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Globalization and the anthropogenic spread of invasive social insects

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Social insects are among the worst invasive species and a better understanding of their anthropogenic spread is needed. I highlight recent research demonstrating that social insects have been dispersed since the early beginnings of globalized trade and in particular after the Industrial Revolution, following two waves of globalization. Many species have complex invasion histories, with multiple independent introduction events and frequent secondary spread. The major source and recipient regions differ markedly across ants, wasps, termites and bees, probably linked to their different introduction pathways. At a more local scale, anthropogenic factors such as irrigation, urbanization or the presence of railways facilitate invasions. In the future, social insect invasions could further accelerate due to intensifying global trade and novel introduction pathways.

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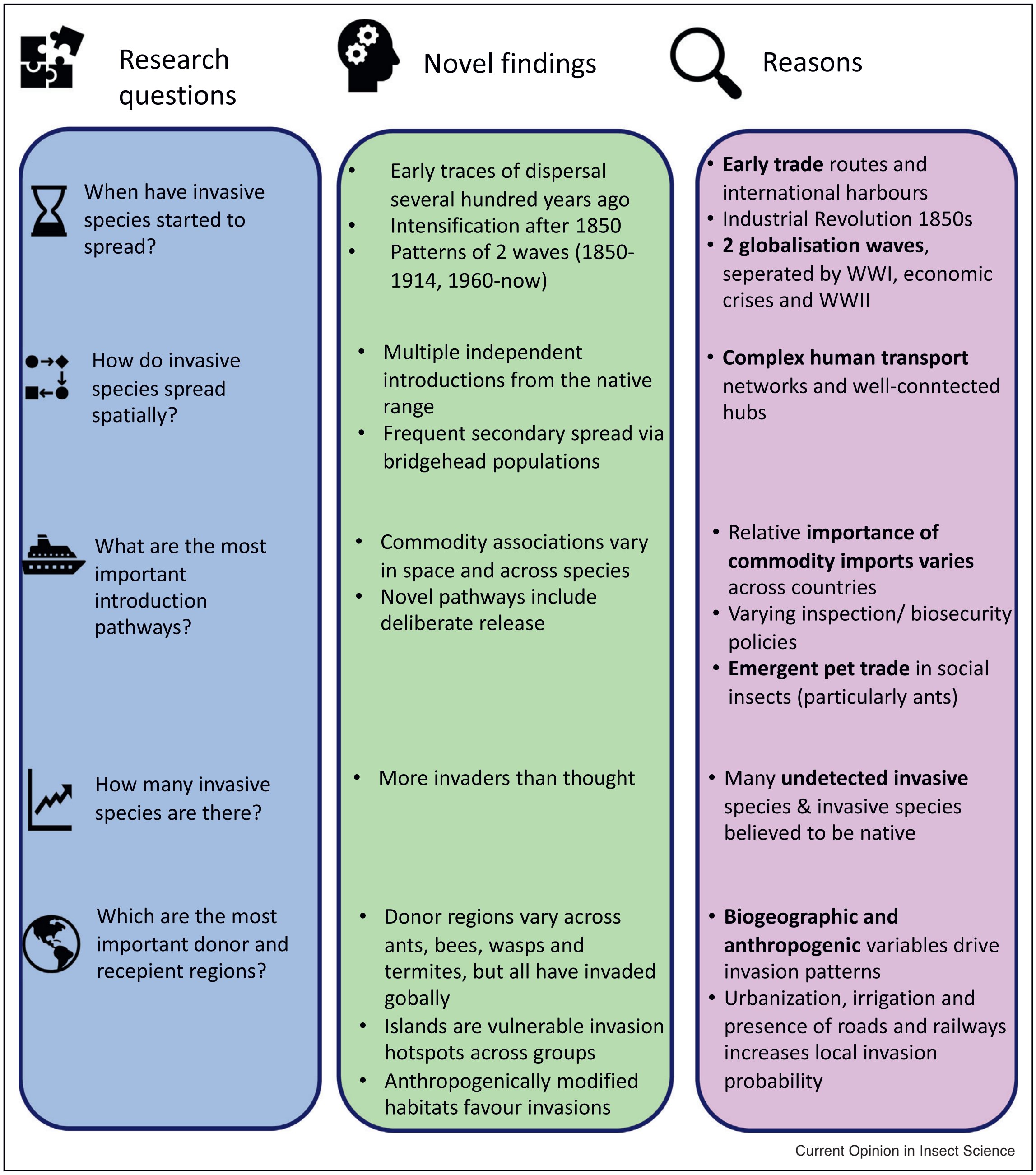
Introduction

