

Recent human history governs global ant invasion dynamics

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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 to 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 world¹, facilitated by the construction of transport networks and the globalization of trade and labour markets since the beginning of the Industrial Revolution². The roles of physical distance and geological barriers in limiting range boundaries have been reduced and species increasingly establish in new regions¹. This spread of alien species has become a major threat to biodiversity and ecosystem services worldwide³ and rates of new establishments are predicted to continue to increase with ongoing effects of globalization^{4,5}.

Previous research has mainly focused on retracing the invasion routes of individual species⁶ and mapping donor and recipient regions for entire taxonomic groups⁷, 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 that is present in almost all terrestrial habitats on all continents except Antarctica¹⁰. Moreover, because of their small size¹¹ 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 communities¹⁴. To investigate the spatiotemporal dynamics of ant invasions, and to test for factors favouring spread, we assembled a dataset 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}.

Results

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 (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 index¹⁶). Thus, species present in adjacent countries have a low spatial diversity while those present in a few countries on 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) included 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 probably the result of a mix between human-mediated land transport and natural dispersal after initial invasion events¹¹. 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 movements¹¹. 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

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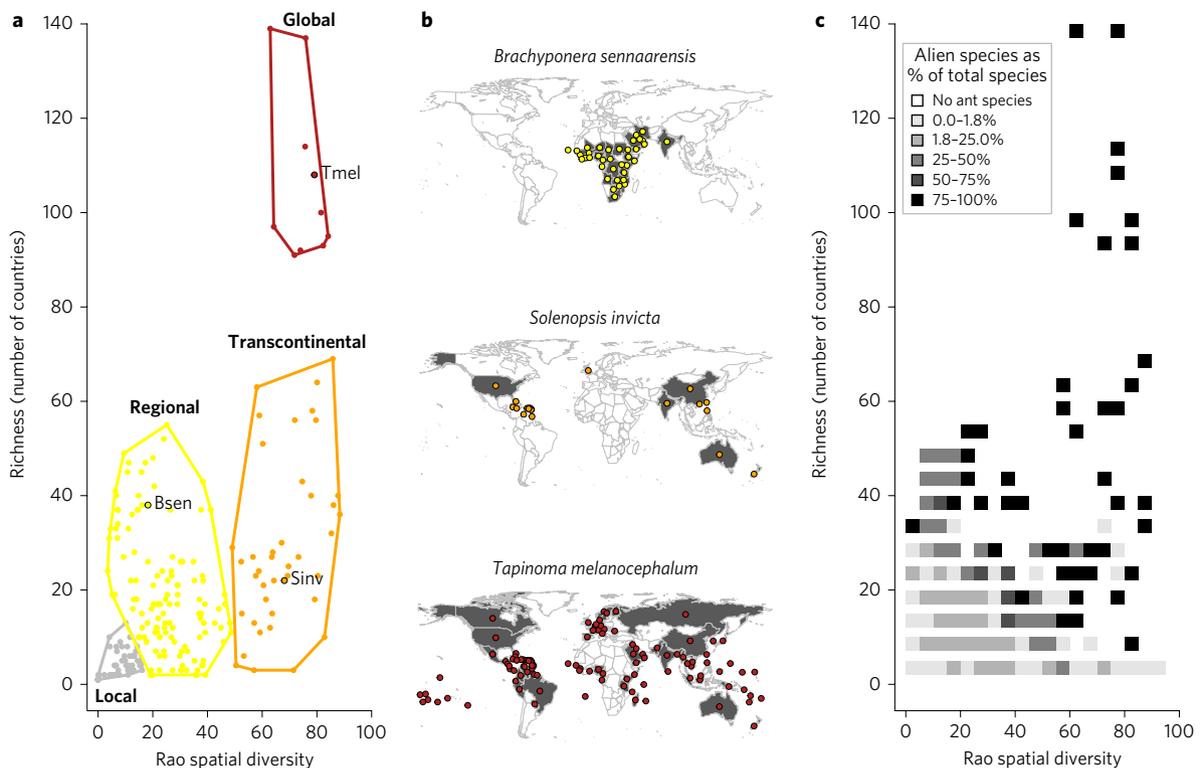


