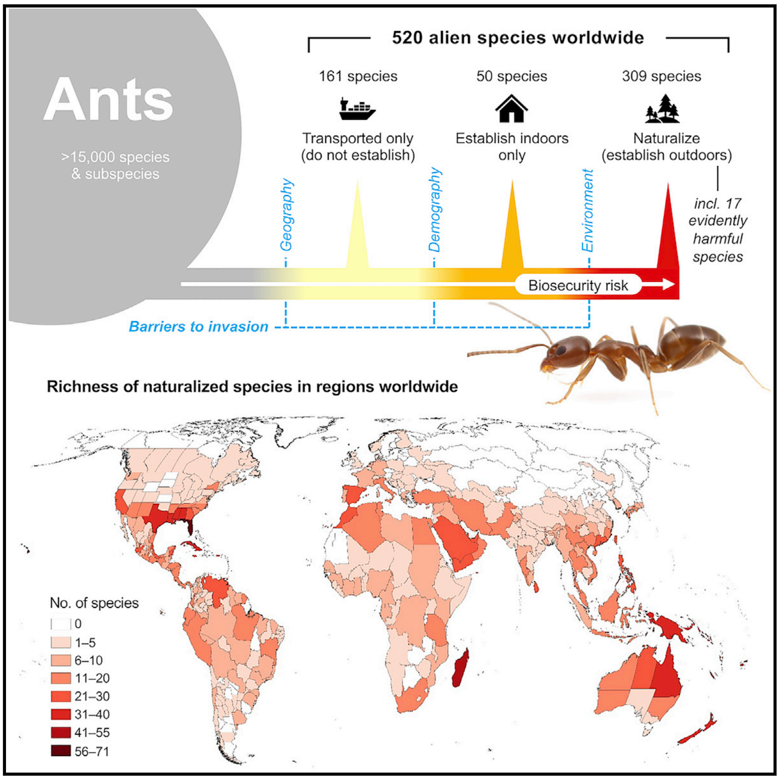
Report

Current Biology

The global spread and invasion capacities of alien ants

Graphical abstract



Highlights

- At least 520 ant species have been transported outside of their native ranges
- 60% of these species naturalize; others establish only indoors or not at all
- Global diversity hotspots for indoor-confined and naturalized species differ
- Border interceptions miss many litter- and soil-dwelling species that naturalize

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In brief

Wong et al. comprehensively map the human-mediated spread of all known alien ant species globally and distinguish their capacities to invade ecosystems. Species of different invasion capacities have contrasting movements and diversity hotspots globally. Border interceptions miss many litter- and soil-dwelling species with a high invasion capacity.

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Report

The global spread and invasion capacities of alien ants

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SUMMARY

Many alien species are neither cultivated nor traded but spread unintentionally, and their global movements, capacities to invade ecosystems, and susceptibility to detection by biosecurity measures are poorly known.[1–4] We addressed these key knowledge gaps for ants, a ubiquitous group of stowaway and contaminant organisms that include some of the world's most damaging invasive species.[5–10] We assembled a dataset of over 146,000 occurrence records to comprehensively map the human-mediated spread of 520 alien ant species across 525 regions globally. From descriptions of the environments in which species were collected within individual regions—such as in imported cargoes, buildings, and outdoor settings—we determined whether different barriers to invasion had been overcome[11] and classified alien ant species under three levels of invasion capacity corresponding to increasing biosecurity threat. We found that alien species of different invasion capacities had different sources and sinks globally. For instance, although the diversity of indoor-confined species peaked in the Palearctic realm, that of species able to establish outdoors peaked in the Nearctic and Oceanian realms, and these mainly originated from the Neotropical and Oriental realms. We also found that border interceptions worldwide missed two-thirds of alien species with naturalization capacity, many associated with litter and soil. Our study documents the vast spread of alien ants globally while highlighting avenues for more targeted biosecurity responses, such as prioritizing the screening of imports from regions that are diversity hotspots for species of high invasion capacity and improving the detection of cryptic alien invertebrates dwelling in substrates.

