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Recent human history governs global ant invasion dynamics

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Abstract

Human trade and travel are breaking-down biogeographic barriers, resulting in shifts in the geographical distribution of organisms, yet it remains largely unknown whether different alien species generally follow similar spatiotemporal colonization patterns and how such patterns are driven by trends in global trade. Here, we analyse the global distribution of 241 alien ant species and show that these species comprise four distinct groups that inherently differ in their worldwide distribution from that of native species. The global spread of these four distinct species groups has been greatly, but differentially, influenced by major events in recent human history, in particular historical waves of globalization (approximately 1850-1914, and 1960-present), world wars and global recessions. Species in these four groups also differ in six important morphological and life-history traits and their degree of invasiveness. Combining spatiotemporal distribution data with life-history trait information provides valuable insight into the processes driving biological invasions and facilitates identification of species most likely to become invasive in the future.

A hallmark of the Anthropocene is range expansion by alien species around the world 1, facilitated by the construction of transport networks and the globalization of trade and labour markets since the beginning of the Industrial Revolution 2. The roles of physical distance and geological barriers in limiting range boundaries have been reduced and species increasingly establish in new regions 1. This spread of alien species has become a major threat to biodiversity and ecosystem services worldwide 3 and rates of new establishments are predicted to continue to increase with on-going effects of globalization 4,5.

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Author contributions

CB and LK have designed the study, CB and AL have collected the data, CB and SO have analysed the data and all authors have discussed the analyses and written the paper.

Competing Financial Interests

There is no conflict to declare.

Author information

All data used in this article will be made available online and can be accessed as supplementary material, together with R code used to conduct all analyses. Reprints and permissions information is available at www.nature.com/reprints. The authors have no competing financial interests to declare.

Previous research has mainly focussed on retracing invasion routes of individual species 6 and mapping donor and recipient regions for entire taxonomic groups 7, sometimes linking colonization probability to environmental factors 8,9. It thus remains largely unknown whether alien species within a taxonomic group follow similar invasion dynamics, if past global trade patterns have affected these species differentially and which species' traits are selected by human-mediated transport. Here, we address these questions in ants, a group of animals particularly suitable to test hypotheses about global invasion dynamics because they are an ecologically diverse group which is present in almost all terrestrial habitats on all continents except Antarctica 10. Moreover, because of their small size 11 and complex social structure, ants are a particularly prominent group of invasive species worldwide 12,13, able to displace numerous native species and rapidly disassemble communities 14. To investigate the spatiotemporal dynamics of ant invasions, and to test for factors favouring spread, we assembled a data set comprising the current distribution and historical spread (establishment) of ants worldwide and compiled data on nine morphological and life-history traits previously suggested to play a role in ant invasions 12,13,15.

Global distribution data were available in the Antweb and Antwiki databases for the majority (13,104) of ant species (see methods), including the currently known 241 alien species (i.e., species that have been introduced outside their native range). For each species, we recorded the number of countries where it had established (spatial richness) and estimated spatial diversity taking into account pairwise distances between countries (Rao index 16). Thus, species present in adjacent countries have a low spatial diversity while those present in a few countries in several continents are characterized by a high spatial diversity. Cluster analysis within this diversity-richness space revealed four distinct groups of alien species (Fig. 1a,b). The first dispersion group (*local* group) was characterized by species with extremely low spread and that have barely invaded beyond their native ranges. The second dispersion group (*regional* group) includes species with low spatial richness and low spatial diversity, indicating that the principal mode of spread of these species is mostly within the same continent. Spread at this spatial scale, mainly among adjacent countries, is likely to be the result of a mix between human-mediated land transport and natural dispersal after initial invasion events 11. The third dispersion group (*global* group) had a high spatial richness and a high spatial diversity; these are species that have successfully dispersed both across continents and among neighbouring countries on several continents, which is likely to result exclusively from human-mediated long-range jump movements 11. Finally, the last dispersion group (*transcontinental* group) fell in between the *regional* and *global* groups, having a low spatial richness but a high spatial diversity. Species of this group were established on several continents but only in a few countries per continent. Importantly, spatial richness and diversity of the four groups greatly differed from the distribution of the remaining 12,863 native ant species listed in the authoritative online databases Antwiki and Antweb (Fig. 1c, all pairwise Wilcoxon tests with Bonferroni correction, $p < 0.0001$).

To investigate whether the distinct spatial distributions of these groups could stem from differences in their response to global trade over the last two centuries, we compared their temporal invasion dynamics, represented as the cumulative curves of the number of countries colonized over time (Fig. 2a). Data were available for only 36 species in the three groups that dispersed most (i.e., the *regional*, *transcontinental* and *global* groups), probably

because these species have attracted more attention due to their wider distribution and greater ecological impact. The first derivative of the smoothed cumulative curves represents the instantaneous colonization rate. Principal Component Analysis (PCA) of these first derivative curves characterized temporal variation among species in their colonization dynamics and revealed general patterns in the spread of species shared among the three groups but also some idiosyncratic differences (Fig. 2b). There were two distinct waves of colonisation (see coordinates of the first PCA axis) that coincide with the two waves of globalization recognized in the economic literature as the dominant feature of global commerce trends during the last two centuries 17,18. To test this statistically, we used time-frequency domain analysis with a Morlet wavelet transform 19 which indicated a significant association between the temporal spread dynamics of all three groups of ants and temporal trends in trade openness, a metric of trade globalization (Fig. 2c, Supplementary Fig. S2). The initial explosive spread coincides with the first wave of globalization but starts declining with World War I, the great economic depression in 1929 and World War II, and increased again with the second wave of globalization during the second half of the 20th century. Although all ant species followed this general pattern (Fig. 2b), the second PCA axis distinguishes between species that had already spread widely among multiple continents during the 1st wave of globalisation (*global* group) and species that did not spread widely until the 2nd wave (*transcontinental* group, Fig. 2c). The main difference between the *regional* and *transcontinental* groups occurred principally during the 2nd wave, which had only a limited effect on species of the *regional* group (Fig. 2c). These data indicate that an important difference between the three groups is the respective importance of the 1st or the 2nd wave of globalization. In these analyses we used dates of first observation per country as proxy for colonization and although lags likely exist between times of introduction and first detection, this should not significantly affect the chronology of records within a given taxonomic group 20. Therefore, we believe that our characterization of species associated with the two globalization waves is robust.