Figure 1 | Global spread of alien ants. **a**, Coordinates of 241 non-native ant species, clustered in four dispersion groups, within a ‘spatial distribution space’ (Jaccard similarity values within the local, regional and transcontinental groups were >0.75 , and in the global group, they were $0.6-0.75$). 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 the spatial distributions of three species belonging to each of the main dispersion groups, regional (yellow), transcontinental (orange) and global (red). 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 Supplementary Fig. 1 and occurrence data for all 241 species can be found in Supplementary Data 1. **c**, The proportion of alien species as a percentage of all species (including native species) for each position in the spatial distribution space.

36 species in the three groups that dispersed most (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 colonization (see coordinates of the first PCA axis) that coincided 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 transform¹⁹, 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 and Supplementary Fig. 2). The initial explosive spread coincides with the first wave of globalization but starts declining with World War I, the great economic depression of 1929 and World War II, and then increases again with the second wave of globalization during the second half of the twentieth 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 first wave of globalization (global group) and species that did not spread widely until the second wave (transcontinental group, Fig. 2c). The main difference between the regional and transcontinental groups occurred

principally during the second wave, which had only a limited effect on species in the regional group (Fig. 2c). These data indicate that an important difference between the three groups is the respective importance of the first or the second wave of globalization. In these analyses we used dates of first observation per country as proxies for colonization and although lags probably existed between the times of introduction and first detection, this should not significantly affect the chronology of records within a given taxonomic group²⁰. 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 colonized 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 (that is, 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