RESULTS AND DISCUSSION

Global alien ant diversity

We compiled 146,917 records corresponding to 17,948 occurrences of alien ant species across 525 non-overlapping regions corresponding to all areas where ants occur on Earth. These regions were delineated to reflect the finest geographic resolution at which data on ant species' occurrences was available; a single region typically corresponded to a country or a smaller administrative area such as a state or an island. From the data,[12] we identified a total of 520 alien ant species, which had been recorded as native in 497 regions and non-native in 486 regions globally, evidence of their massive worldwide spread. This doubled the most recent estimate of alien ant diversity and improved the geographic resolution for mapping their global distributions (cf. 252 species distributed across 195 country-level units in Bertelsmeier[10]).

Alien ant invasion capacities

To determine alien ant species' invasion capacities, we organized the data according to a well-established conceptual framework of ecological barriers to invasion.[11] Specifically, we inspected all records of each ant species' non-native occurrences for information about the localities and conditions in which they were collected (e.g., in imported cargo and interceptions from quarantined items, in buildings and other indoor environments, or in native ecosystems) and thereby classified alien ant species under three levels of invasion capacity that corresponded to increasing biosecurity threat, as follows. "Level I: Transport Only" species had non-native records that only reported individuals in border interceptions at ports of entry. While these species could overcome barriers to their uptake and transport, thereby entering new destinations, they could not overcome demographic and environmental barriers to their establishment of populations at those destinations, and therefore were of lower biosecurity concern. "Level II: Establish Indoors Only" species could overcome the same barriers as Level I species, as well as demographic barriers to establish non-native populations, but only in locations buffered from external environments (e.g., buildings and greenhouses), where they could impact human activity as pests. "Level III: Naturalize" species were of most concern to biosecurity. These species could

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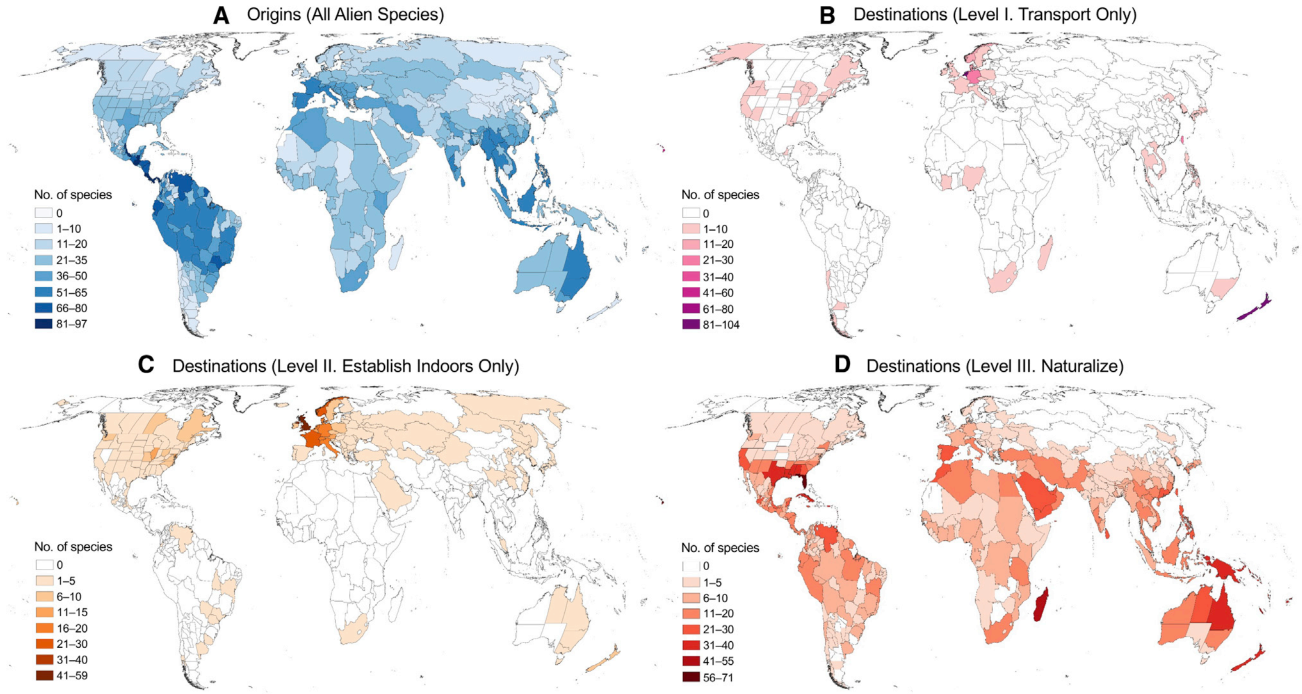