Social insects are among the worst invaders worldwide. Only about 2% of all insect species are estimated to be social, but 57% of the worst invasive insect species listed by the IUCN are social insects [1]. Ants and termites contribute the highest number of species to the pool of social insect invaders (defined here as species that have established and spread outside of their native range). But recently, invasive wasps, such as the Asian hornet (*Vespa velutina*) [2] and bees, such as the African honeybee (*Apis mellifera scutellata*) [3], have also spread at a fast rate across their invaded areas, raising concerns by conservationists and the general public. Impacts of invasive social insects include the competitive displacement of native species, hybridization with native species, changes of ecosystem functions, damage to infrastructure, threats to human or animal health through stings or the transmission of pathogens [2,4,5]. The two insect species estimated to generate the highest economic costs globally are both social, the termite species *Coptotermes formosanus* (30 US$ billions annually) and the ant species *Solenopsis invicta* (8 US$ billions annually) [6]. Impacts of social insects are now well documented, but much less is known about how these invasive species have arrived in their introduced range. Here, I argue that a better understanding of the anthropogenic spread of social insects is needed to better predict and prevent future invasions and I highlight recent progress in the field (Figure 1).

Globalization has a long history

Social insects have probably been transported accidentally by humans over long distances since the early establishment of long-distance trade routes, but it is extremely difficult to provide evidence for such early introductions [7]. Research has focused on the last decades when dated records of observation are available for many species. Based on such recent data, it has been suggested that species introductions accelerate with intensifying trade and travel [8]. Yet, it is unclear how much of this steep increase in species invasions can be attributed to the surge in scientific activities recording invasions and to what extent the early phases of globalization have already contributed to the global movement of species. For example, *Coptotermes formosanus* is thought to have invaded Japan at least 300 years ago, based on the current extent of its spatial distribution and the slow reproduction of colonies requiring 5–10 years to mature [5]. Several population genetic studies have also suggested that social insects have started dispersing early. Precise dates are difficult to calculate using this approach, but it allows building potential invasion scenarios. For example, the tropical fire ant, *Solenopsis geminata*, has probably become a global invader in the 16th century when Spanish trade routes connected the New World with Europe and Asia [9]. Similarly, the clonal raider ant, *Oocerea biroi*, is thought to have spread from its native range in Bangladesh via the harbors in the Bay of Bengal which had become major sources of international shipping activity roughly between 1600 and 1800 [10•]. Shipments of agricultural products and timber during the 18th century are thought to have dispersed the subterranean termite species *Reticulitermes flavipes*. This species was introduced from Louisiana to mainland France when Louisiana was still a French territory and has spread subsequently over the western half of the country from Marseille to Paris [11].

Figure 1



Recent research on the anthropogenic spread of social insects: the main types of research questions addressed in the literature, novel findings and underlying reasons explaining these discoveries.