A possible explanation for the distribution pattern of the *transcontinental* group is that these species are similar to species in the *global* group but that their more recent spread reflects historical contingency, such that they have not yet colonised a large number of neighbouring countries. To test this hypothesis, we reconstructed the spatiotemporal trajectories (within the spatial diversity space) of all 36 species between 1750 and 2010 (Fig. 3a). This analysis revealed that ants of the *global* group first increased spatial diversity through long-distance spread and subsequently increased richness through regional spread (Fig 3a,b). Importantly, species of the *global* group had a spatial distribution similar to that of ants of the *transcontinental* group at an early stage of spread, supporting the view that ants of the *transcontinental* group represent species at an earlier stage of global invasion that will eventually follow the same pattern of distribution as ants of the *global* group (i.e., they will also spread locally to colonize many neighbouring countries, thus increasing their richness and decreasing spatial diversity indexes). Further support for this conclusion comes from the analysis of yearly transition of species among groups between 1750- 2010 (see Supplementary Notes).

Despite previous interest in spread dynamics 21, historical introduction rates 22 and even the link between trade and invasions 23–25, such distinct spread dynamics and in particular the

relative importance of two waves of globalization (mid 19th century-1914, and 1960-present) have hitherto gone unnoticed in the literature. Furthermore, alien species are typically treated as a homogeneous group when testing the effects of trade on their spread dynamics. These studies have not identified groups of species that are affected differentially by globalization. The distinction between the two waves of globalization is all the more important as it suggests that some species of the *transcontinental* group will further spread in the future, eventually reaching a distribution similar to ants of the *global* group. The study of spatiotemporal trajectories further reveals that most species in the *regional* group seem to be limited in their capability for global spread.

To investigate whether these group-specific spatiotemporal trajectories might be explained by morphological and life-history differences, we analysed nine traits previously suggested to be associated with ant invasions 12,13,15, using the Antprofiler database 26. Remarkably, all nine traits were significantly associated with spatial diversity and/or richness (Table 1). The four groups also exhibited significant differences for six of the nine traits (Table 1). These differences among groups were confirmed by Principal Component Analysis with respect to Instrumental Variables (PCAIV) using spatial diversity and richness as instrumental variables (Fig. 4). Species of the *regional* group tended to have large body sizes and to live in undisturbed habitats. While previous work had shown that non-native ants are smaller than native ants 27, our analyses revealed that among non-native ants, smaller body size was associated with higher spatial diversity and additional life-history traits, including Colony Founding (Dependent Founding), Queen Number (Polygyny) and Nesting Generalism are significantly associated with both spatial diversity and richness (Table 1, for relative importance of the traits in explaining the variance in spatial diversity and richness see Fig. S3), suggesting that they are important for establishment and subsequent spread. Finally, the *transcontinental* and *global* groups are further structured along an axis of increasing spatial richness, which is tightly linked to Habitat Generalism (Fig. 4, Table 1). Thus, among species that readily move across long distances, this trait influences whether a species is likely to invade a large number of adjacent countries. This is probably explained by the fact that Habitat Generalism confers a flexibility to exploit many different habitats and spread over heterogeneous landscapes 28.

In a final analysis we investigated whether there was an association between the spatiotemporal distribution of species, morphological and life-history traits 13,15 and “invasiveness” defined as a serious impact on biological diversity and/or human activities (IUCN Invasive Species Specialist Group, www.iucngisd.org). Ants are very prominent among invasive species, with 19 species in the IUCN list of the 360 “invasive” animals. Eighteen of these 19 ants are alien species that were greatly over-represented in the *global* group of our analysis ($\chi^2=67.8$, $df=3$, $p<0.001$; see methods) where they represent seven of the nine species. Interestingly, ants listed as invasive by the IUCN also differ in their life-history traits compared to the remaining 100 alien ant species for which data are available, as evidenced by their coordinates on the 1st axis of the PCAIV (Welch $t=-13.1$, $df=41.2$, $p<0.0001$). To identify additional species with traits characteristic of invasive species we determined the 99% confidence interval around the position of the invasive species on the 1st axis of the PCAIV. This analysis identified nine additional species (Fig. 4b). Strikingly, these nine species had a significantly faster spread over the last 10 years (11.6 ± 1.2

countries) than other alien species (7.5 ± 1.7 countries, Welsh $t = 1.96$, $df = 18.5$, $p = 0.03$), further supporting the view that these are likely to also become invasive in the future.

Using global spatial patterns of ant invasions, we have identified four groups of species exhibiting specific spatiotemporal patterns of global spread and differences in key morphological and life-history traits. So far, the majority of studies linking traits to invasiveness have compared invasive to alien species 29, treating them as two homogeneous groups. Here, we were able to identify traits that influence specific spatiotemporal trajectories of the four dispersion groups. Interestingly, several of these traits have been shown to also influence invasiveness in other taxonomic groups. For example, association with habitat disturbance has been implicated in plants 30, habitat generalism in birds 31 and body size in amphibians 32 and bivalves 29. Most of the other traits analysed in our study (Queen Number, Nest Structure, Colony Founding and Colony Size) are specific to social insects and have not been mentioned in the literature on invasive traits of other taxonomic groups, which has mainly focused on plants 33.