Figure 1. Origins and destinations of alien ant species across 525 regions
(A) Origins of alien ant species.
(B–D) Destinations of alien ant species of different invasion capacities (at region scale).
See also Figure S1 for a summary of widespread alien ant species.

overcome all geographical, demographic, and environmental barriers to their establishment of non-native populations in outdoor settings, thereby increasing their chances for subsequent uptake and transport to expand their non-native ranges.

Patterns in alien ant diversity at different geographical scales

We applied the classification to examine whether differences in species' invasion capacities influenced (1) the distribution of alien species richness across 525 regions, (2) the exchanges of species between eleven major zoogeographic realms, and (3) the overall composition of alien species globally. Specifically, we asked whether our view of these fundamental patterns changed when species of a different invasion capacity were considered.

First, we classified species' invasion capacities relative to individual geographic regions (n = 525) and mapped the non-native distributions of species of different invasion capacities across all regions globally (Figures 1A–1D). We found that the distributional patterns changed markedly when different invasion capacities were considered (Figures 1B–1D). Among 525 potential destination regions globally, the hotspots where most alien species naturalized correlated poorly with those where most were confined to indoor populations ($r = -0.06$) and those where most had arrived but had failed to establish ($r = 0.13$) (Figures 1B–1D).

Second, we classified species' invasion capacities relative to eleven major zoogeographic realms (after Holt et al.[13]) and determined flows in the numbers of species of different invasion capacities exchanged between the realms (Figures 2A–2E). Although the Palearctic realm recorded the highest diversity of alien ant species worldwide (170 species), just 42% of those had overcome environmental barriers and naturalized (72 species) (Figure 2A). In contrast, most species had naturalized in the Nearctic (111 species) and Oceanian (102 species) realms (Figure 2A). Flow patterns in the exchange of species between realms also differed with the invasion capacity considered (Figures 2B–2D). For instance, the Panamanian, Neotropical, and Nearctic realms were major donors of Level I and Level II but not Level III species to the Palearctic realm. Additionally, the importance of the Oriental realm as a source of alien species increased with increasing invasion capacity; resampling tests showed that it was a significant exporter of species with naturalization capacity to as many as six realms globally, exporting 19–52 species to these realms (Figure 2E; results for all realms in Figure S2).

Third, we distinguished the 520 alien ant species by their maximum invasion capacities at the global scale and tested whether species of different invasion capacities were taxonomically and ecologically different (Figure 3; Data S1). We identified 161 Level I: Transport Only species and 50 Level II: Establish Indoors Only species. Most known alien species had a high invasion capacity of Level III: Naturalize (n = 309). These included 17 species which had direct impacts on biodiversity and ecosystems, as evidenced in the literature (Table S1). Nonetheless, this did not imply that the other Level III species were of low concern. Although it is true that some naturalized species may not strongly impact native biota, others may have less detectable but