With the beginning of the Industrial Revolution (roughly 1850's), these human-mediated movements of species around the globe have increased with the development of better transport networks and technology. A study on 36 ant species found that invasion rates rapidly increased towards the end of the 19th century, decreasing after World War I and the economic crisis of 1929 until World War II and exploding again after the 1970's when the levels of trade openness (an indicator of international exchanges) exceeding those before the world wars [12]. These invasion dynamics follow the two waves of modern globalization (1850–1914 and 1960–today), known in the economic literature as defining features of the recent world history [13]. The first wave is characterized by exchanges among European countries and their former colonies, while the second wave is defined by more equal exchanges among countries and the emergence of new economic powers [13]. Interestingly, some ant species were more associated with the first wave of globalization, while others benefited mainly from the second wave. Studying these spatiotemporal dynamics allows identifying whose spread has accelerated recently but follows the same trajectory of more ancient global invaders, suggesting that these species have a great potential to invade further in the future [13].

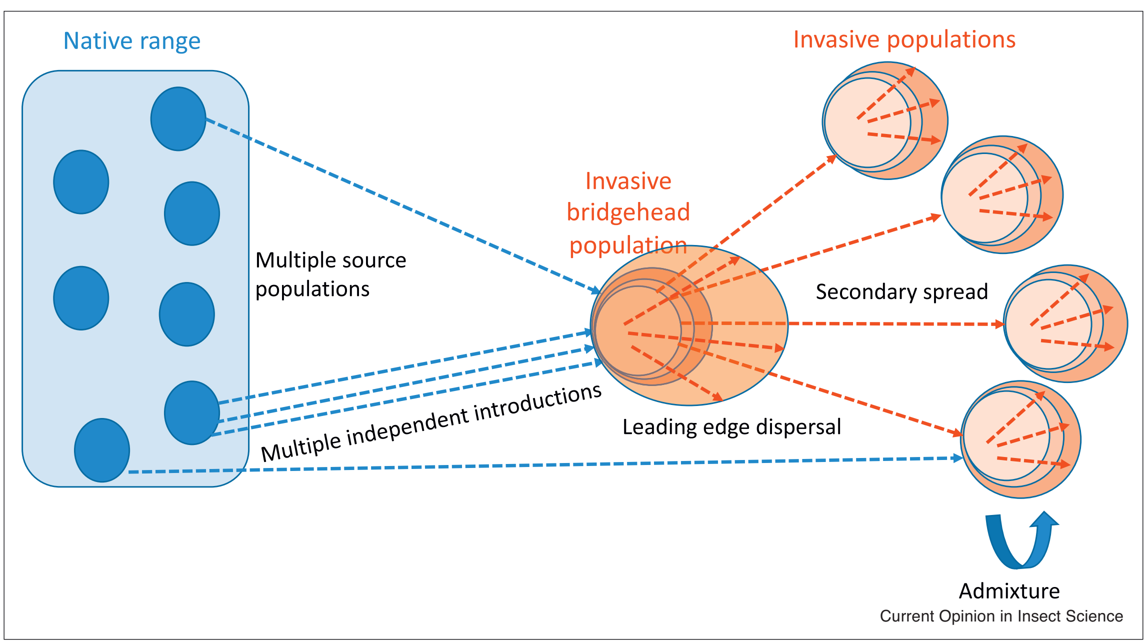
Invasion histories are complex

Evidence has accumulated that spread patterns are often complex, and do not simply follow a sequential invasion process where an introduction from the native range is followed by establishment, population growth and natural dispersal at a local scale in the introduced range [14] (Figure 2).

First, the introduction process is not a single event. Repeated introductions from the native range to the introduced range occur frequently, increasing the propagule size [15–17,18•]. In addition, propagules sometimes arrive from different source populations, increasing the genetic diversity of the introduced population through admixture [18•].

