Biological invasions: the secret domination of alien ants

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Summary

Globalization has contributed to the spread of thousands of species, yet a few harmful species have attracted most attention. However, evidence is accumulating that introduced ants are a particularly important group of global invaders and can dominate native insect communities.

The global biodiversity crisis is a hallmark of the Anthropocene, with numerous species declining in abundance or even going extinct due to human activities [1]. There are many ways in which humans may threaten wildlife, ranging from direct exploitation to pollution, urbanization, deforestation, and climate change. One of the most important drivers of current biodiversity loss is the global ongoing movement of thousands of species around the planet [2]. Once introduced outside of their native range, some may displace resident species through competition, predation, herbivory or the transmission of deadly diseases. The reason why some and not all introduced species wreak havoc is still debated and probably quite case specific. But potential causes of the sudden explosive population growth include the release from enemies present in the native but not in the introduced range, the availability to exploit new resources, the filling of an empty niche, or the possession of “novel weapons” -traits of the invader- that harm a naïve recipient community which has not co-evolved with the invader [3]. Collectively, introduced species have become a major part of communities worldwide, contributing to biotic homogenization [4] and breaking classic biogeographic boundaries [5]. Worse still, invasion rates are steeply rising with increasingly globalized trade and transport. The economic development of more and more countries will open new pools of species that have lacked the opportunity to travel so far [6].

Among the poster children of biological invasions figure species like the tiger mosquito (vector of many human diseases), the Asian longhorn beetle (destroyed millions of hectars of hardwoods), chytrid fungus (threatening half of all amphibian species), or Japanese knotweed (clogging waterways). Generally, species that threaten directly human health, infrastructure or the economy are more noticed by the public and more intensely studied by scientists. It is therefore unsurprising that the secret domination of ants is far less well known. Occasionally ants annoy humans because they may sting, bite or chose to relocate their nests inside human houses and bite through electrical equipment [7]. However, these nuisances are dwarfed by their impacts on native insects (Fig. 1). Introduced ants may wipe out almost entire native ant communities [8] and can also severely impair ecosystem processes like pollination, seed dispersal or soil aeration [9]. To make matters worse, they are everywhere! Introduced ants have spread into almost all countries on all continents and all major terrestrial habitats over the past 250 years [10]. There is also no end in sight, as they are hitchhikers on many plant and fruit products and continue to spread around the plant with traded commodities [11]. Two new studies quantify the intense intercontinental exchanges of invasive ant species and their pervasive impacts on native ant communities in Florida.

Wong et al. [12] have compiled and analyzed an impressive dataset of introduced ants and their spatial distributions across 525 regions globally. In total, at least 520 out of more than 14,000 described ant species have been moved outside of their native range, likely through human-mediated transport. The spatial resolution and extent of this dataset is remarkable and constitutes to my knowledge the most comprehensive dataset for any insect taxon so far. This is no small feat as such data is extremely scarce despite the fact that insects represent 80% of all animal species, with more than 1 million described species worldwide and an estimated actual number of species of around 5.5 million [13], and invasive insect species outnumbering all other invasive animal species together [14]. This lack of knowledge on biogeographical patterns has been called the "Wallacean shortfall" and it is clearly a major obstacle for understanding macroecological patterns of insect invasions and their underlying drivers for insects which are far less well known than mammals or birds for example [15]. The data compiled by Wong et al. [12] will help filling this knowledge gap for a major insect family and establish ants as an exceptional insect model system to test hypotheses about invasion macroecology and biogeography.

They also list separately species that have been intercepted in ports of entry and have thus been transported but have not been able to establish outside of their native range (risk "level 1"), species that survive and reproduce outside of their native range but only indoors ("level2") and species that have established outdoors ("level 3"). This distinction is useful to analyze the different filters that act during the invasion process at different stages. Previous work on mammals has shown that different biological traits can be under selection during transport and establishment [16] and is confirmed by the data by Wong et al. [12] showing that the proportion of ants nesting in different habitat strata changes from 36% of arboreal nesting ants during the transport stage to only 16% of outdoor established species. This adds a layer to previous findings that the extent of spatial spread in alien ants (at a regional, transcontinental or global scale) is related to their use of habitat and nesting requirements in addition to other life-history traits [10]. Wong et al. [12] also use their distinct groups to assess intercontinental species flows (Fig. 2). For example, some regions like the Panamanian, Neotropical and Nearctic realm were major donors of level 1 and 2 species (not established outdoors) to the Palearctic, but not for level 3 species. This illustrates nicely that these species have the opportunity to travel there but are unable to establish self-sustaining populations perhaps because of climatic barriers. These findings open avenues for future research that could test the importance of potential drivers of species flows (trade, human movements, species traits, recipient communities or environmental factors) acting at different invasion stages. One possible limitation to this understanding of species flows is the secondary spread of species from areas where they are already invasive [17]. This phenomenon is known as the “bridgehead effect” and may blur our vision of species flows since ant species are frequently introduced from parts of their invaded range [18].

