exacerbate homogenization patterns by favouring non-native insects. For example, urban areas in Quebec favour a few abundant non-native butterflies while native species richness is reduced, leading to more homogenized butterfly communities in urban compared with rural habitats[106].

## Future invasions

Future insect invasions can be predicted in space (for instance, identifying areas that are expected to accumulate many new non-native insects based on current invasion debts) and in time (for instance, estimating rates of change in invasion dynamics).

### Predicting invasions using trade metrics

The history of biological invasions clearly demonstrates that connectivity via trade is a major driver of species transfer among regions[53,56,92]. Therefore, invasion science can use these human activities to predict new invasions[1]. A correlation of the number of non-native species per country or region with GDP, with population density or with the extent of human footprint on the environment provides an indication that human activities are linked to the overall level of invasion[107–110]. However, these proxies of trade are heavily generalized and are poor predictors of new invasions[111]. General proxies of trade have also been used to assess the relative importance of trade compared with environmental factors in shaping the distributions of non-native species, with conflicting results. Trade (or a related socio-economic proxy) has been flagged as either the most important driver of invasions[96], as an important factor among others[112], or even as not linked to invasion patterns at all[113].

There are several possible explanations for these inconsistencies in the importance of trade to species invasions. First, time lags between current species flow and past socioeconomic indicators could obscure the link between species flows and trade[114,115]. The contemporary distribution of non-native species is better explained by historical rather than by current human activities[115]. Second, determining the importance of trade can depend crucially on using relevant metrics of trade. Different commodities can have very different global trade networks (Fig. 5). Moreover, linking trade with invasions is complicated by the fact that specific countries can change trading partners over time[15] and that trade networks vary in space, with different countries using different trading partners to import the same commodities (Fig. 5). These patterns illustrate the complexity of using trade flows to predict invasions: because researchers need to deter