Our analyses also revealed that the spread of the four distinct groups of species has been greatly influenced by major events in recent human history, in particular historical waves of globalization. Previously, it has been shown that historical bird introductions in the 19th century were driven to a large extent by British colonialism 34 and alien insect spread rates in Europe seem to have been influenced by the East-West divide 35. Temporal analyses also revealed that invasion rates increased towards the end of the 20th century 20, and were associated with development and governance socio-economic indicators of trading partners 36, but colonization rates have not previously been associated with specific events driving global trade.

Finally, the identification of four different groups with different spatiotemporal dynamics linked to the species' invasiveness may have practical applications to assess the likelihood of further spread by species. Predicting future invasions is all the more important as time lags of several years to decades between establishment and spread of invasive species are frequent 37. Therefore many of the ant invasions that international trade has already caused during the second wave of globalization will only reach their full extent in years to come 4. In the future, it would be useful to test and extend our framework in other taxonomic groups, in particular for species that spread through different invasion routes and pathways than ants. Overall, this study shows that understanding spatiotemporal trajectories and associated morphological/life-history traits not only provides valuable insights into the processes driving biological invasions, but additionally can be used to identify species most likely to become invasive in the future.

Methods

Data

Distribution and establishment—We compiled distribution data for all 241 known alien ant species (i.e. species that have established outside of their native range through human-mediated transport, Supplementary Data S1). Our list is based on existing alien ant lists from the literature 38,39 and the public databases Antprofiler 26 (www.antprofiler.org),

Antweb (www.antweb.org), the Invasive Species Specialist Group (ISSG) of the IUCN (www.issg.org) and Delivering Alien Invasive Species for Europe (www.europe-aliens.org).

We classified 19 species as invasive using the ISSG Global Invasive Species Database (<http://www.iucngisd.org/gisd>) list of “invasive” species with documented impacts on biological diversity and/or human activities. Eighteen of these 19 invasive species were also in our list of alien species. The exception was *Acromyrmex octospinosus*, which has not been transported outside its native range although it has impacts on native biodiversity within this range (Supplementary Data S1). Species names were checked for synonymy using the authoritative AntWeb database (v. 6.0.13) (<http://www.antweb.org>), which contains 15,961 valid species and subspecies names based on the Bolton World catalogue 40 and the taxonomic history of senior synonyms that have become outdated due to taxonomic revisions. We compiled global country-level distribution data for each of these species using the geo-referenced AntWeb v. 6.0.13 specimen database, species lists from the literature assembled by AntWiki (www.antwiki.org, an authoritative database maintained by ant experts, which contains 255 regional ant fauna lists from different countries or smaller political entities over the world and is interlinked with the Encyclopedia of Life, the New Zealand Landcare research database 41 which records exact occurrences of alien and invasive ant species, a dataset of recorded alien ants in the US 38,42 and a dataset of alien ant species worldwide 39. We compiled historical global establishment records for the 36 most widespread alien ant species across the world (1750-2010) for which dates of first observation at the country-level were available from the literature (Supplementary Data S1, Supplementary Table S2). Additionally, we extracted country-level distributions from AntWeb and AntWiki for all 12,863 native species for which occurrence data had been recorded. As countries have sometimes changed names over the course of the last century, we revised the country names using ISO code 3166, which provides an international standard for country codes and their subdivisions.

Trade Openness—Trade Openness is an economic index measuring the level of international trade: it is the sum of all world trade (exports and imports from every country) divided by world GDP. Data from 1870 until 2002 were compiled by Martin et al. 43 based on Direction of Trade Statistics (DOTS) by the International Monetary Fund (IMF) and the Barbieri dataset for trade data, in addition to the World Bank’s Development Indicators (WDI) and the Maddison dataset for GDP data 43. Trade Openness from 2003-2010 was extracted from the UNCTAD dataset (United Nation Conference on Trade and Development).

Species traits—We used the Antprofiler database 26, which is a database on ecological, morphological and life-history traits of ants based on the literature and the contribution of the myrmecologist community. We selected 9 traits that had been previously suggested to be associated with invasiveness 12,13,15. We transformed the variables in that database in order to record (1) Queen Number, i.e., if species can have multiple queens within the same nest (*Polygyny*) or if they always have a single queen (*Monogyny*), (2) Nest Structure, i.e., if colonies construct a single nest (*Monodomy*) or if they inhabit multiple nest sites with transfer of brood and/or resources between these sites (*Polydomy*), (3) Colony Founding,

i.e., if queens found their colonies alone after a mating flight (*Independent founding*) or if they have been observed to disperse on foot from their natal colony taking with them some workers to start a new colony (*Dependent founding*), (4) Habitat Disturbance, i.e., if they construct their nests in disturbed habitats (*Habitat Disturbed*) or not (*Habitat Not Disturbed*), (5) Colony Size, i.e. the typical size of mature colonies, expressed as the log-transformed number of workers, (6) Size Smallest (worker), i.e., the log-transformed body length of the smallest workers within a colony (7) Size Largest (worker), i.e., the log-transformed body length of the largest workers within a colony (8) Habitat Generalism, i.e., the number of habitats where the species has been recorded using the following classification: rain forest, tropical dry forest, temperate forest, boreal forest (taiga), grasslands, scrubland, tundra, riparian zones, desert, coastland, urban areas, agricultural areas, and (9) Nesting Generalism, i.e., the number of different nest types that the species can inhabit using the following categories: canopy, leaf litter, ground, twigs and logs, underground, nomad (no nest). We had information on all traits for 108 alien ant species, 26 of which were among the species also studied in the spatiotemporal analyses. In order to be able to include in the trait analysis all 36 alien species previously used in the spatiotemporal analyses, we then imputed 13 missing values (in total) for 10 additional species (1.2% of the dataset). The imputation of this mixed dataset was done using an iterative factorial analysis for mixed data (FAMD) with the `imputeFAMD` function in the `missMDA` R package 44. Because the imputation uses the principal axes and components, the prediction of the missing values is based on the similarity between species and on the relationships between variables 44.