Gaining a better understanding of how exactly globalization impacts the human-mediated transport of ants is urgent given the large number of introduced species and their capacity to spread globally, as the study of Wong et al. [12] illustrated. However, it is not clear to what extent the ubiquity of introduced ants at a large spatial scale translates into an ecological domination of ant communities. Since ants are small-sized organisms, they may be easier to overlook by humans even when they are quite abundant, contrary to other invasive organisms that become conspicuous features of the landscape such as kudzu or rabbits. This is not to say that they cannot have as dramatic impacts on other small-sized organisms. Studies assessing the consequences of ant invasions on insect communities typically compare invaded and uninvaded plots at a local scale [19]. But this is problematic because invasive ants might be more likely to colonize disturbed areas where the native species richness was already lower before their arrival. To study the long-term consequences of multi-species invasions in natural ecosystems, Booher et al. [19] have studied the composition of 6483 local leaf litter ant communities across the whole state of Florida over more than 50 years. To achieve that, the researchers leveraged data from museum collections and contemporary sampling. They found that the proportion of introduced ants in ant communities increased across the whole state, and reached a staggering 73% in southern Florida, which is the most densely populated area of the state.

Booher et al. [19] ranked the species that showed the largest decreases ('losers') and increases ('winners') in abundance over time. Strikingly, nine out of ten greatest losers were native species, while nine of the top ten winners were introduced species. This has obviously massive impacts on community composition. Studying changes in relative abundances of 177 species allowed also identifying the characteristics of winners and losers. Interestingly winners – whether native or not – shared a propensity to be opportunistic, both in terms of their habitat and dietary requirements. On the other hand, losers tended to be much more specialized predators or seed dispersers and included for example one species that selectively feeds on oribatid mites. This erosion of functional diversity is also expected under other anthropogenic changes such as climate change or habitat loss [20]. As a consequence, species assemblages worldwide become more and more similar to each other, a process that has been called biotic homogenization [4]. The greatest victims of homogenization are likely to be faunas with a high degree of endemicity. These communities will gradually be swamped by introduced species and sadly lose their most fascinating and unique species.

Together, the two new studies by Booher et al. [19] and Wong et al. [12] emphasize that it would be a grave mistake to neglect the rapid spread of introduced ants. Although many humans may still be unaware that ants can be highly problematic, they are have already reached almost every region on the planet and increasingly dominate local communities.

This is extremely concerning, since their spread is likely to accelerate over the coming years [18].

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Figure legends

Fig. 1. Invasive ants are dominant members of insect communities worldwide. a) The yellow crazy ant (*Anoplolepis gracilipes*) can alter ecosystem processes and is famous for killing more than 20 million red land crabs on Christmas island where they have caused major changes to the rainforest ecosystem, b) the electric ant (*Wasmannia auropunctata*) is among the four introduced ant species with the greatest increase in abundance in Florida according to Booher et al. The species may reduce native insect diversity and is an important nuisance especially in agricultural areas due to its powerful sting. Pictures © Alex Wild

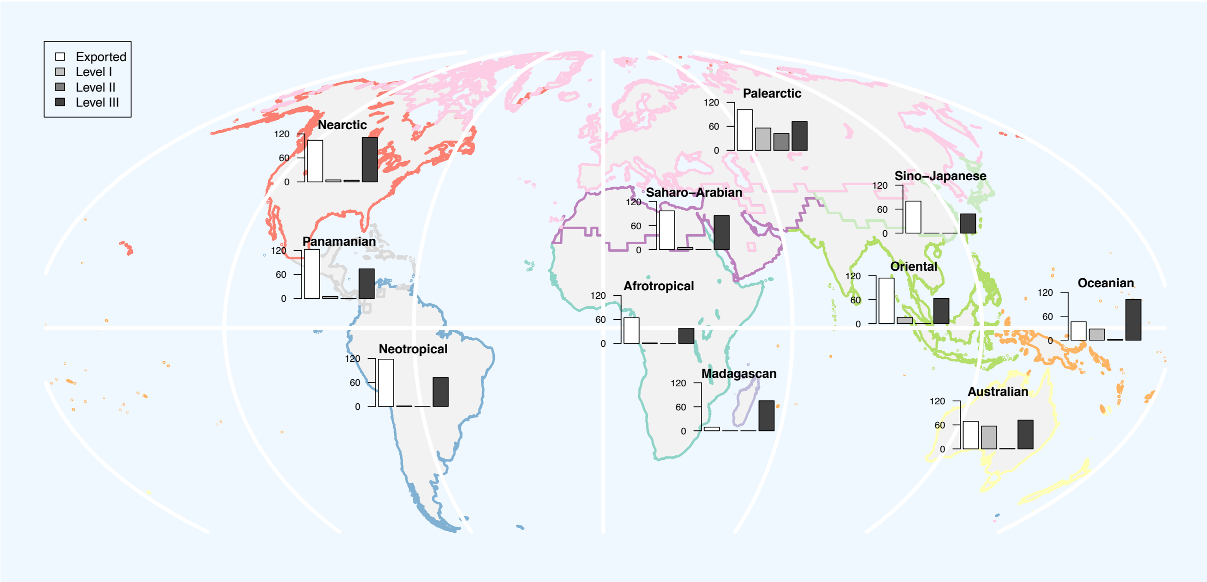

Fig. 2 Numbers of exported and imported (level 1-3) species by bioregions, illustrating that some regions are greater exporters of ant species that have become invasive elsewhere (e.g., Neotropical, Panamanian, Oriental, Palearctic region) and other regions have greater numbers of species that have arrived and established (e.g., Nearctic, Oceanian, Madagascan region). Level 1 species (intercepted) are mainly found in the Palearctic, Oceanian and Australian region), potentially due to the availability of interception data from only these regions. Map based on data from Wong et al.