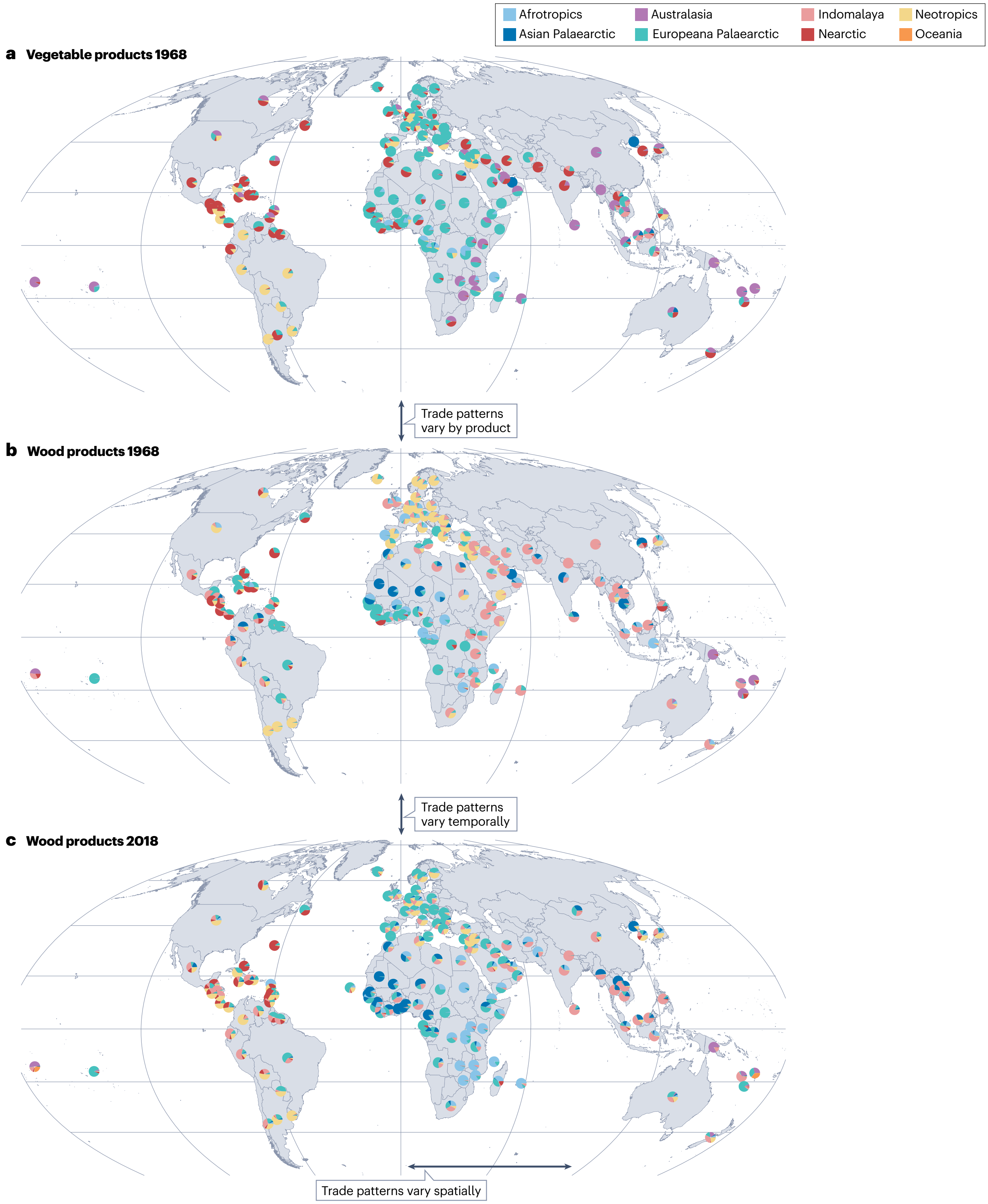

Afrotropics
Asian Palaearctic
Australasia
Europeana Palaearctic
Indomalaya
Nearctic
Neotropics
Oceania
a Vegetable products 1968
Trade patterns vary by product
b Wood products 1968
Trade patterns vary temporally
c Wood products 2018
Trade patterns vary spatially

**Fig. 5 | The variability of global trade flows. a**, Global vegetable imports in 1968. **b**, Global wood imports in 1968. **c**, Global wood imports in 2018. Pie charts show the proportion of imports originating from each continental region. Each map depicts the geographic origin of trade imported by country. Trade flows can vary by commodity (**a** and **b**), by time (**b** and **c**) or by space (**c**). Data for all panels are from the United Nations, downloaded using the 'tradestatistics' R package[147]. Administrative borders of countries are from the Database of Global Administrative Boundaries (GADM 4.1) (ref. 148).

commodities, the time span and the spatial focus of their data to be able to use trade data to understand or predict future invasions of specific species, it might be necessary to have prior knowledge about the biology of a particular taxonomic group and its propensity to be associated with different commodities[116]. For example, flows of ants to the USA are linked to trade in plants and fruits (which from import–export interception records are known to transport ants) but not to agricultural or general trade[117]. However, it is unknown whether such specificity is the rule and whether specific metrics of trade are needed to predict future invasions of particular insect species, or to build risk assessments for focal countries. This understanding would be particularly valuable in the light of ongoing globalization, with emerging economies opening up markets and changing trade networks[15].

Predicting future invasions based on current trade networks is further complicated by transport technologies shifting towards greater speed and efficiency, reducing the time spent in transit and increasing the survival probability of hitchhiking insects in the absence of concomitant advances or investment in monitoring or mitigation[53]. Finally, novel introduction pathways are continually emerging. For example, insects have risen in popularity as exotic pets and are now traded in online stores and shipped by post[19]. If this deliberate movement of insects becomes more widespread, invasions resulting from accidental escapes after intentional introduction could become an important, if unexpected, pathway of spread.

### Invasion debts

Although current socioeconomic activities and transportation are causing new invasions, past activities have also caused important invasion debts[115]. One reason for these debts is the long time lag between establishment and discovery of the non-native species. Some species have been introduced in the past but go unnoticed for decades because they are small and inconspicuous, or because they have not yet reached the critical population size required to cause noticeable effects[118]. It is estimated that 20–40% of established non-native insects remain undiscovered[119].