Second, established invasive populations can also serve as sources of new invasions via secondary introductions, a phenomenon known as 'bridgehead effect' [19]. Several studies have retraced invasion histories of a few well-known invasive social insects either at global or local scales and identified bridgehead effects [9,11,18•, 20–28]. To quantify the overall frequency of bridgehead effects, studies have used border interception data of ants [29,30] and termites [31•] at air and maritime borders. They have shown that a high proportion of interceptions arise from the invaded versus the native range of arriving species. In the United States and New Zealand, the vast majority of ant interceptions (76% and 88% respectively) arose from bridgehead populations [29], while this was the case for 36% of ant interceptions in Taiwan [30] and 46% of termite interceptions in the United States [31•]. Bridgehead effects are a self-acceleration process, whereby invasion begets invasion. Indeed, a higher frequency of introduction increases the probability of establishment, which in turn increases the probability of further transport [29]. A potential explanation for bridgehead effects is that an introduced population has evolved greater invasiveness favouring secondary spread. Yet, no conclusive evidence for adaptive evolution generating bridgehead effects is currently available [32]. A more parsimonious explanation for the phenomenon is that secondary spread stems from higher abundance in the introduced range or establishment at a busy transport hub, which may increase the chance of accidental transport [32]. Supporting the idea that bridgehead effects are at least in part the result of the properties of transport

Figure 2



Complex introduction histories of social insects.
The invasion process often includes multiple independent introductions (different arrows pointing from the native range to the same introduced population), sometimes from different source populations within the native range, admixture in the introduced range (arising from the encounter of different source populations in the introduced range) and secondary spread over long distances in addition to local leading-edge dispersal (represented visually by several circles of different sizes, symbolizing progressive outward movement from an initial point of introduction).

networks, studies have found that most secondary introductions arise from geographically nearby hub regions [29,30,31•,33•,34].

Social insects have different introduction pathways

Variations in overall trade openness are strongly correlated with ant invasions over the last two hundred years [12]. But, it is necessary to understand more precisely what types of trade transport different taxa of invasive species. Ants, wasps and termites are mainly transported by accident on cargo [2,5,35]. But not all types of cargo carry the same risk of being infested [36] and species may differ in their commodity associations. Ants intercepted in Australia have been found mainly on live plants, wood, vegetables and fruit [33•], while ants intercepted in Taiwan are most frequently associated with wood [30]. Some of these differences among interception datasets reflect differences in biosecurity policies of different countries (e.g., a focus on wooden products or searching for particular taxonomic groups), but others are linked to genuine differences among species and commodities imported by different countries. It is a challenge for future research to try and tease apart these factors and quantify species-commodity associations across multiple countries.

Most social insects have been introduced accidentally, hitchhiking on human transport or contaminating traded goods. However, bees have been mostly introduced deliberately for agricultural pollination. For example, the iconic African honeybee (*Apis mellifera scutellate*) was introduced to Brazil in 1956 to establish honey bee populations better adapted to tropical conditions [3]. This sub-species then spread rapidly across South America and hybridized with European honey bees [3]. Similarly, the bumblebee species *Bombus terrestris* and *Bombus ruderatus* have been introduced for pollination in agricultural landscapes but have escaped and spread rapidly across Chile, displacing native species. In addition to such 'classic' deliberate introductions, there is a new phenomenon of voluntary spread of social insects: the global trade in invertebrates as pets. More than 500 species of ants are proposed by online sellers worldwide, including 13 of the 19 most invasive species listed by the IUCN (Gippet *et al.*, unpublished data). So far, this emergent trade is too recent to be responsible for many introductions yet. However, it is well established that pet owners of species belonging to other taxonomic groups often release animals, which can subsequently become invasive. Therefore, it is likely that trade in ants as pets will become a future invasion pathway.

