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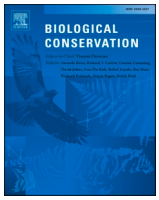

Monitoring the online ant trade reveals high biological invasion risk

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ABSTRACT

Ants are traded as pets across the globe, but if introduced outside of their native ranges they could become invasive with dire environmental and economic consequences. We demonstrate how geotagged e-commerce information can be utilized for biosecurity risk assessment. We monitored online pet ant sales in China and found that 58,937 ant colonies from 209 species were sold by 206 sellers in 89 cities across the country in six months. More than a quarter of the traded species were not native to China. Trait-based analysis revealed that the most sought-after ants have higher invasive potential than less popular species. Climate-based distribution models suggest that 24.7 % of the non-native species could find suitable climatic conditions in the cities from which they were sold. If released, pet ants could interfere with urban ecosystems, rural agriculture, and spill over to threaten back-country habitats with high biodiversity. Based on our analysis we offer guidelines on wildlife trade policy and management: (1) we provide a list of potentially invasive ants sold in each Chinese city; (2) we identify the highest risk of a non-native ant introduction at the Greater Bay area of subtropical southern China; (3) we highlight the absence of within-country permitting requirements which resulted in invasive species being transported across Chinese provincial lines. Worldwide, similar wildlife trade records are only accessible to conservation practitioners cognizant of local languages and customs. We encourage grassroot web scraping of under-monitored, fast-developing economies to gather information crucial for guiding regional policy decisions.

1. Introduction

Ants are becoming popular pets around the world (Gippet and Bertelsmeier, 2021). Compared with vertebrates, ants are more diverse in morphology and behavior, require less husbandry, and since they follow r-selected reproductive strategies, are easier to propagate when environmental conditions are met (Lach et al., 2009). Individual pet owners fascinated by insect eusocial behavior house entire ant colonies, including reproductive queens, in exhibition-style indoor formicaria (AntsCanada, 2022; Ant Keeping Depot, 2022). To meet this demand, sellers advertise local and non-native species online and send colonies across the globe (Gippet and Bertelsmeier, 2021; Gippet et al., 2022). Ants transported outside of their native ranges could establish themselves as invasive species. Invasive ants are already among the most widespread and economically destructive species on earth (Angulo et al., 2022). Just 12 species of invasive ants have been responsible for $51.93 billion worth of economic damage since 1930 (Angulo et al., 2022), with dire environmental consequences, including the replacement of native biota, alteration of nutrient cycles, and the disruption of agriculture and human affairs (Diagne et al., 2021). In light of these threats, it is necessary to assess the potential biosecurity risk of the increasingly popular online ant trade.

Central to such an assessment is the establishment of a baseline of trade volume, trade species and seller distributions (Gippet et al., 2022). In particular, since environmental similarity is commonly used as a proxy for the likelihood of an invasive species establishing itself outside of its native range (Byeon et al., 2020; Chen et al., 2020; Morrison et al., 2005), fine-scale locality data of ongoing transactions could instruct researchers on which local climatic data to use in their models. Habitat suitability, coupled with species specific traits (e.g. polygyny, caste polymorphism) and other environmental variables (e.g. soil quality, microbiota), allows for the preemptive identification of regions of high

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biosecurity concern (Fournier et al., 2019; Kaiser and Burnett, 2010). Understanding general patterns of trade will also assist border control agencies in anticipating shipments of incoming non-native species (Sánchez-Mercado et al., 2016; Stringham et al., 2021).

Theoretically, global wildlife transport must comply with export-import reporting requirements, and relevant locality records of trades can be obtained from centralized databases (e.g. Scheffers et al., 2019; Liew et al., 2021). However, recent decades have seen wildlife trade thriving in the loosely regulated cyberspace. A surprisingly high number of species are being shipped in parcels without regulatory oversight (Marshall et al., 2020, 2022; Nijman et al., 2021). While official trade records are hard to obtain, e-commerce can be monitored through systematic web scraping (e.g. Chaber et al., 2021; Gippet and Bertelsmeier, 2021; Kubo et al., 2022). Since some platforms mandate their sellers to report monthly sale volume and shipping locations, e-commerce data can provide fine-scale locality information on where and how many potentially invasive species are being sold.

Our goal is to assess the biological invasion risk of online ant sales by monitoring ant trading on the largest e-commerce platform in China for one year. Over the past decade, China has experienced a boom in the digital economy (Jiang and Murmann, 2022), but its Chinese language e-commerce platforms have largely evaded conservation analysis. We plan to record species, trade volume and seller locality for each pet ant item sold online and apply a standard assessment framework (Stohlgren and Schnase, 2006) to analyze the risk of each traded species becoming invasive. Specifically, for each sold ant species we plan to use web-scraped information to assess (1) its chance of introduction, (2) the abiotic (climatic) match between its seller location and its native range and (3) whether it possesses biological traits associated with invasiveness. Based on our assessment, we will identify regions of high invasive concern and discuss potential changes in policy and legislation to better monitor the online trade in pet ants.