For each morphological and life-history variable, we had data for most of the 241 species: Queen Number (n=174 species), Nest Structure (n=171 species), Colony Founding (n=166 species), Habitat Disturbance (n=238 species), Colony Size (n=133 species), Size Smallest (n=240 species), Size Largest (n=240 species) Habitat Generalism (n=241 species) and Nesting Generalism (n=222 species).

Statistical analyses

Spatial patterns—The current spatial distribution of the 241 alien ant species was represented in a ‘spatial distribution space’ where the X-axis represented the Rao diversity index 16 calculated using the species’ spatial distribution in 2010 (presence-absence data per country), based on the pairwise distances between countries where a species was present. These distances were calculated by using the geographical coordinates of the centers of country polygons according to the haversine method 45. The Y-axis of the spatial distribution space represented the number of countries where a species was present (spatial richness). We used a cluster analysis to identify groups of species within this space, according to the hierarchical Ward’s minimum variance clustering method. We have confirmed the cluster-wise stability of the cluster analysis using a resampling method based on bootstrapping (B=1000 resampling runs). Observed Jaccard similarity value exceeded 0.6 for the main four nodes (0.845: *local* group; 0.766: regional group; 0.774: transcontinental group, 0.623: global group). This method is described in more detail by Hennig46 and was computed by the `clusterboot()` function in the `fpc` R package.

We then represented the position of all 12,863 native ant species in this spatial distribution space and calculated the percentage of alien species as a fraction of all (alien plus native) species per 5x5 square of the graph in order to identify areas of the graph with relatively low or high proportions of alien species. We used pairwise Wilcoxon rank sum tests with Bonferroni corrections to test if the four alien species groups differed from the position of native species and among each other in their spatial diversity and richness. To test if invasive species were differentially represented among the four *dispersion* groups we used a Chi-square test.

Temporal dynamics—Using earliest detection dates per country (proxy for dates of establishment), which were available from the literature for 36 invasive and alien ant species, we calculated cumulative curves of the number of countries colonized by each species over time. These species belonged only to the three groups that dispersed most (i.e., the *regional*, *transcontinental* and *global* groups) and not to the *local* group, probably because these species have attracted more attention due to their wider distribution and greater ecological impact. To quantify the temporal variation of this spatial spread, we then calculated the first derivatives of these curves after they were first smoothed using a cubic spline (with smoothing parameter 0.65) prior to the analysis. A Principal Component Analysis (PCA) was performed on these yearly first derivatives and the three most widespread groups of species (*regional*, *transcontinental* and *global*) were represented on the factorial map, using the *ade4* package in R v.3.1.1. We estimated average group spread rate as the mean derivative per dispersion group and compared these group spread rates to historical trade openness between 1870 and 2012. To test for coherence between the temporal spread data and trade, time-frequency domain analysis was performed using the wavelet transform with the Morlet wavelet which is a powerful method for the analysis of non-stationary systems, in particular for environmental and ecological time series 19. Wavelet transform of the trade openness annual time series was used to describe its frequency time-spectra and reconstruct large-scale tendencies between 1870 and 2012. Cross-wavelet transform of the three mean derivatives and trade openness were done to determine and test their coherence at large scales. All wavelet analyses were performed using the *WaveletComp* package in R v.3.1.1.

Spatiotemporal dynamics—The spatiotemporal trajectories of each group were then represented in the ‘spatial distribution space’. Coordinates of each species were calculated for different dates and grey arrows connected the previous position with the position for each date (1860, 1910, 1960, 2010).

For each species and every year between 1750-2010, we calculated spatial richness and diversity and determined to which of the four groups these points belonged using a k-nearest neighbor’s method based on single-linkage clustering. For species that are currently in the *transcontinental* and *global* groups, we calculated the time they have spent in the *transcontinental* stage. Similarly, we calculated for the *regional*, *transcontinental* and *global* groups the amount of time they spent in the *regional* stage. We compared species dispersion groups using Wilcoxon rank tests.

Morphological and life-history traits—We tested whether the nine morphological and life-history traits were linked to the species position in the spatial distribution space, using univariate tests: (1) Generalized linear models (GLMs) with a binomial link function to test for a link between spatial richness or spatial diversity and Queen Number, Nest Structure, Colony Founding, or Habitat Disturbance, (2) linear models (LM) to test for a link between spatial richness or spatial diversity and Colony Size, Size Smallest or Size Largest and (3) GLMs with a Poisson link function to test for the link between spatial richness or spatial diversity and Habitat Generalism or Nesting Generalism. We also tested if these traits were able to discriminate the four spread groups, using Chi-square tests (Queen Number, Nest Structure, Colony Founding, Habitat Disturbance) and ANOVA (Colony Size, Size Smallest, Size Largest, Habitat Generalism, Nesting Generalism). We carried out a Principal Component Analysis with respect to Instrumental Variables (PCAIV) on 118 species for which we had information on all 9 traits using the *ade4* package in R v.3.1.1. This analysis is a particular case of a Principal Component analysis (PCA) in which we used spatial richness and spatial diversity (Rao) as explanatory variables. We tested pairwise differences among groups in this traits space using a Wilcoxon rank sum test with Bonferroni correction on the species' coordinates on the first PCAIV axis. We then tested if invasive species have greater values on the first PCAIV axis than non-invasive alien species using a one-tailed two-sample Welch t-test with an alpha-level of 0.005 to reduce the probability of making a type I error. Finally, we calculated a confidence interval (99% level) around the group of invasive ants, using the coordinates of the first PCAIV axis. This confidence interval allowed identification of alien ant species that shared the traits with invasive ants. Finally, to assess the relative importance of traits in predicting the variance in spatial diversity and richness, we did a randomization test for hierarchical partitioning and averaged over orderings of predictive variables, using the *hier.part* R package to calculate the Lindeman, Merenda and Gold metric (*lmg*). We used a Gaussian error model for spatial diversity and a Poisson error model for spatial richness.