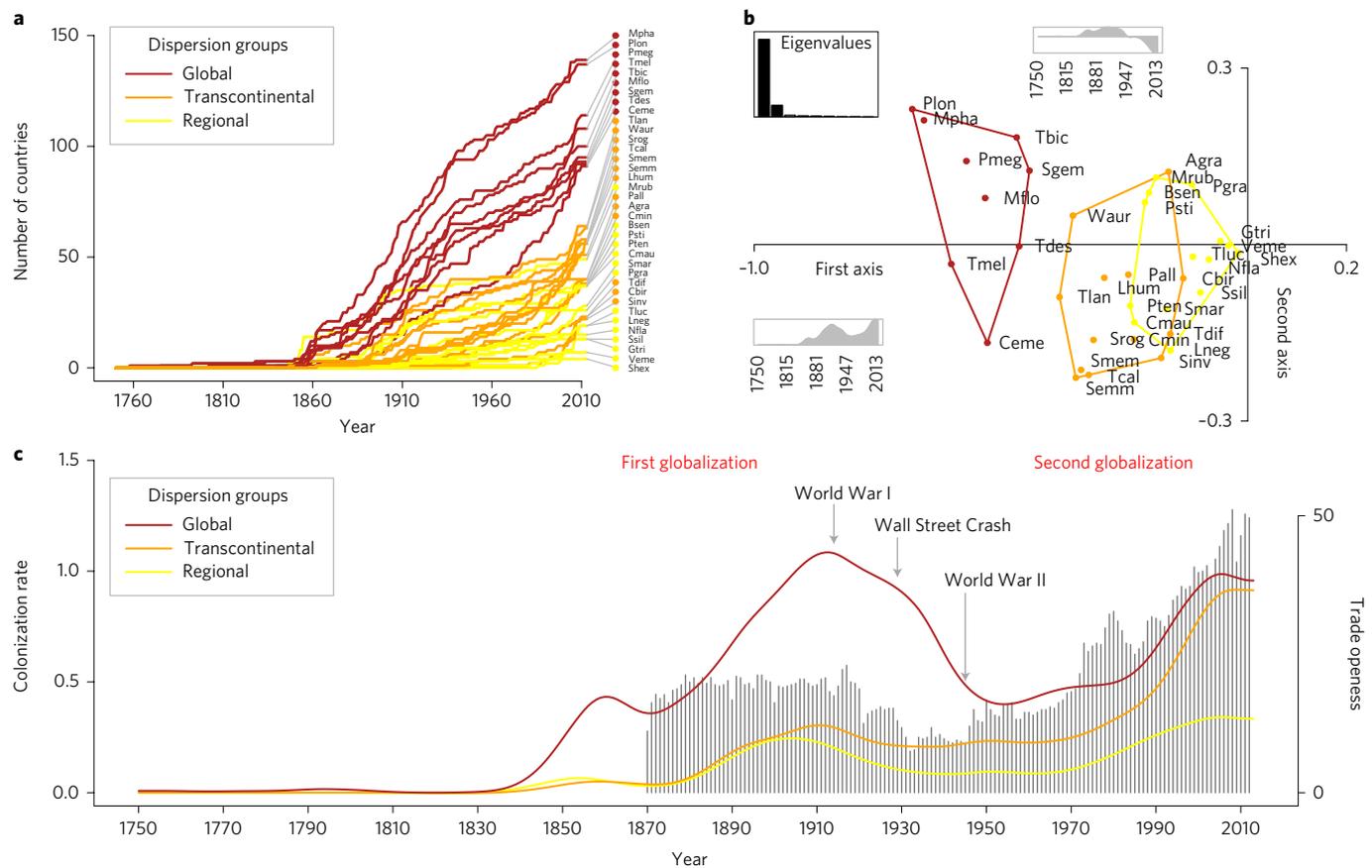


Figure 2 | Temporal colonization dynamics. **a**, Historical time series of cumulative numbers of countries colonized by 36 ant species. Colours indicate the dispersion group to which the species currently belong. For species codes see Supplementary Table 1. **b**, Factorial map: the three dispersion groups (colours as for **a**) 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 nineteenth and twentieth centuries, in particular the two waves of globalization. The second axis contrasts the first and the second wave. The coordinates of the first and second PCA axis are shown in the lower left and upper right inset charts and the eigenvalues of the first PCA axes are displayed in the upper left chart. **c**, Time series (1750–2010) of the mean colonization rates for the regional, global and transcontinental dispersion groups (coloured lines), and the yearly trade openness ((exports + imports)/world gross domestic product; grey bars).

yearly transition of species among groups between 1750 and 2010 (see Supplementary Notes).

Despite previous interest in spread dynamics²¹, historical introduction rates²² 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 nineteenth century to 1914 and 1960 to the 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 database²⁶. 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 PCA 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 ants²⁷, 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 that 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 Supplementary Fig. 3), 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 and 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 landscapes²⁸.

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 (International Union for Conservation of Nature (IUCN) Invasive Species Specialist Group, www.iucngisd.org). Ants are very prominent among invasive species, with 19 species in the IUCN list of