2. Methods

2.1. Data collection

Taobao (www. taobao.com) is the largest e-commerce site in China (a dedicated website for selling pet ants in the country does not exist). We used all ant genus names in Chinese from a curated list as search terms (Ran, 2022). In April 2021, we searched through each term and used a customized JavaScript snippet (Supplementary Material 1) to record the item link, item description, seller name, seller location and monthly sale volume of each display item matching the search term. We excluded irrelevant items (e.g. dead ant specimens) from our analysis. After an initial round of scraping, we revisited the same item links each month to record the change in monthly sale volumes from May to October 2021 (six months). In October 2021 and April 2022, we again searched for all terms and incorporated any new item links: this allowed us to track item turnover at six-month intervals. We classified each ant species on sale as native or non-native based on whether it has ever been recorded in China as non-invasive (Janicki et al., 2016).

Our analysis of online ant trade was based on verified seller localities. We assumed that for each seller, its self-reported business locality was where ant colonies were stored (and from where they were shipped to potential buyers). Although it is not illegal on Taobao.com to ship goods from a locality other than a seller's business location, the practice is associated with proxy sellers and uncommon among sellers of live animals that need pre-transaction maintenance.

2.2. Climate-based assessment

For each traded ant species, we obtained their native range distribution records (Janicki et al., 2016) to train Maximum Entropy Species Distribution Models (MaxEnt, Phillips et al., 2006, implemented in maxent function in the R package dismo). Since we used a 2.5-min resolution world map grid with 19 current climatic variables (Fick and Hijmans, 2017), we conducted spatial thinning at 4.6 km so that no two distribution points used for modelling fell within the same grid (Aiello-Lammens et al., 2015, implemented in R package spThin). Only species with >10 post-thinning distribution records were used for modelling; this cutoff was shown to provide robust modelling results for both simulation and ground-truthed studies of similar scale and sample prevalence to ours (van Proosdij et al., 2016).

For each species, we built two sets of MaxEnt models using different selection criteria for climatic variables. First, we conducted a principal component analysis (PCA) on all 19 climatic variables (rasterPCA function in R package RStoolbox, Leutner, 2022) and used the first two principal components (PC) that captured most of the climatic variances as MaxEnt training inputs. This approach served to reduce the co-linearity of model predictors, but the biological meaning of the MaxEnt response curves was difficult to interpret because the PC contained loadings of multiple climatic variables. We referred to these models as "PC-based models". To complement our first approach, we evaluated a preliminary MaxEnt model built with all 19 variables, and subsequently re-built the MaxEnt model using only variables that had higher than 5 % contribution in the initial iteration (equivalent to using the contributionthreshold function in R package MaxentVariableSelection, Jueterbock et al., 2016). This approach selected for variables that were most biologically relevant for each ant species, although each variable could still be correlated. We referred to these models as "climate-based models". All models used a combination of linear, quadratic, product, threshold and hinge response curve feature classes depending on the number of distribution records (see explanation of MaxEnt default setting in Merow et al., 2013)—we did not change this default setting because we had little a priori information on each ant species' response to selected climatic variables.

For model training, 10,000 pseudo-absence points were randomly generated (on terrestrial surfaces) within 10 degrees of longitude and latitude of each species' native distribution range, following best practices outlined in Barbet-Massin et al. (2012). Each model was cross-validated using five replicate folds (i.e. a total of five replicates, each following a 1:4 training/testing regime). Model accuracies were verified by calculating their area under the receiver operating characteristic curve (AUC). Following the guidelines of Hanley and McNeil (1982), only models with higher than 0.8 mean AUC (for either PC-based models or climate-based models) were used to make distribution predictions. We projected the replicate model with the highest AUC onto the climatic map of Chinese mainland (using the predict function in R package dismo) to calculate the habitat suitability of each city that had been transacting that species of ant (PC-based models were projected onto the map with principal components as raster layers). These suitability projections were "clamped" such that when projecting onto an environmental condition not encountered in MaxEnt training, the suitability value was constrained to its limit in the training range—providing a conservative estimate of species suitability in unencountered habitats.