Data availability

All analyses have been carried out in R v. 3.1.1 and a script (Supplementary Data S2) is supplied to generate all figures using the R workspace, which contains all data used here (Supplementary Data S1).

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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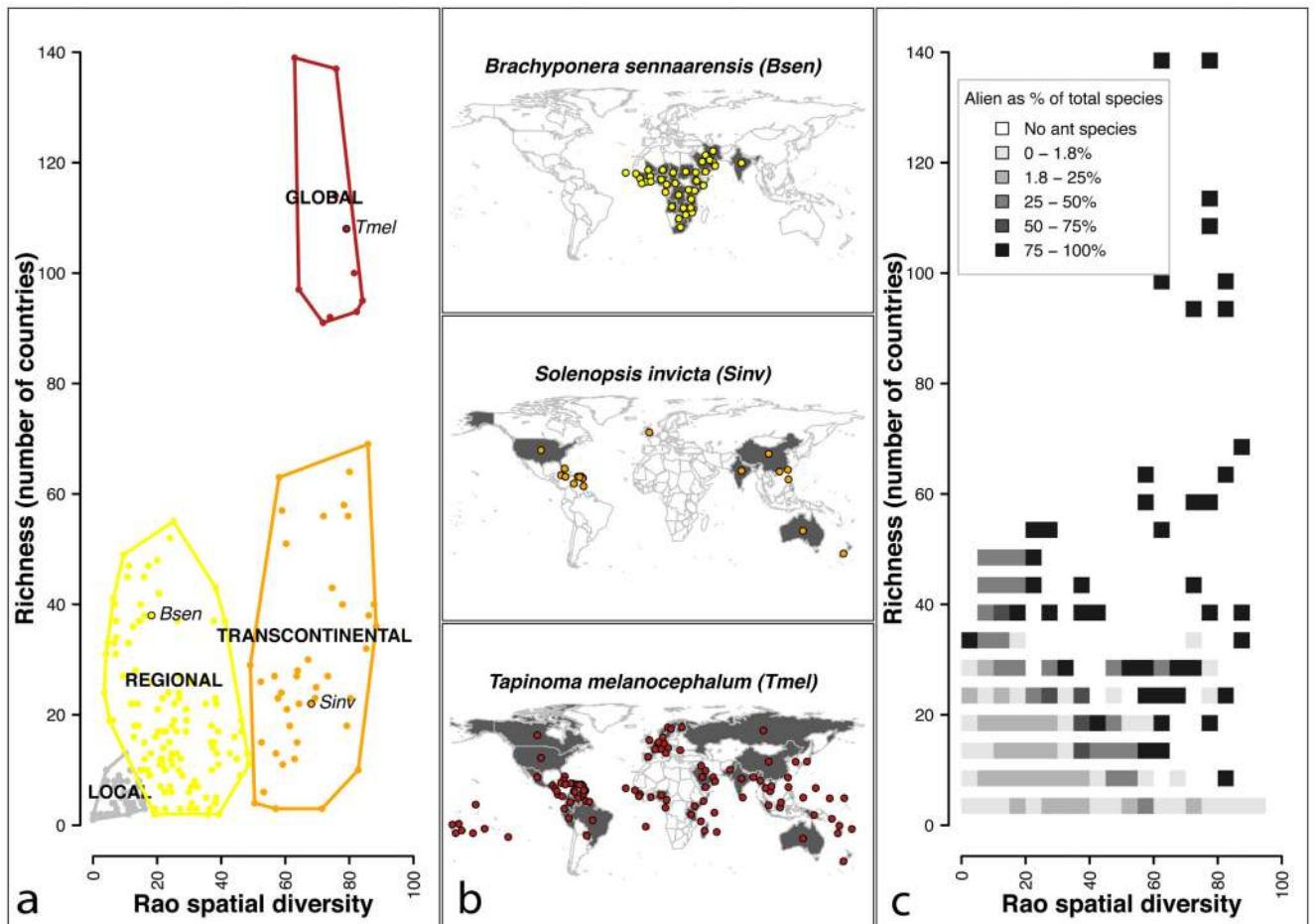


Fig. 1. Global spread of alien ants

- a. Coordinates of 241 non-native ant species, clustered in 4 dispersion groups, within a ‘spatial distribution space’ (Jaccard similarity values within the local, regional and transcontinental group >0.75 , and in the global group $0.6-0.75$). The Y-axis (richness) represents the number of countries in which a species is currently established. The X-axis (Rao) represents the diversity of these countries (based on pairwise distances between colonized countries).
- b. Examples of spatial distributions of three species belonging to each of the main dispersion groups (*regional*, *transcontinental* and *global*). Colonized countries are shown in grey with a dot in the colour of the corresponding dispersion group at the centre of each country. Maps for all 241 alien ant species can be accessed in the Supplementary Material (Fig. S1), occurrence data for all 241 species can be found in Data S1.
- c. The proportion of alien species as a percentage of all species (including native species) for each position in the spatial distribution space.