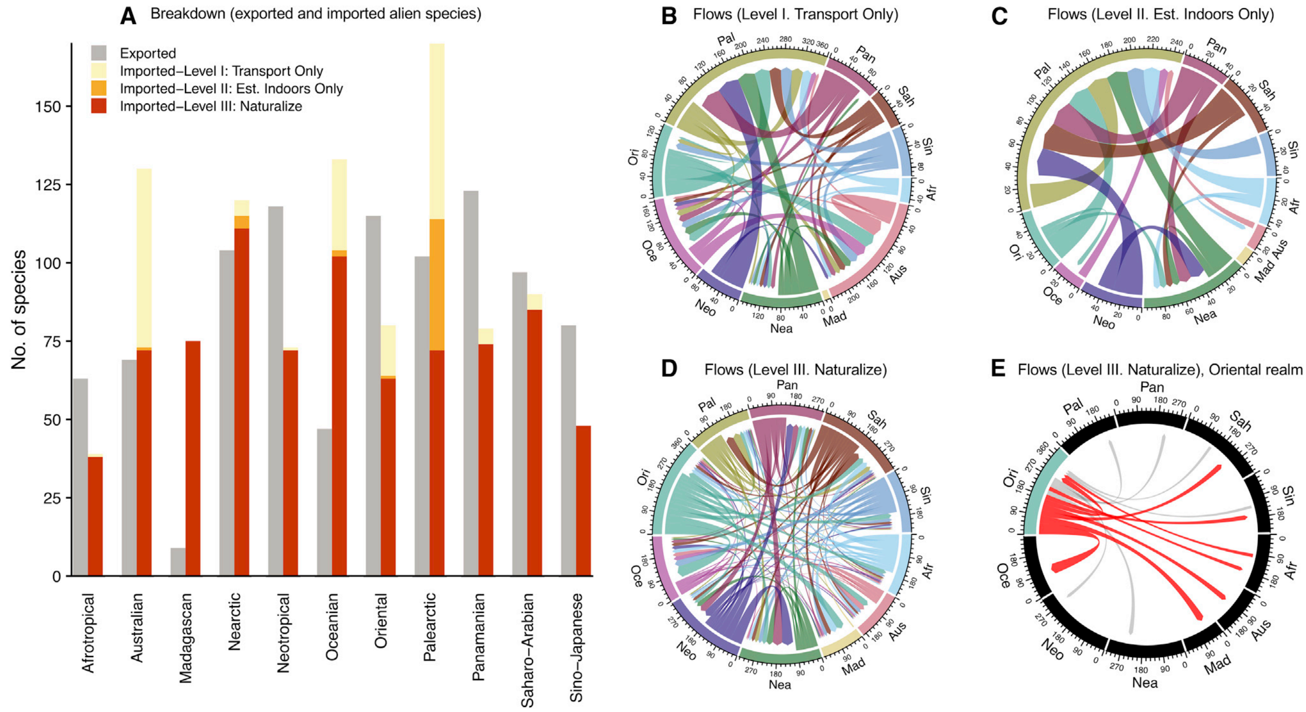

Figure 2. Breakdown and exchanges of alien ant species among eleven zoogeographic realms
(A) Numbers of species exported and imported by individual realms.
(B–D) Flows in the numbers of species of different invasion capacities (at realm scale) exchanged among realms (flows with <5 species are not shown).
(E) Flows in the numbers of Level III species to and from the Oriental realm, with statistically significant flows highlighted in red.
See also Figure S2 for flows of Level III species to and from each realm.

nonetheless severe impacts on species as well as phylogenetic and functional diversity, which represent an urgent knowledge gap.[14]

Alien ants comprised a non-random subset of total ant diversity, with disproportionate contributions of species from individual subfamilies. For instance, although the proportions of alien species from the three largest subfamilies (Myrmicinae, Formicinae, and Ponerinae) did not differ substantially from their contributions to total ant diversity, species of Dorylinae and Dolichoderinae were under- and over-represented among alien ants, respectively (Table S2). Indeed, many Dorylinae species display an army ant syndrome characterized by behaviors and ecologies (e.g., nomadism and obligate collective foraging) that would make them particularly prone to detection during the initial intake and transportation phases of the invasion process; the more widespread alien species from this subfamily tend to be the more cryptic, soil-dwelling species (e.g., *Ooceraea biroi*).[15] Further underscoring the need to account for species' invasion capacities in invasion research, alien ants of different invasion capacities differed significantly in taxonomic composition (Table S2; Data S1), as well as ecological composition—in terms of their use of different vertical habitat strata in terrestrial systems (Figure 3) (chi-square tests, $p < 0.05$; Data S1). The proportion of formicines roughly halved from Levels I (42%) and II (40%) to Level III (21%). Showing an opposite trend, ponerines constituted 3% of Level I species but as much as 13% of Level III species; likewise, myrmicines were under-represented in Levels I (42%) and II (28%) relative to Level III (50%) (Table S2).