Invasion debt captures the reality that many non-native species have not yet been detected or have not yet caused any discernible effects. In addition, many species are transported around the world, as is evident from border interceptions, but have so far failed to establish outside their native range[120]. This failure to establish could, in part, be attributed to the absence of suitable host plants. Many insects are specialist herbivores[121] and depend on host plants from their native range for their establishment. As plants are introduced to more regions worldwide, they form new niches for insects, creating the conditions required for insect establishment[90]. On a global scale, some world regions (particularly tropical Asia and Africa) have imported many non-native plants but have not yet observed the non-native insects associated with them[2].

### Global acceleration of invasions

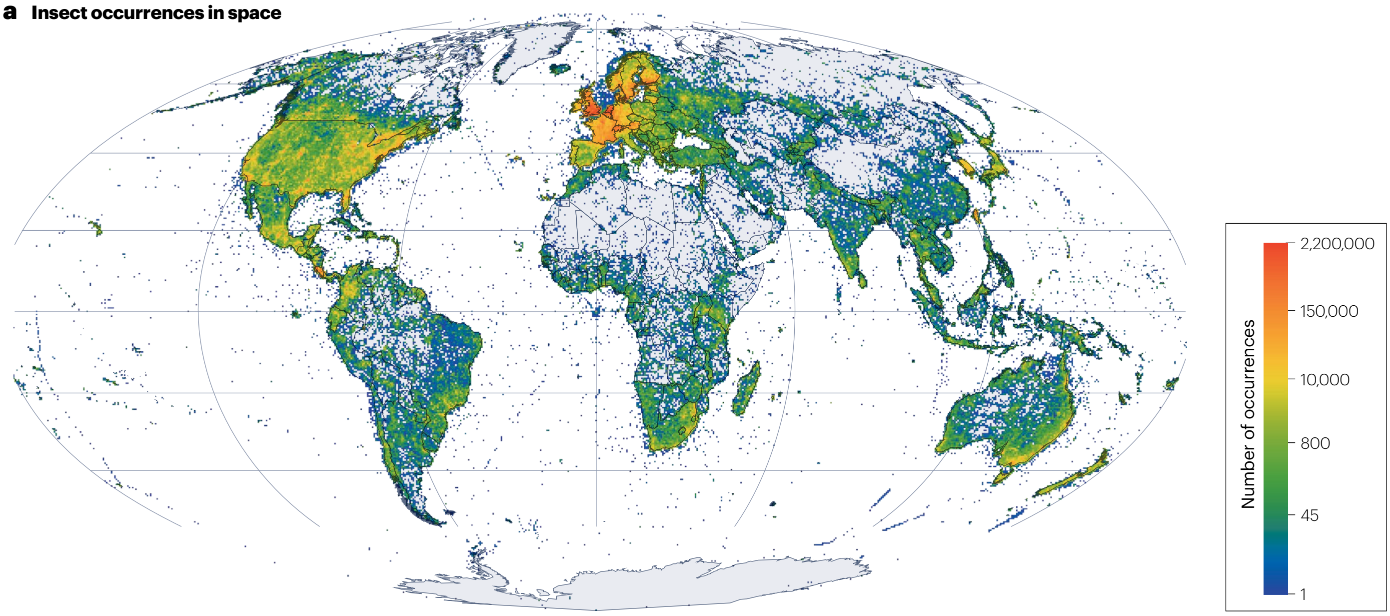
Based on modern invasion dynamics and the size of available species pools, models of the future accumulation of non-native insects until 2050 predict further accelerating global spread[122]. The world regions in which non-native insect richness is predicted to increase most over the next decades are Europe, temperate Asia and North America[122]. Remarkably, this future acceleration is possible because the pool of potential insect invaders has not yet been depleted. As globalization continues to move new species around the planet, an increasing number will establish in regions outside their native ranges[4].