In each model, a binary cut-off for invasive ant establishment (referred to as a "threshold") was estimated based on MaxEnt predicted suitability (threshold function, spec_sens option, in R package dismo). We further averaged this value within 10 km of the city from which the species was sold (i.e. across 16 grid cells on our 2.5 min map). With the exception of a few megacities, this 10 km radius covered both the urban area of a city and its surrounding forest or agricultural land. Temperature effects specific to urban environments (e.g. urban heat islands) were not noticeable at this scale. We referred to this value as "species-city" suitability, but it principally forecasts a species suitability in the city and its surroundings. Species-city suitability values were calculated for all modeled species in all the cities trading them. For climate-based models, we further calculated species-city suitability values of climate predictions using a pessimistic high-emission future climate change scenario (CMIP5 RCP8.5 scenario for 2070, with a predicted 4–5 °C annual temperature increase across the region, Taylor et al., 2012) to explore

whether invasive ant suitability would change under extreme regional warming scenarios.

2.3. Trait-based assessment

To investigate whether traded ants possessed biological traits associated with invasiveness, we assembled a dataset of ecological traits for all species with more than ten sales. (1) Worker body size as a continuous variable: we measured worker head width of three specimens per species from museum specimens at Harvard Museum of Comparative Zoology. We measured the maximum head width in full-frontal view excluding eyes; only minor workers were measured if the species had distinct major and minor workers. Body size has been shown to be related to the commercial success of ants because buyers prefer larger workers (Gippet and Bertelsmeier, 2021). (2) Polygny (whether the species has multiple queens within the same colony) as a binary variable was recorded from online databases (AntWiki, 2022; AntWeb, 2022). Polygynous ant species have a competitive advantage over other species in dominating local habitats quickly (Hölldobler and Wilson, 1977). (3) Record of worker caste polymorphism (i.e. sufficient intraspecific variation in worker body size, defined in Wills et al., 2018) as a binary variable: we surveyed whether each species had been described as having either major/ minor worker caste differentiation or exhibiting continuous size variation in online databases—we interpreted both types of descriptions as indicating presence of worker caste polymorphism (AntWiki, 2022; AntWeb, 2022). Although there is mixed evidence linking worker caste polymorphism to invasiveness (e.g., monomorphic species such as Argentine ants *Linepithema humile*, ghost ants *Tapinoma melanocephalum*, and yellow crazy ants *Anoplolepis gracilipes* are highly invasive), worker caste polymorphism promotes colony efficiency and colonization success, and is often correlated with colony size (Anderson and McShea, 2001; Wills et al., 2018). (4) Degree of habitat generalism, defined as the number of habitats where the species has been recorded (see Gippet and Bertelsmeier (2021)) was reported as a count variable: ant distributions were classified into 12 habitat types according to Bertelsmeier et al. (2013). Species with a high degree of habitat generalism are more likely to survive outside their native ranges (Lach et al., 2009).

We investigated the importance of these biological traits in predicting the commercial success of ants by fitting generalized linear models (GLM, without phylogeny, implemented in R package stats, R Core Team, 2022) and Bayesian phylogenetic generalized linear mixed models (BPMM, with phylogeny, implemented in the R package MCMCGLM, Hadfield, 2010). We used either a species' total six-month sale volume or the number of sellers as response variables. We combined all predictor variables (body size, worker caste polymorphism, degree of habitat generalism) as factors in a single model, with phylogeny as a random effect. Degree of habitat generalism (count variable)