Most intriguingly, the proportion of arboreal species halved, whereas that of species associated with litter and soil tripled along the gradient of increasing invasion capacity from Level I to Level III (Figure 3). One possible explanation for this pattern is that stronger environmental barriers may hinder the establishment of arboreal ant species. For instance, arboreal alien ants may face direct biotic resistance from interspecific competition, which is often especially intense in vegetation, owing to the patchy distribution of limiting resources such as nest space and food.[16] Arboreal alien ants may also depend on mutualistic or facilitative interactions with plants or herbivorous insects that fail to establish in new regions owing to climatic factors.[17] It is also conceivable that litter- and soil-associated ant species have exploited a greater volume or diversity of invasion pathways than arboreal species to date. Notably, soil was often used as ballast in ships throughout the expansion of European maritime trade routes in the 16th century and into the 20th century.[18] Imported soils continue to be used in horticulture, agriculture, and construction, and soil is a contaminant of imported plant products as well as containers and vehicles.[4,19,20] Still, information on the specific invasion pathways used by alien ant species have largely been anecdotal, with many established populations only being detected years, if not decades—and even centuries in the case of *Solenopsis geminata* in Asia[18]—after introduction events. This dearth of information on when and how species were unintentionally introduced further underscores the value of examining their habitat preferences and traits to clarify invasion pathways. Finally, the patterns observed may

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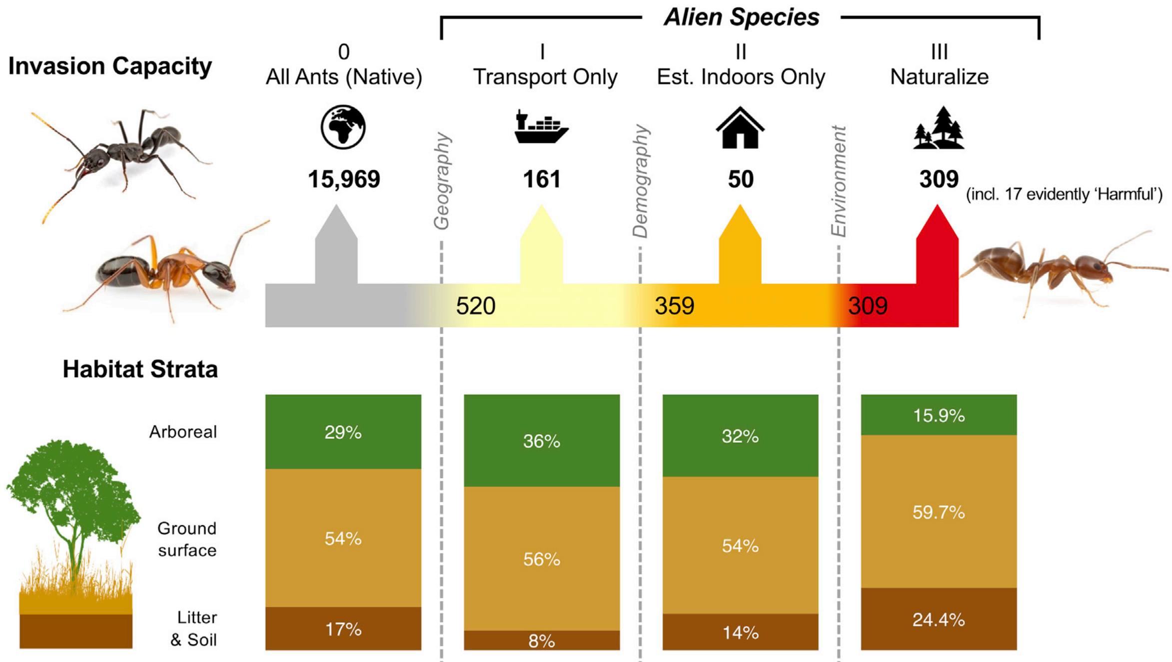

Figure 3. Differences in ant species' invasion capacities and use of vertical habitat strata at global scale

Top row (invasion capacity) summarizes the diversity of species (and subspecies) for the global pool of ants (all ants [native]) and for 520 alien ant species in three levels of invasion capacity and biosecurity threat that increase from left to right. Invasion capacities reflect species' capacities to overcome successive barriers to invasion (vertical dotted lines) at the global scale. For species in each group, the second row (habitat strata) shows their distribution across three major vertical habitat strata of terrestrial ecosystems. See also Table S1 for a list of 17 Level III species with evidently harmful impacts; see Figure S3, Table S2, and Data S1 for comparisons of the taxonomic and ecological compositions of alien ant groups. Images by Alex Wild.

also have been an artefact of detection biases associated with species from specific vertical strata, as discussed below.