## Possible mitigation

Despite the long history of the intentional and unintentional movement of species, there is little evidence of efforts to limit global anthropogenic spread of organisms prior to the twentieth century[123]. The existence of non-native species was recognized in various parts of the world in the nineteenth century[124–126], including occasional reference to their status as pests[127]. In 1878, the grape phylloxera conference in Bern, Switzerland, led to the first international phytosanitary agreement in recognition of threats due to a non-native plant pest, the North American aphid (*Daktulosphaira vitifoliae*)[128]. A few decades later, the United States Plant Quarantine Act of 1912 created the Animal and Plant Health Inspection Service as an arm of the United States Department of Agriculture (USDA), with the power to regulate the movement of harmful non-native species. This act stands in stark contrast with the numerous acclimatization societies popular in Europe and America in the mid- to late 1800s[128], and with the charter mandate of the USDA "to procure, propagate and distribute among the people new and valuable seeds and plants"[129].

Preventing biological invasion via manual inspection of imports is a daunting task as global trade volumes have grown dramatically. Inspection is difficult, expensive and is often inadequate, with high rates of slippage[53]. Most countries use a black-listing approach, where only species previously identified as potentially harmful and/or likely to establish are denied entry[130]. Several countries have proposed white-listing (where only species deemed acceptable by formal risk assessment are permitted entry) and/or grey-listing approaches (where pre-identified watch-list species are denied entry pending assessment). However, such policies have been challenged under World Trade Organization rules[131], and stricter import regulations (as seen in New Zealand and Australia) have not successfully prevented the arrival of some high-profile biotic threats, including myrtle rust (*Puccinia psidii*)[132]. In addition to inspection, considerable effort has focused on shutting down pathways of non-native pest invasion[133]. In 2022, the International Plant Protection Convention (IPPC) adopted ISPM 15, a binding rule among signatory countries requiring bark removal as well as chemical or heat treatment of wooden shipping pallets, a known pathway for the spread of non-native bark and wood-boring insects. Although apparently effective in reducing interceptions of these insects, concerns about compliance and efficacy persist, prompting some importers to favour processed or non-wood alternatives[134]. Other major pathways of introduction, notably those linked to the horticultural trade, have so far proved more difficult to manage via national or international regulation, despite clear evidence of their role in the spread of non-native species among regions[59].

Other prevention or mitigation approaches have gained traction in recent years. The planting of sentinel gardens and ta using biological attractants (such as insect pheromones and plant stress kairomones) as part of an early detection rapid response network both offer the potential to detect nascent invasive insect populations[135,136]. Technological approaches are also in development for monitoring and mitigation purposes. For example, passive sampling of air or water coupled with rapid sequencing of environmental DNA has potential to aid in the detection of non-native species, particularly as sequence databases, bioinformatic pipelines and high-throughput sequencing platforms continue to improve[137]. Detection of insects via machine-learning-enabled visual, chemical or acoustic monitoring is receiving some focus in biosecurity interceptions or around ports of entry, although such technologies are still largely in their infancy or are tailored to only a small subset of species[138]. Distributed citizen science initiatives such as iNaturalist, EDDMapS or WildSpotter have