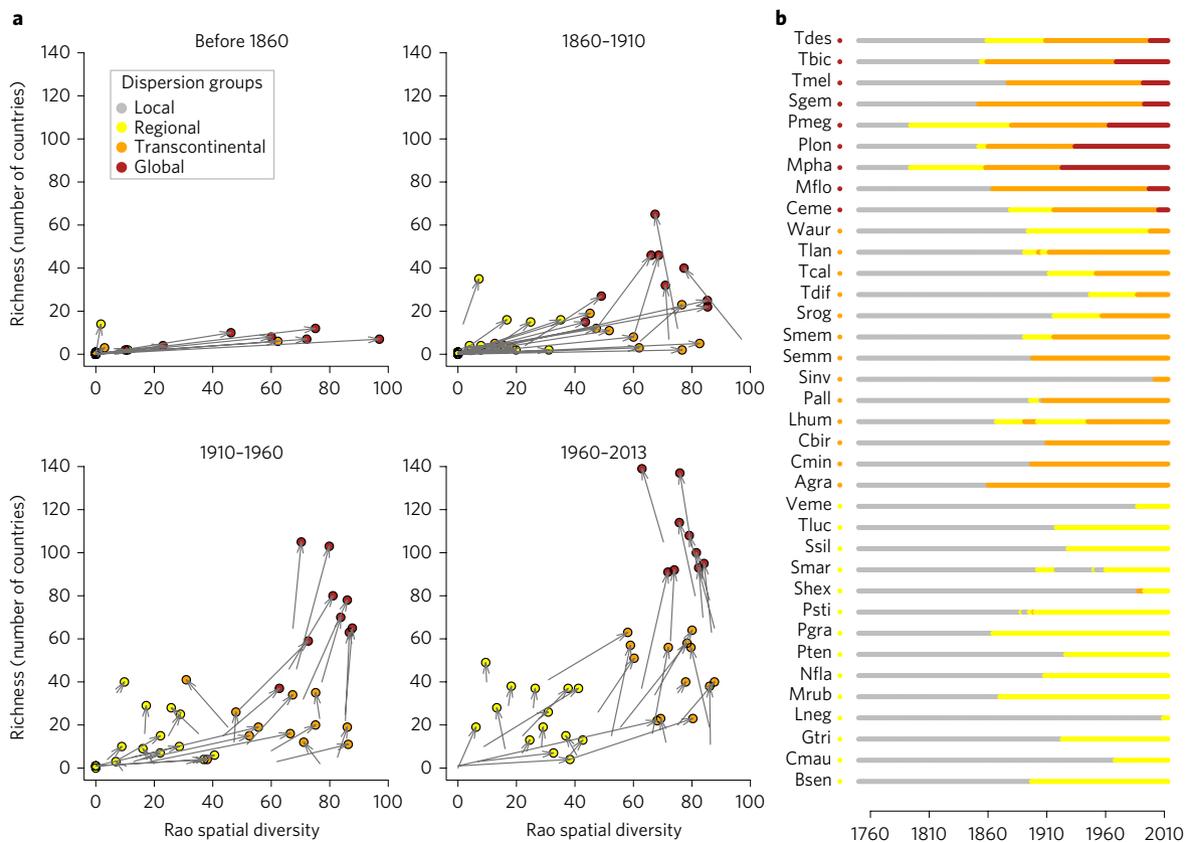


Figure 3 | Spatiotemporal trajectories. **a**, Historical progression of each species through spatial distribution space. Colours indicate the dispersion group to which the species currently belong. Species currently in the transcontinental group seem to follow the spatiotemporal trajectory of species in the global group. **b**, Historical transition of each species among dispersion groups from 1750 to 2010. For species codes see Supplementary Table 1. The colours indicate the dispersion group to which each species belonged in the past. Group membership was calculated on the basis of the species' annual position within the spatial distribution space (as in Fig. 1). Species in the transcontinental and global group spent less time at the regional stage than species currently in the regional group (Supplementary Notes).

the 360 'invasive' animals. Eighteen of these nineteen ants are alien species that were greatly over-represented in the global group of our analysis ($\chi^2 = 67.8$, d.f. = 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 with the remaining 100 alien ant species for which data are available, as evidenced by their coordinates on the first axis of the PCAIV (Welch $t = -13.1$, d.f. = 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 first axis of the PCAIV. This analysis identified nine additional species (Fig. 4b). Strikingly, these nine species had a significantly faster spread over the last ten years (11.6 ± 1.2 countries) than other alien species (7.5 ± 1.7 countries; Welch $t = 1.96$, d.f. = 18.5, $P = 0.03$), further supporting the view that these are likely to also become invasive in the future.

Discussion

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 species with alien species²⁹, 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 plants³⁰, habitat generalism in birds³¹ and body size in amphibians³² and bivalves²⁹. 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 plants³³.

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 nineteenth century were driven to a large extent by British colonialism³⁴ and alien insect spread rates in Europe seem to have been influenced by the East–West divide³⁵. Temporal analyses also revealed that invasion rates increased towards the end of the twentieth century²⁰, and were associated with development and governance socioeconomic indicators of trading partners³⁶, 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 in assessing 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 frequent³⁷. 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

Table 1 | Univariate tests of nine morphological and life-history traits; across dispersion groups, linked to spatial richness and linked to spatial diversity.