Many unknown species could be invasive

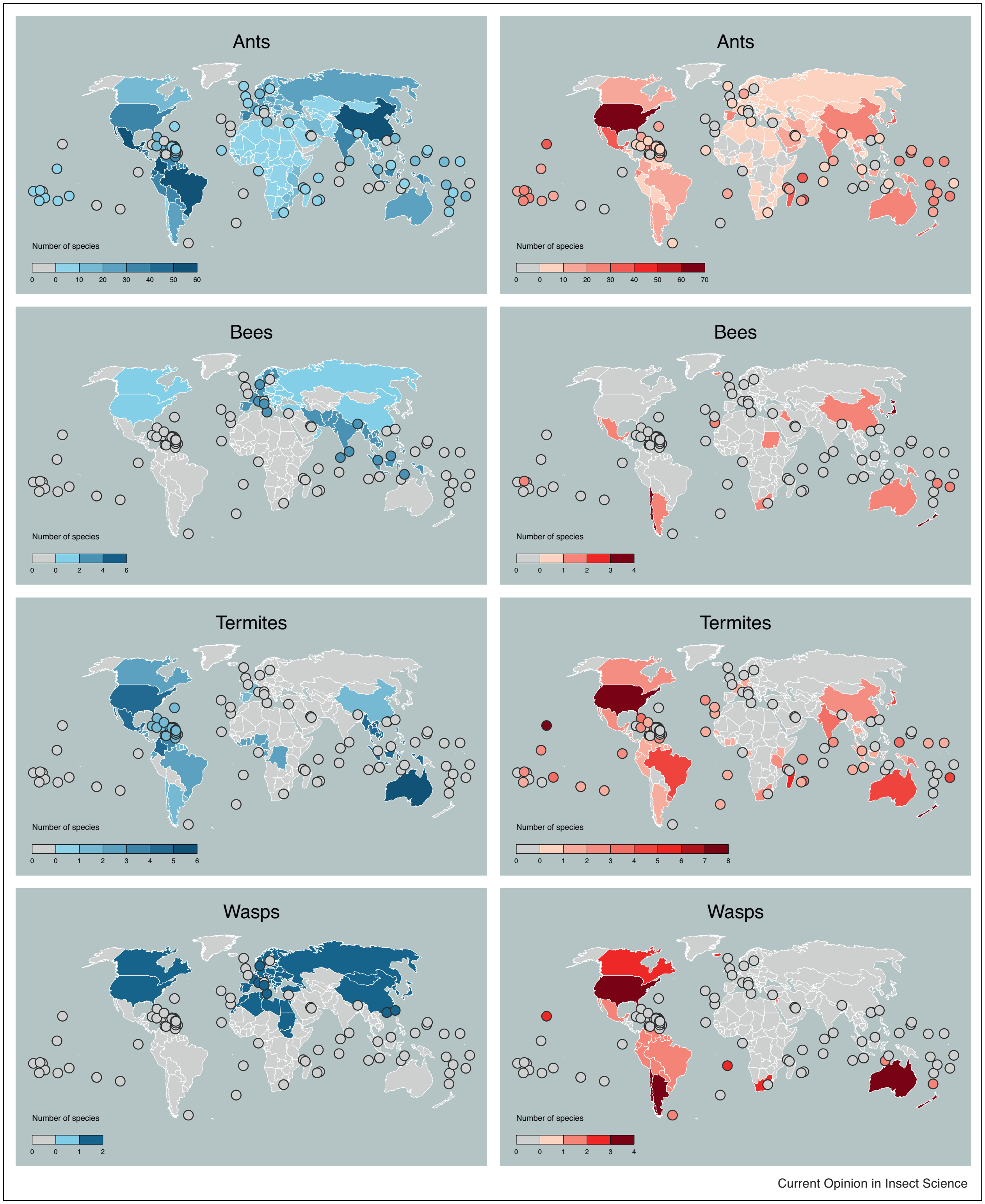
Currently 252 ant and 28 termite species have recorded populations outside of their native range, but their true number might be much higher. Interception records indicate that many more ant [37] and termite [31•] species are dispersed accidentally than actually established. To infer the total number of worldwide established species, the frequency of rare species detected in interception and establishment records has been used to estimate species richness [37]. This approach has yielded an estimated number of 593 established ant species, which is more than twice the number of currently known introduced ant species [37]. It would be useful to detect these potentially established species as early as possible in order to prevent further spread. As sampling efforts by researchers are necessarily limited by the available resources, a promising approach is to involve the general public. While participating in a recent citizen science project in Denmark, children have discovered the introduced ant species *Tetramorium immigrans* in the Botanical Garden of the Natural History Museum of Denmark [38]. As citizen scientists tend to sample ants in more disturbed anthropogenic habitats than professional scientists, they may have a greater chance of detecting invasive species early as they collect in areas of likely introduction of invasive species.