**a** **Insect occurrences in space**

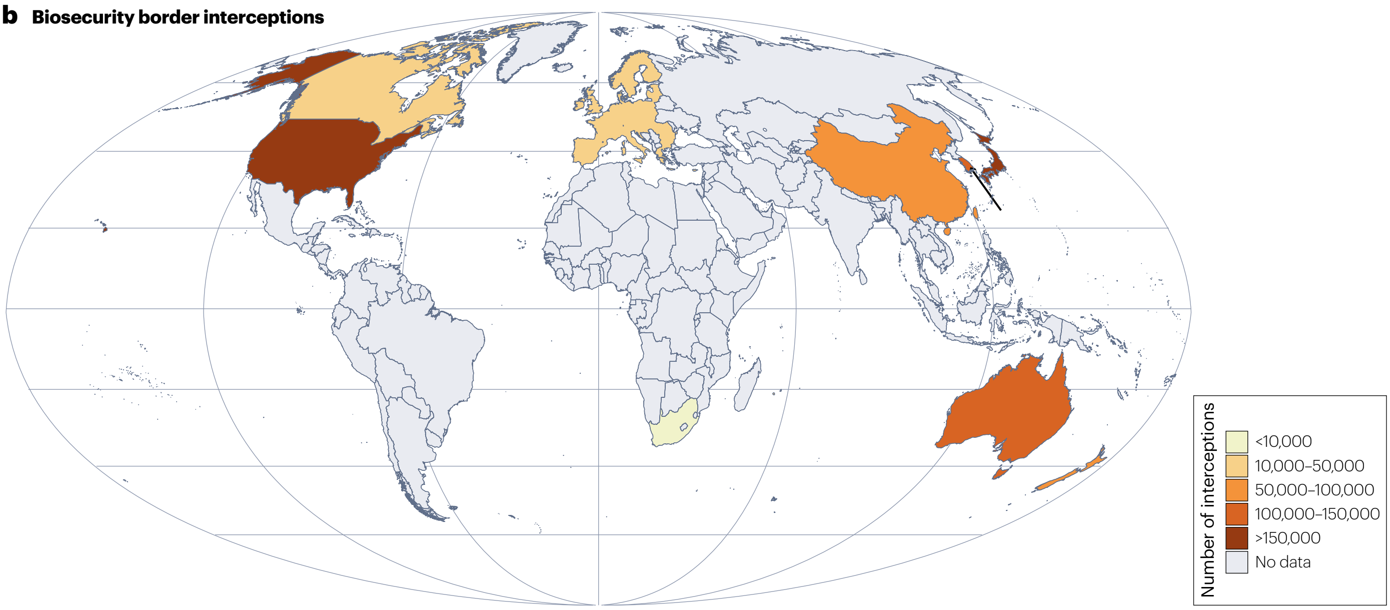

**b** **Biosecurity border interceptions**

**Fig. 6 | Geographic knowledge gaps in insect occurrence. a**, Recorded occurrences of insects (both native and non-native) in space. **b**, Number of border interceptions by biosecurity services per country or region. The spatial pattern of known insect occurrences reveals geographic gaps in our understanding of the transport stage, reflected by border interceptions, with particular scarcity in South America, most of Africa, the Middle East and large parts of South and Southeast Asia. Data in panel **a** are from the Global Biodiversity Information Facility (ref. 149). Data in panel **b** are from refs. 120,150,151.

been successful in mapping species distributions by voluntary contributors using smartphone applications[138,139]. Improved databases and algorithms for automatic and accurate detection of new potential non-native species are powerful tools against established non-native species, although early detection or prevention will require improving research facility infrastructure and technological tools to create portable field-ready devices without automated identification capacities[138]. Finally, web crawling or scraping to detect and mitigate the online trading of living organisms[140] can be useful, facilitating data capture and/or promotion of public awareness via social media platforms. Other mitigation strategies include crowdsourced inspection for the detection of non-native species, either at ports as an outsourced arm of existing inspection agencies or via distributed, web-enabled sensors around the world. These all represent plausible avenues for the mitigation of biological invasion in the years and decades to come[138,139].

## Summary and future directions

Several thousand insect species have already established in areas outside their native range and many more are predicted to arrive in the near future, threatening biodiversity and human livelihood[1,2]. The spread of non-native insects on a global scale has been influenced by multiple facets of globalization, including geopolitical events in history such as wars and economic crises[52], the types of traded product[117], and the topology of trade and mobility networks[84], and by technological innovations such as steam ships, containerization and the internet[1]. This complex multitude of aspects of change demands a much better understanding of how precisely these socio-economic aspects influence invasions[70]. Direct evidence of spread, particularly of causal links between invasions and globalization, is not always clear. Challenges lie in identifying the most pertinent indicators of globalization to predict invasions, given that many metrics of trade and connectivity can vary in time, space and by type of commodity (Fig. 5). Overall, there is a substantial body of literature indicating the importance of a better understanding of human-mediated transport of insects[1,53,141], a necessary starting point for predicting and preventing future invasions. More interdisciplinary work among invasion biologists, ecologists, entomologists, economists, data scientists, social scientists and archaeologists, among others, is essential for this field of research to progress. Here, we suggest key future directions of research for the field to develop a better understanding of the temporal dynamics and spatial patterns of insect invasions.