Possible detection biases

The apparent compositional differences among ant species of different invasion capacities at the global scale were likely shaped to some extent by differences in the likelihood of detecting species in different invasion stages or environments. For instance, it is conceivable that individual queen ants or young, small colonies dwelling in imported products would be less easily detected at border interceptions compared with mature, large colonies from naturalized populations in the wild. Similarly—and evidencing a key blind spot in invasion management—we found that roughly two-thirds of Level III: naturalize species (n = 199) were not among species recorded in border interceptions worldwide (n = 291). Moreover, litter- and soil-dwelling ants constituted a significant proportion (29%) of the missing species; this was almost triple the proportion of such ants (11%) detected in border interceptions worldwide (chi-square tests, $p < 0.001$; Figure S3; Data S1). Such patterns were likely shaped by obstacles to detecting alien invertebrates in substrate, in contrast to the widely implemented border screening protocols targeting agricultural and domestic pests associated with vegetative matter (e.g., leaf-chewing and wood-boring insects).[21,22] To this end, our results indicate that current gatekeeping biosecurity measures may be ill-equipped to deal with alien invertebrates, in particular those that impact the biodiversity and ecosystem functioning of brown food webs.[23]

As with all global biodiversity assessments, the documented patterns were inevitably shaped by variation in sampling effort and data availability.[2,24,25] For instance, the large number of Level I alien ant species recorded in the Australian and Palearctic realms (Figure 2) was likely influenced by the extensive data on border interceptions in countries such as Australia and the United Kingdom and the shortage of comparable data for countries in Asia and Africa.[2,26] The large number of studies on biological invasions in the United States may have also contributed to the many Level III species detected in the Nearctic.[2] Our classification of alien ant species' invasion capacities system is conservative in requiring positive evidence for species classified at each higher level. However, it is difficult to prove a negative, thus it is quite possible that some species may have been classified at a level lower than they should be due to a lack of knowledge. Although introduced ants are a major concern and have been studied quite extensively, and we made every effort to consolidate existing information, we are far from a complete picture. Our analysis is intended to provide a state of knowledge and framework for putting further observations in context, but the status of each species will need to be continuously revisited in the future. A major challenge for future studies will be to determine whether differences in records of alien species between geographic regions relate to differences in the flows of species, sampling effort, or data reporting.

Conclusions

Our findings provide the most comprehensive picture thus far of the global non-native distributions of a terrestrial invertebrate group. Terrestrial invertebrates constitute a large portion of the biota exchanged worldwide but many species are poorly known.[27] Moreover, taxonomic impediments are a major obstacle to identifying species, determining their native and exotic ranges and developing effective control measures.[28–31] To this end, knowledge of specific donor regions of species with high invasion capacity (Figure S2) may help with the allocation of limited resources for measures such as the screening of imports in a country. At the same time, novel methods to detect alien invertebrates in litter and soil (e.g., eDNA) can be explored in conjunction with the development of robust taxonomic and molecular DNA libraries.[32,33] The distribution data and classifications we provide should also allow future studies to explore the mechanisms underlying ant species' varying invasion capacities among different regions (Figure S1); why species cannot establish or are confined indoors in some regions and yet able to naturalize in others. Although our study comprehensively documents current knowledge of the global spread and invasion capacities of alien ant species, management protocols for specific regions will have to be developed in collaboration with key stakeholders such as border authorities and local landowners. Overall, our research demonstrates how basic information describing the environments in which species were found, how they were collected, as well as their functional traits and ecological preferences can be leveraged to distinguish alien species' invasion capacities, advancing efforts to identify the biological correlates of invasiveness to predict and manage future invaders.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- METHOD DETAILS
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- ADDITIONAL RESOURCES

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2022.12.020.