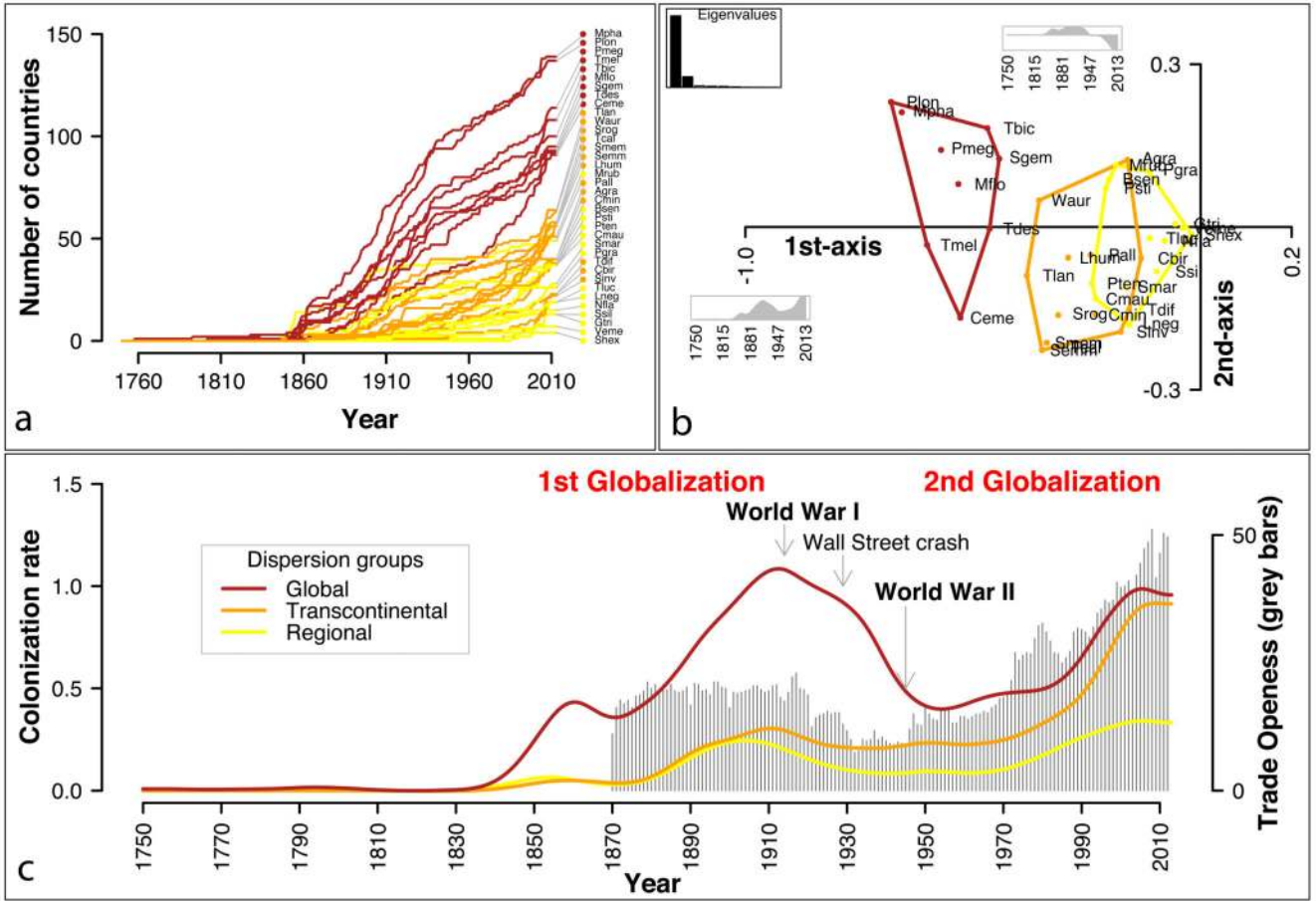


Fig. 2. Temporal colonization dynamics

- a. Historical time series of cumulative numbers of countries colonized by 36 ant species. Colours indicate the dispersion group to which the species currently belong. For species codes see table S1.
- b. Factorial map: the three species groups are represented on the first two axes of the PCA on the 36 annual colonization rates (1750-2010). The first axis is linked to the general trade pattern over the 19th and 20th centuries, in particular the two waves of globalization. The second axis contrasts the first and the second wave.
- c. Time series of mean colonization rates for the *regional*, *global* and *transcontinental* dispersion groups and yearly Trade Openness ((Exports+ Imports)/World GDP) 1750-2010