Obtaining evidence of the earliest human-mediated movements of insects is particularly important to characterize how human history has shaped the distributions of insects worldwide[13]. Research focusing on insects found in archaeological sites worldwide would improve our understanding of the early dispersal of insects. Currently, the evidence is limited to a few well studied sites and species. Targeted efforts to develop more comprehensive evidence of prehistoric dispersal of insects or the role of the Roman Empire and the Spice and Silk Roads in large-scale dispersal of insects could inform a more nuanced understanding of invasion processes and dynamics. To this end, it might be possible to explore genetic tools for analysis of ancient DNA to reconstruct these early dispersal routes[142,143]. To explore insect dispersal over the past two hundred years, it will be important to improve the current datasets of first records of early observations. Despite the growing importance of these datasets, many records remain buried in the scientific and grey literature and are not yet accessible for analysis.

The insect dispersal dynamics leading to present-day distribution are of the utmost importance for characterizing the state of insect invasions now and for predicting future invasions. We suggest that it will be fruitful to explore emergent tools such as data mining of social media websites (such as Instagram) and community sources (such as iNaturalist) where the public can enter observational data for different species[144,145]. These data can be usd in fundamental and applied research to build models for the early detection of accelerating invasions that could in turn be used to prioritize mitigation efforts. Moreover, it is important to improve and better standardize sampling efforts, which are highly heterogeneous worldwide, with some regions still poorly sampled[146] (Fig. 6a). Further key questions include which commodities transport which insects, how specific the association between insects and their transport vectors is[117], and what the time lags between introduction and detection are for different taxa[118]. To address these questions, more extensive databases of border interception data will be useful, as they provide insight into ongoing species transport[120] (Fig. 6b).

Overall, the field of invasion science is still young. Despite progress in building large datasets and analysing global patterns of insect invasions, important geographic knowledge gaps remain (Fig. 6). Disentangling relevant socio-economic factors is not straightforward and the importance of specific geopolitical events, including European colonialism and early trade routes, is still uncertain. We believe that the field of invasion science will make substantial progress in the near future, thanks to increasing interdisciplinary collaboration.

## Glossary

| | |
|---|---|
| Acclimatization societies | Societies dedicated to the establishment of non-native species for the perceived improvement of the local flora and fauna for aesthetic and economic purposes. |
| Bridgehead effects | Secondary spread of species from established non-native populations. |
| Invasion debts | Invasions predicted to occur on the basis of past events. |
| Jump dispersal | Discontinuous long-distance dispersal. |
| Native species | Species that have not established outside their native range. |
| Non-native species | Species introduced outside their native range that have established a self-sustaining population. |
| Propagule pressure | Number of individuals introduced or the frequency of introduction events. |
| Sentinel gardens | Plantation of a variety of host plant species, which can provide early warning of non-native insect species that can use them as hosts. |
| Slippage | Introduction of a known quarantine pest that was not detected at port. |

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## Acknowledgements

The authors acknowledge support by grants from the Swiss canton Vaud, the Swiss National Science Foundation (SNSF grant 310030_192619) and the SERI-funded ERC grant SPREAD (MB22.00086). C.B. and J.R.G. also acknowledge support from Fondation Herbette for the sabbatical visit of J.R.G. to the University of Lausanne.

## Author contributions

The authors contributed to all aspects of the article.

## Competing interests

The authors declare no competing interests.

## Additional information

**Peer review information** *Nature Reviews Biodiversity* thanks Núria Roura-Pascual and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

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