In addition to undetected introduced species, there may be detected invasive species, but which are commonly thought to be native because they have been established for a long time. This was the case in several termite species, including *Reticulitermes santonensis* formerly thought to be native to France and *Nasutitermes polygynus* formerly considered native to New Guinea, until molecular tools demonstrated that they were actually invasive there [5].

Invasion hotspots of social insects

A major challenge of invasion biology is to understand which continents serve as donor and recipient regions of invasive species. Past research has found striking differences in plants [39], amphibians and reptiles [40]. To explore if there are such differences among four groups of social insects, I extracted distribution data from the literature (see Material and Methods) (Figure 3). The source regions of ants include almost all continents with the exception of Africa where only few invasive species are native. Invasive social bees (of the genera *Apis* and *Bombus*) primarily originate from Western Europe and South-East Asia. Invasive termites are mainly native to the Americas, Oceania and South-East Asia and invasive social wasps (genera *Polistes* and *Vespula*) are native to the Northern hemisphere. Future research could explore to what extent these differences are linked to different invasion pathways or native source pools (number of species potentially exported by each region). Hotspots of species establishment are distributed globally for all four groups (Figure 3). Islands are particularly vulnerable to invasion, which may be because they import much, are

Figure 3



Native regions (left colum, blue) and invaded regions (right column, red) of invasive ants, bees, termites and wasps.
The colour gradient corresponds to increasing numbers of species.

more connected through the transport network over large spatial scales, or, alternatively, because they have a depauperate native fauna unable to resist invaders [5,41]. Among islands, those that have denser human settlements and which are less isolated from the continent have higher densities of invasive wasp species, suggesting that both biogeographic and anthropic variables are important in determining invasion hotspots [42•]. The relative importance of these factors may vary. For example, it has been found that the current distribution of Argentine ants is mainly determined by climatic factors and not international imports [43]. However, this could be scale-dependent. At more local scales, most studies on the spread of invasive insects have found that anthropogenic influence was crucial. For example, the distance to railroad tracks and the presence of buildings influenced the spread of the invasive termite species *Reticulitermes flavipes* [11,44]. Irrigation has also been found to increase the spread of certain invasive wasps [45] and ants [46].

Conclusions

Historically, research has concentrated on the biology of social insect invaders highlighting important life-history traits (e.g., [4]) favouring invasiveness, characteristics of abiotic environments increasing their invasibility (e.g. [47]) and species interactions that can influence community vulnerability or resistance to invasion (e.g., [48]). Until recently, anthropogenic factors have been neglected despite their obvious importance for invasive species. Here, I have synthesized recent progress in understanding the influence of globalization on temporal and spatial patterns of social insect invasions. Understanding how exactly past movements of goods and people have transported invasive species will help making predictions about future spread. This is particularly important as additional anthropogenic drivers of global change, such as urbanization [49] and climate change [47], will also increase the likelihood of invasions. The potential synergies between these factors need to be explored in more detail to better assess future invasion risks. To achieve that, biologists need to do more cross-disciplinary work that investigates the details of human movements and trade and how they may influence the accidental spread of species.

Material and methods

The data distribution data for ants was sourced from the Antmaps [50], for bees from Russo [51], for termites from Evans et al. [5] and for wasps from Manfredi et al. [52]. The country list for each species was supplemented by data sourced from the Invasive Species Specialist Group of the IUCN when possible [1]. When a region larger than a country was mentioned as part the species range (e.g 'Western Europe'), I considered that all countries within that region as part of the species range. Additional occurrence data (point locations) were sourced from the GBIF [53] and a country was added as part of the species range if it included at least 10 occurrence points to avoid erroneous observations.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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