Response	Trait	Trait value	Association	Test	n	d.f.	Statistic	P value
Dispersion groups	Queen number	Polygyny	+	Chi-square	174	3	$\chi^2 = 15.8$	0.001
	Nest structure	NS	0		171	3	$\chi^2 = 6.9$	0.07
	Colony founding	Dependent founding	+		166	3	$\chi^2 = 26.8$	<0.0001
	Habitat disturbance	Habitat disturbed	+		238	3	$\chi^2 = 38$	<0.0001
	Colony size	NS	0	ANOVA	133	3, 129	$F = 1.77$	0.15
	Size smallest	Quantitative	-	ANOVA	240	3, 236	$F = 4.38$	0.005
	Size largest	Quantitative	-	ANOVA	240	3, 236	$F = 3.52$	0.016
	Habitat generalism	Quantitative	+	GLM (Poisson)	241	3	$\chi^2 = 67$	<0.0001
	Nesting generalism	NS	0	GLM (Poisson)	222	3	$\chi^2 = 6$	0.1
Richness (countries)	Queen number	Polygyny	+	GLM (binomial)	174	1	$\chi^2 = 10.4$	0.001
	Nest structure	NS	0	GLM (binomial)	171	1	$\chi^2 = 2.1$	0.15
	Colony founding	Dependent founding	+	GLM (binomial)	166	1	$\chi^2 = 18.3$	<0.0001
	Habitat disturbance	Habitat disturbed	+	GLM (binomial)	238	1	$\chi^2 = 27$	<0.0001
	Colony size	Quantitative	+	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	Quantitative	+	GLM (Poisson)	241	1	$\chi^2 = 70$	<0.0001
	Nesting generalism	Quantitative	+	GLM (Poisson)	222	1	$\chi^2 = 5.4$	0.02
Diversity (Rao)	Queen number	Polygyny	+	GLM (binomial)	174	1	$\chi^2 = 13.7$	0.0002
	Nest structure	Polydomy	+	GLM (binomial)	171	1	$\chi^2 = 3.9$	0.05
	Colony founding	Dependent founding	+	GLM (binomial)	166	1	$\chi^2 = 22.7$	<0.0001
	Habitat disturbance	Habitat disturbed	+	GLM (binomial)	238	1	$\chi^2 = 47$	<0.0001
	Colony size	NS	0	LM, ANOVA	133	1, 131	$F = 0.48$	0.49
	Size smallest	Quantitative	-	LM, ANOVA	240	1, 238	$F = 10.8$	0.001
	Size largest	Quantitative	-	LM, ANOVA	240	1, 238	$F = 7.3$	0.007
	Habitat generalism	Quantitative	+	GLM (Poisson)	241	1	$\chi^2 = 51$	<0.0001
	Nesting generalism	Quantitative	+	GLM (Poisson)	222	1	$\chi^2 = 6.8$	0.009

The association of the trait with the response variable is indicated as '+' for positive and '-' for negative, if significant. Here, the dispersion groups are considered ranked (from 'local' (1) to 'global' (4)) and the trend across dispersion groups is given. For dichotomous variables, the variable value with a positive association is indicated. NS, not significant; ANOVA, analysis of variance; GLM, generalized linear model.

to come⁴. In the future, it would be useful to test and extend our framework for 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 also 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 (species that have established outside of their native range through human-mediated transport; Supplementary Data 1). Our list is based on existing alien ant lists from the literature^{38,39} and the public databases AntProfiler²⁶ (www.antprofiler.org), Antweb (www.antweb.org), the Invasive Species Specialist Group of the IUCN (www.issg.org) and Delivering Alien Invasive Species for Europe (www.europe-alien.org).

We classified 19 species as invasive using the Invasive Species Specialist Group's 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 nineteen invasive species were also on 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 1). 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 Bolton's world catalogue⁴⁰ 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 throughout the world and is interlinked with the Encyclopedia of Life); the New Zealand Landcare Research database⁴¹, which records exact occurrences of alien and invasive ant species; a dataset of recorded alien ants in the United States^{38,42}; and a dataset of alien ant species worldwide³⁹. 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 1 and Supplementary Table 2). In addition, 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 the International Organization for Standardization 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 gross domestic product. Data from 1870 until 2002 have been previously compiled⁴³ on the basis of the International Monetary Fund's Direction of Trade Statistics and the Barbieri dataset for trade data, in addition to the World Bank's Development Indicators and the Maddison dataset for gross domestic product data. Trade openness from 2003 to 2010 was extracted from the United Nations Conference on Trade and Development dataset.