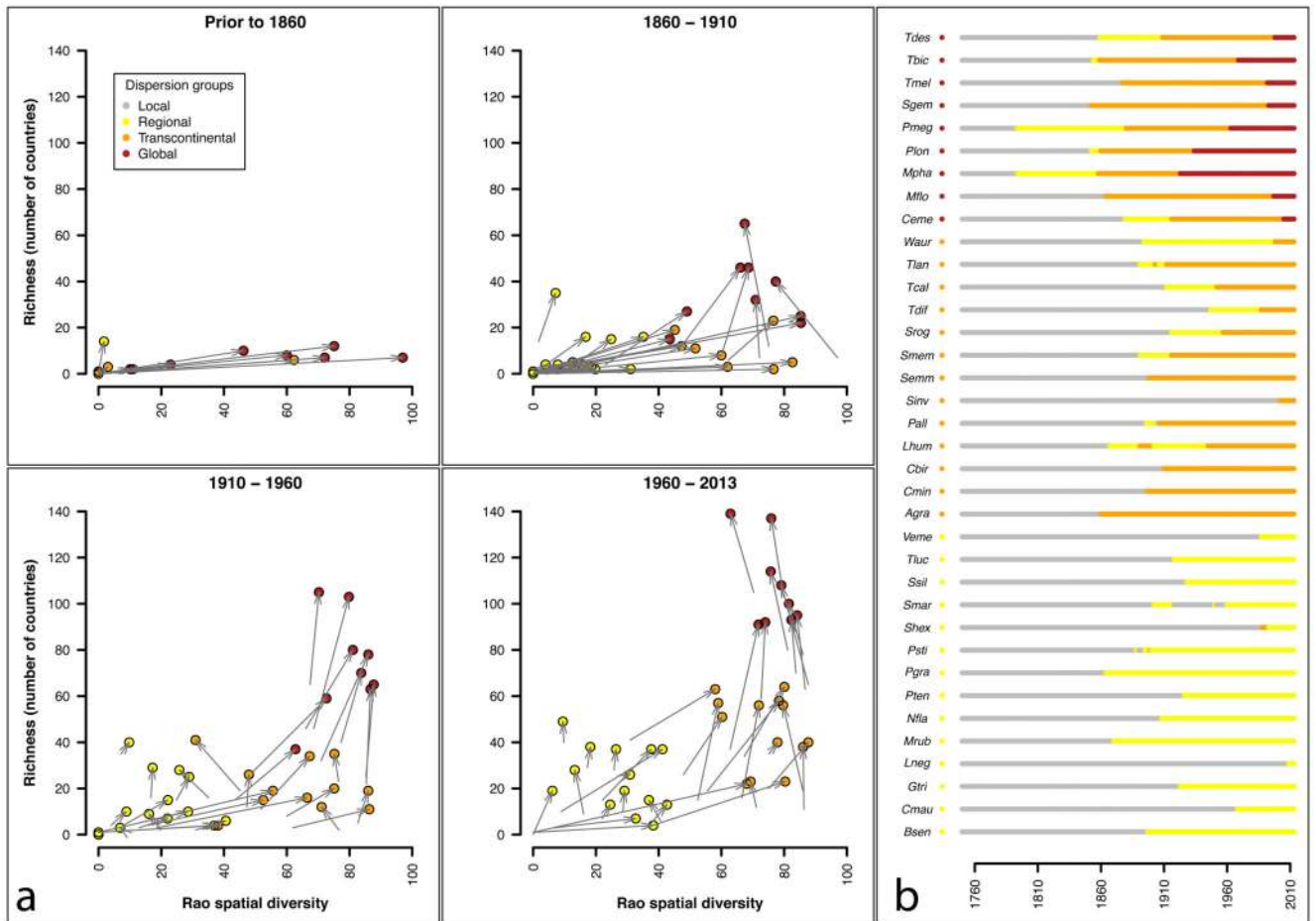


Fig. 3. Spatiotemporal trajectories.

- Historical progression of each species through spatial distribution space. Colour indicates the dispersion group to which the species currently belong. Species currently in the transcontinental group seem to follow the spatiotemporal trajectory of species in the global group.
- Historical transition of each species among dispersion groups 1750 – 2010. The colours indicate the dispersion group to which each species belonged in the past. Group membership is calculated based on the species' annual position within the spatial distribution space (as in Fig. 1). Species in the transcontinental and global group spent less time in the regional stage than species currently in the regional group (Supplementary Notes).