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AUTHOR CONTRIBUTIONS

Conceptualization, M.K.L.W., B.G., and E.P.E.; methodology, M.K.L.W., B.G., and E.P.E.; formal analysis, M.K.L.W.; writing – original draft, M.K.L.W.; writing – review & editing, M.K.L.W., B.G., and E.P.E.; funding acquisition, B.G. and E.P.E.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Data on alien ant species' occurrences in geographic regions and zoogeographic realms globally, and species' occupancy of different vertical habitat strata	This paper; Figshare[12]	https://doi.org/10.6084/m9.figshare.21666191
Software and algorithms		
R version 4.1	R Development Core Team	N/A

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Mark Wong (mark.wong@uwa.edu.au).

Materials availability

This study did not generate any new reagents.

Data and code availability

- Data on alien ant species' occurrences in geographic regions and zoogeographic realms globally, and species' vertical habitat strata have been deposited at Figshare and is publicly available as of the date of publication. DOIs are listed in the key resources table.
- All original code has been deposited at Figshare and is publicly available as of the date of publication. DOIs are listed in the key resources table.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

This study did not use experimental models.

Data on ant species occurrences

Data on ant species occurrences across regions globally was sourced from the Global Ant Biodiversity Informatics (GABI) database.[34]

Data on vertical habitat strata

Data on ant species' affinities for vertical habitat strata was sourced from Lucky et al.[35] and a literature search.

METHOD DETAILS

Data compilation and organization

Data were compiled as part of the Global Ant Biodiversity Informatics (GABI) project. The details of data compilation have been described fully previously[25,34] and a brief update is presented here. In total, nearly two million records for nominal species were compiled from 10,342 scientific publications, as well as 82 and 16 public and private databases, respectively [major components included data from AntWeb,[36] the Global Biodiversity Information Facility (GBIF), the Integrated Digitized Biocollections (iDigBio), the Commonwealth Scientific and Industrial Research Organisation (CSIRO) collection and others; see Kass et al.[25]]. Dubious and erroneous records were identified based on their mentions in the literature, cross-referencing when updates to checklists of species were available, and through direct communication with numerous experts since 2012.

Native and non-native ranges were identified for each species based on their mentions in the literature and the number of records present for the species (or in a few cases genera) within a particular zoogeographic realm or part of it. Information about the locality and habitat of collection were also used to determine the native or non-native status of a species within a particular region. For instance, species encountered only within highly disturbed habitats within a particular region, one of the characteristics of tramp species,[37] and with an uncertain native range were considered non-native within the region. For several species that displayed extensive and continuous distributions, some uncertainty was inevitable when demarcating the precise limits of their native and non-native ranges at the scale of individual regions; nonetheless these uncertainties would have limited influence on patterns of species distributions at the larger scale of zoogeographic realms. The resultant dataset, which included all ant species that had at least one non-native record globally, consisted of 146,917 records (including native and non-native records); 4,127 of these were subsequently identified as dubious records. We further summarized the data by geographic regions to yield 17,948 occurrences of alien ant species across 525 non-overlapping regions (i.e., all areas where ants occur on Earth).[34]

Details about the collection locality, sampling method, or any other relevant information associated with each non-native record of a species were used to identify the geographical, demographic, and environmental barriers to invasion that the species had overcome (or failed to overcome) and therefore its invasion extent within that particular region, based on positive evidence. In particular, we distinguished among non-native records that reported three different types of information: (i) occurrences of species in border interceptions (i.e., species overcoming geographical barriers to transport); (ii) occurrences of species established in indoor settings such as buildings and greenhouses (i.e., species overcoming demographic barriers and some environmental barriers to establishment); and (iii) occurrences of species established in outdoor settings including semi-natural and natural habitats (i.e., species overcoming most barriers to establishment). We then compared the invasion extents of all non-native records for individual species to determine their invasion capacities (Level I: Transport Only, Level II: Establish Indoors Only, or Level III: Naturalize) at the scale of individual regions and zoogeographic realms, as well as at the global scale. In the common case where a species had multiple non-native records with differing invasion extents at a given scale, we used a hierarchical approach and inferred the species' invasion capacity from its maximum invasion extent at that scale.