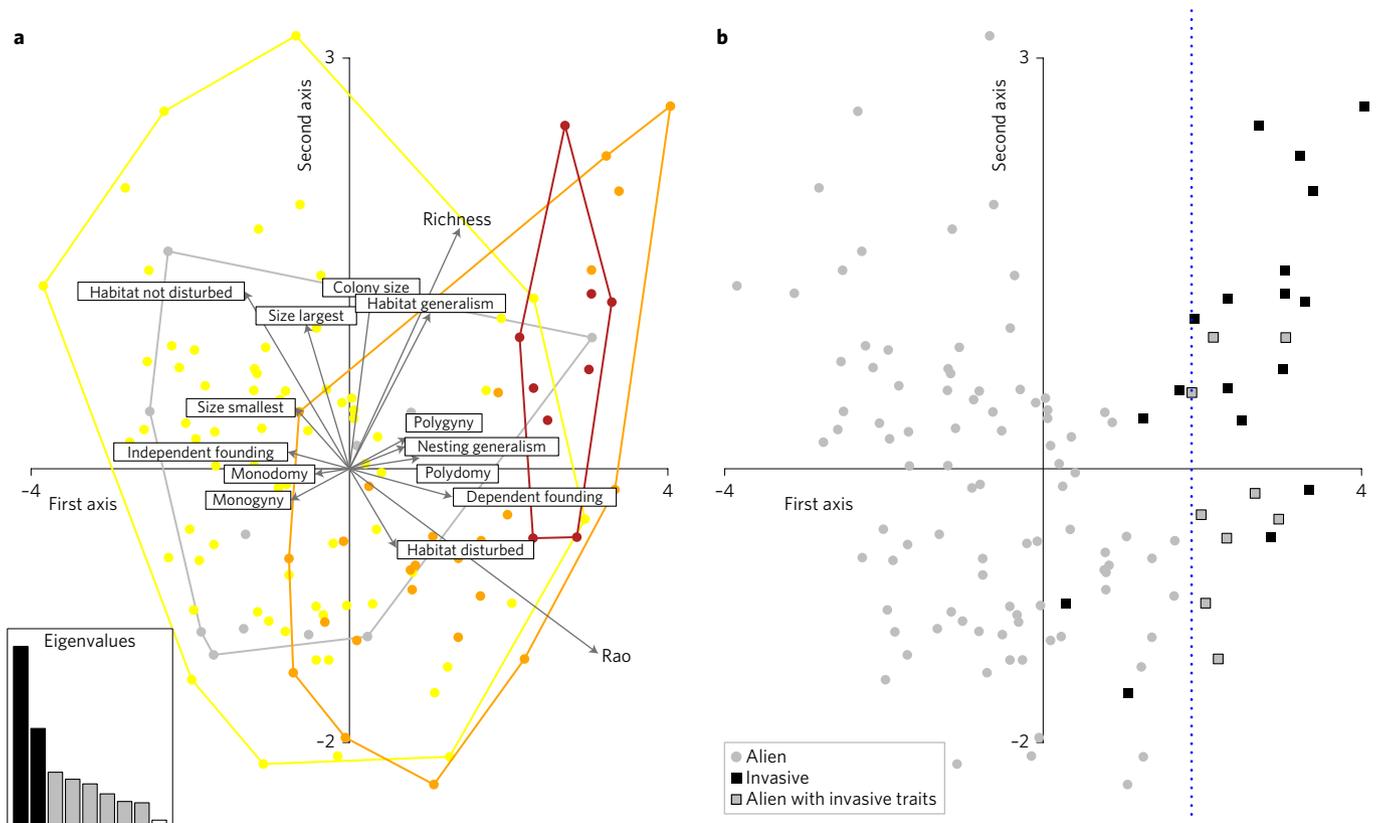


Figure 4 | Morphological and life-history traits. **a**, PCAIV on 9 traits and 118 alien ant species; eigenvalues of the PCA axes are shown in the lower-left chart (black bars represent the first two axes). The polygon (convex hull) boundaries show the contour of the most extreme points in each dispersion group (local, grey; regional, yellow; transcontinental, orange; global, red). The grey arrows indicate the vectors of the species' traits, spatial richness (Richness) and diversity (Rao). All pairwise comparisons between groups of the coordinates on the first PCAIV axis were significant (pairwise Wilcoxon, $P < 0.0001$ for all comparisons). For the species represented by each point, see Supplementary Fig. 3 and the species codes in Supplementary Table 1. **b**, Invasiveness status of the 118 ant species. Alien ant species that fell within a 99% confidence interval (lower confidence limit indicated by the dotted blue line) along the first PCAIV axis around invasive species are represented by grey squares. These species were *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 first PCAIV). For the species represented by each point, see Supplementary Fig. 4 and the species codes in Supplementary Table 1.

Species traits. We used the Antprofiler database²⁶, which is a database of the ecological, morphological and life-history traits of ants based on the literature and the contribution of the myrmecologist community. We selected nine traits that had been previously suggested to be associated with invasiveness^{12,13,15}. We transformed the variables in that database to record (1) queen number, that is, if species can have multiple queens within the same nest (polygyny) or if they always have a single queen (monogyny); (2) nest structure, that is, 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, that is, 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, that is, if they construct their nests in disturbed habitats (habitat disturbed) or not (habitat not disturbed); (5) colony size, that is the typical size of mature colonies, expressed as the log-transformed number of workers; (6) size smallest (worker), that is, the log-transformed body length of the smallest workers within a colony; (7) size largest (worker), that is, the log-transformed body length of the largest workers within a colony; (8) habitat generalism, that is, the number of habitats where the species has been recorded (using the following classifications: rainforest, tropical dry forest, temperate forest, boreal forest (taiga), grasslands, scrubland, tundra, riparian zones, desert, coastland, urban areas and agricultural areas); and (9) nesting generalism, that is, the number of different nest types that the species can inhabit (using the following categories: canopy, leaf litter, ground, twigs and logs, underground, and 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. 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 package⁴⁴. 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 variables⁴⁴.