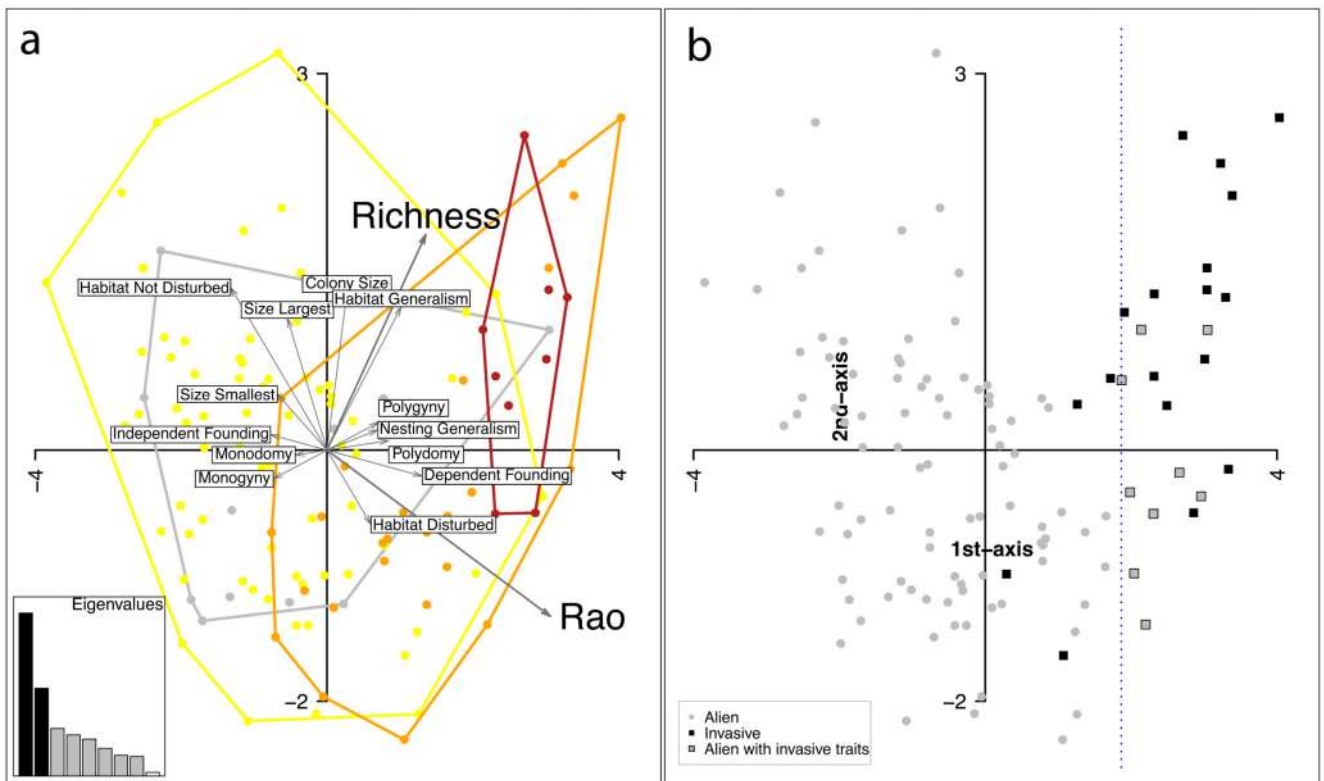


Fig. 4. Morphological and life-history traits

a. PCAIV on 9 traits and 118 alien ant species. The polygon (convex hull) boundaries show the contour of the most extreme points in each group. All pairwise comparisons between groups of the coordinates on the 1st PCAIV axis were significant (pairwise Wilcoxon, $p < 0.0001$ for all comparisons). For species names see Supplementary Fig. S3 and species codes in Supplementary table S1.

b. Invasiveness status of the 118 ant species. Alien ant species that fall within a 99% confidence interval (lower confidence limit indicated by the dotted blue line) along the 1st PCAIV axis around invasive species are shown in grey squares. These species are: *Hypoponera opacior*, *Monomorium minimum*, *Plagiolepis alluaudi*, *Tapinoma sessile*, *Technomyrmex difficilis*, *Tetramorium bicarinatum*, *Tetramorium simillimum*, *Cardiocondyla emeryi* and *Pheidole teneriffana* (ordered by increasing position on the PCAIV x-axis). For species names see Supplementary figure S4 and species codes in Supplementary table S1.

Table 1

Univariate tests of 9 morphological and life-history traits; across dispersion groups, linked to spatial richness and linked to spatial diversity. The association of the trait with the response variable is indicated as “+” for positive and “-” for negative, if significant, if significant. Here, the dispersion groups are considered ranked (1=“local” to 4=“global”) and the trend across dispersion groups is given. For dichotomous variables the variable value with a positive association is indicated.

Response	Trait	Trait value	Association	Test	n	d.f.	Statistic	p-value
Dispersion groups	Queen Number	<i>Polygyny</i>	+		174	3	$\chi = 15.8$	0.001
	Nest Structure	NS	0	Chi-Square	171	3	$\chi = 6.9$	0.07
	Colony Founding	<i>Dependent Founding</i>	+		166	3	$\chi = 26.8$	<0.0001
	Habitat Disturbance	<i>Habitat Disturbed</i>	+		238	3	$\chi = 38$	<0.0001
	Colony Size	NS	0	ANOVA	133	3, 129	$F = 1.77$	0.15
	Size Smallest	<i>quantitative</i>	-	ANOVA	240	3, 236	$F = 4.38$	0.005
	Size Largest	<i>quantitative</i>	-	ANOVA	240	3, 236	$F = 3.52$	0.016
	Habitat Generalism	<i>quantitative</i>	+	GLM (Poisson)	241	3	$\chi = 67$	<0.0001
	Nesting Generalism	NS	0	GLM (Poisson)	222	3	$\chi = 6$	0.1
Richness (countries)	Queen Number	<i>Polygyny</i>	+	GLM (Binomial)	174	1	$\chi = 10.4$	0.001
	Nest Structure	NS	0	GLM (Binomial)	171	1	$\chi = 2.1$	0.15
	Colony Founding	<i>Dependent Founding</i>	+	GLM (Binomial)	166	1	$\chi = 18.3$	<0.0001
	Habitat Disturbance	<i>Habitat Disturbed</i>	+	GLM (Binomial)	238	1	$\chi = 27$	<0.0001
	Colony Size	<i>quantitative</i>	+	LM, anova	133	1, 131	$F = 9$	0.003
	Size Smallest	NS	0	LM, anova	240	1, 238	$F = 3.8$	0.054
	Size Largest	NS	0	LM, anova	240	1, 238	$F = 0.018$	0.89
	Habitat Generalism	<i>quantitative</i>	+	GLM (Poisson)	241	1	$\chi = 70$	<0.0001
	Nesting Generalism	<i>quantitative</i>	+	GLM (Poisson)	222	1	$\chi = 5.4$	0.02
Diversity (Rao)	Queen Number	<i>Polygyny</i>	+	GLM (Binomial)	174	1	$\chi = 13.7$	0.0002
	Nest Structure	<i>Polydomy</i>	+	GLM (Binomial)	171	1	$\chi = 3.9$	0.05
	Colony Founding	<i>Dependent Founding</i>	+	GLM (Binomial)	166	1	$\chi = 22.7$	<0.0001
	Habitat Disturbance	<i>Habitat Disturbed</i>	+	GLM (Binomial)	238	1	$\chi = 47$	<0.0001
	Colony Size	NS	0	LM, anova	133	1, 131	$F = 0.48$	0.49
	Size Smallest	<i>quantitative</i>	-	LM, anova	240	1, 238	$F = 10.8$	0.001

Response	Trait	Trait value	Association	Test	n	d.f.	Statistic	p-value
	Size Largest	<i>quantitative</i>	-	LM, anova	240	1, 238	F = 7.3	0.007
	Habitat Generalism	<i>quantitative</i>	+	GLM (Poisson)	241	1	$\chi = 51$	<0.0001
	Nesting Generalism	<i>quantitative</i>	+	GLM (Poisson)	222	1	$\chi = 6.8$	0.009