To provide additional information for supporting biosecurity efforts, we also scrutinized the pool of species with an invasion capacity of ''Level III: Naturalize'' and from these distinguished 17 ''harmful'' species for which there was evidence of their impacts on native biota in any of their invaded regions globally (Table S1). It should be noted that while some studies of biological invasions have considered species to be ''invasive'' or ''harmful'' solely based on their geographic spread,[38] such parameters are far more difficult to establish for ants because most parts of the world have received very limited sampling efforts[39]; even in frequently sampled areas, important habitat strata are often overlooked.[40] Furthermore, species of some genera are extremely hard to identify in the absence of taxonomic expertise (e.g., *Cardiocondyla*, *Nylanderia*, *Pheidole*). Not all naturalized species subsequently impact native biota, but those that do often cause the most severe ecological and economic damage.[3] Thus, we emphasized alien ant species' impacts on native biota (as compared to their geographic spread) when flagging species that would be of the greatest priority for biosecurity. In this regard, our list of 17 harmful alien ant species differs slightly from the species listed in IUCN's Global Invasive Species Database (GISD),[41] which includes 19 species but for which, to the best of our knowledge, seven are lacking in evidence of impacts on native biota but may act as pests that are restricted to indoor environments or highly modified systems (Table S1). In addition, the GISD lacks some species, such as *Nylanderia fulva*, for which impacts on native biota have already been demonstrated.[42]

We identified the vertical habitat strata used by each alien ant species based on a literature search as well as the genus-level classification of vertical habitat strata-use as reported in Lucky et al.[35] with necessary updates to adhere to recent taxonomic changes. Three habitat strata were considered: the arboreal, ground-surface, and the litter-and-soil strata.[35] Ant species' affinity for each of these strata was determined based on their foraging and nesting behaviors; see Lucky et al.[35] for details. In coding the habitat strata of alien ant species in the present study, any species belonging to a genus that exclusively used a single stratum as reported in Lucky et al.[35] was coded as that stratum; for instance, all species of *Hypoponera*, which nest and forage in leaf litter or soil, were coded as ''litter-and-soil.'' For all other species, a literature search—typically using Google Scholar as well as the web resources AntWiki[43] and AntWeb[36] to identify primary literature—was conducted to determine the stratum or strata used. If we found clear evidence for a species' use of more than one stratum, all relevant strata (i.e., up to a maximum of three) were coded for that species. For instance, the Ghost Ant, *Tapinoma melanocephalum*, a species displaying extremely high environmental plasticity, was coded as ''arboreal'' and ''ground-surface'' and ''litter-ant-soil'' as it has been observed foraging and nesting in all three strata.[44]

QUANTIFICATION AND STATISTICAL ANALYSIS

All data analysis was conducted in R version 4.1.[45] We used Chi-square tests to compare the frequency distributions of alien ant species in the different invasion capacities (defined at the global scale) in terms of their taxonomic composition (proportions of species in different ant subfamilies) and use of vertical habitat strata (proportions of species in each of the three strata). We also compared each of these to the taxonomic composition of all ants and vertical habitat strata of all ant genera (using updated data from Lucky et al.[35]). Details of Chi-square tests are in Data S1. We characterized flows of Level III: Naturalize ant species within and between different zoogeographic realms, and used resampling tests (after Van Kleunen et al.[46]) to assess whether the observed flows were statistically larger or smaller than expected. The resampling tests involved comparing the observed flows to flows based on 9,999 random draws from the full list of naturalized ant species. If the observed number was in the upper or lower 2.5% quantiles of the resampled values, the flows were significantly higher or lower, respectively, than expected. Results of the resampling tests are shown in Figure S2.

ADDITIONAL RESOURCES

Data on ant species occurrences globally is compiled in the Global Ant Biodiversity Informatics (GABI) database,[34] which is regularly updated. Information on the literature and database sources corresponding to species occurrences is available from GABI, and range maps for ant species across regions globally can be viewed at: https://antmaps.org.