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 index¹⁶ calculated using the species' spatial distribution in 2010 (presence-absence data per country), on the basis of the pairwise distances between countries where a species was present. These distances were calculated using the geographical coordinates of the centres of country polygons according to the haversine method⁴⁵. 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 (1,000 resampling runs). The observed Jaccard similarity value exceeded 0.6 for the main four nodes (local group, 0.845; regional group, 0.766; transcontinental group, 0.774; global group, 0.623). This method is described in more detail in ref. ⁴⁶ and was computed using 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 5×5 square of the graph 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 whether 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 (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 calculated the first derivatives of these curves after they were first smoothed using a cubic spline (with a smoothing parameter value of 0.65). A 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.3.1.1⁴⁷. We estimated average group spread rate as the mean derivative per dispersion group and compared these group spread rates with 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 series¹⁹. 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 arrows (see Fig. 3a) connected the previous position with the position for each date (1860, 1910, 1960 and 2010).

For each species and every year between 1750 and 2010, we calculated spatial richness and diversity and determined to which of the four groups these points belonged using a *k*-nearest-neighbour 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 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 to test for a link between spatial richness or spatial diversity and colony size, size smallest or size largest; and (3) generalized linear model 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 analysis of variance (colony size, size smallest, size largest, habitat generalism, nesting generalism). We carried out a PCAIV on 118 species for which we had information on all nine traits using the *ade4* package in R v.3.1.1. This analysis is a particular case of a PCA in which we used spatial richness and spatial diversity (Rao) as explanatory variables. We tested pairwise differences among groups in this trait 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 Welsh *t*-test with an alpha level of 0.005 to reduce the probability of making a type I error. 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 were carried out in R v.3.1.1 and a script (Supplementary Data 2) is supplied to generate all figures using the R workspace, which contains all data used here (Supplementary Data 1).

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Author contributions

C.B. and L.K. designed the study, C.B. and A.L. collected the data, C.B. and S.O. analysed the data and all authors discussed the analyses and wrote the paper.

Additional information

Supplementary information is available for this paper.

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Competing interests

The authors declare no competing financial interests.