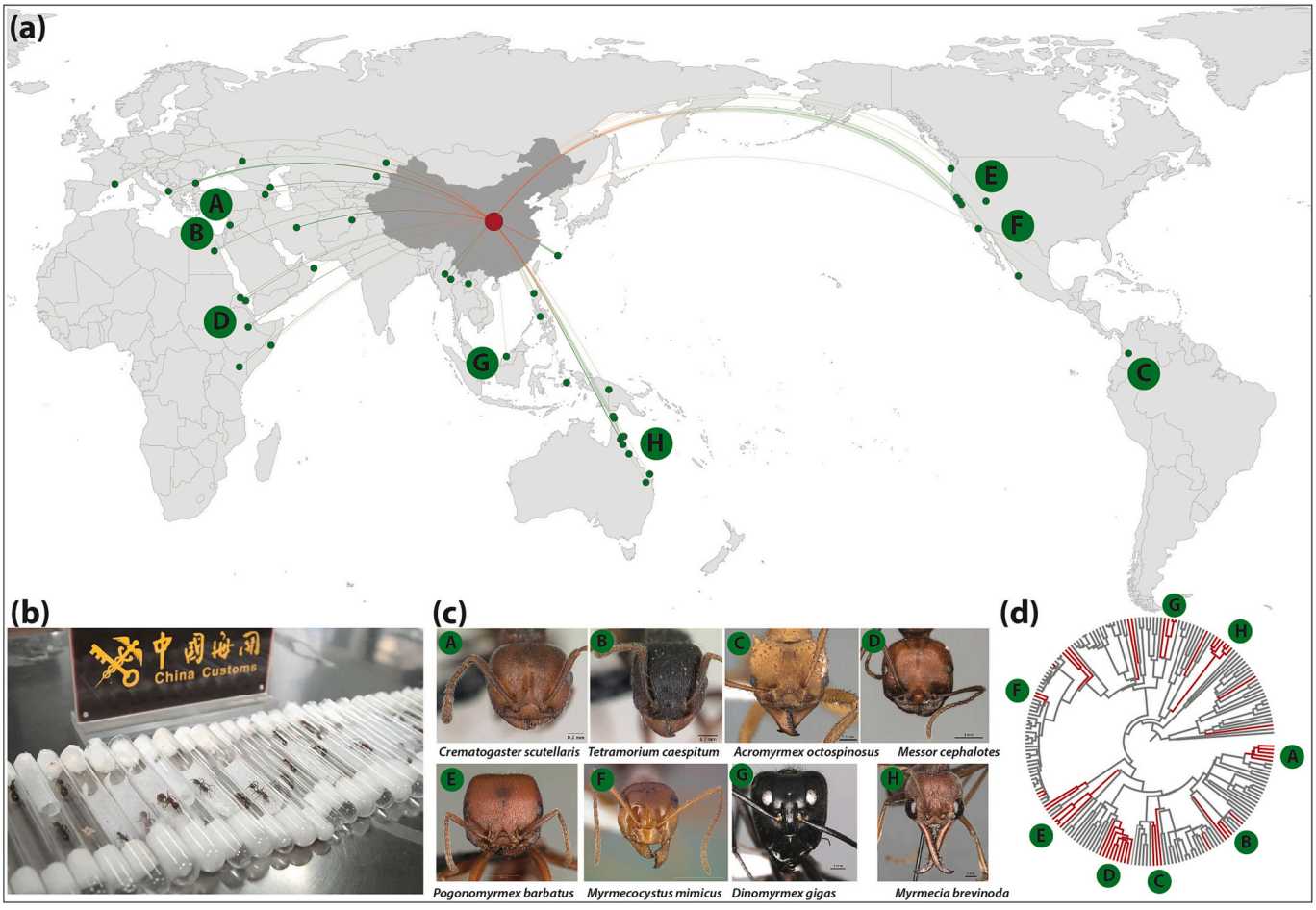

Fig. 1. Non-native pet ants sold in Chinese mainland. (a) Distribution of 56 non-native species. Lines connect Chinese mainland (excluding islands) to the closest point of each species' native distribution (depicted by small green points, the closest point of six species overlapped and were not shown). Larger green points with letters indicate the centroid of the native range of the top eight best-selling ant species. (b) Ants not native to China shipped from overseas intercepted by Chinese custom at Qingdao (photo credit: Xuan Li). (c) Eight of the most traded ant species that are not native to China (photo credit: AntWiki), and (d) phylogenetic position of non-native ants (red branches) among all traded species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

was log-transformed (following Gippet and Bertelsmeier, 2021). Body size (continuous) was z-transformed to facilitate effect size comparison. Phylogeny was obtained by pruning posterior sets of a large-scale ant phylogeny (Economo et al., 2018, Fig. 1D). Each model was run for 240,000 iterations, with a burn-in period of 40,000 and thinning interval of 100. We used priors with an inverse-Wishart distribution (we set the variance to 0.5 and the belief parameter *nu* to 0.002, as recommended by Hadfield, 2010). We assessed model convergence using the Gelman-Rubin diagnostic of potential scale reduction factor (PSR), and selected models with PSR under 1.1 (see Gelman and Rubin, 1992).

3. Results

3.1. Extensive trade

A total of 209 ant species from 72 genera were sold online from 2021 to 2022 (see Supplementary Material 2 for raw trade data). More than a quarter of the traded species (56) are non-native (Fig. 1, a tally of 4 species from Asia, 6 from Africa, and 12 each from America, Europe and Oceania). The 153 native species traded represent 14.7 % of all ant species (and 46.1 % of all ant genera) in China. Among them, 75.7 % were sold outside of the province where they had previous distribution records (see Supplementary Material 3). Two known invasive species (as defined in the Global Invasive Species Database, 2022, not native to China), *Monomorium pharaonis* and *Pheidole megacephala*, were traded (Fig. 3a).

A total of 58,937 ant colonies were sold from May to October 2021, from 206 sellers located in 89 cities across the Chinese mainland (Fig. 2a, Fig. 3a, excluding Taiwan and Hainan). Seller cities ranged from 0.05 to 22 million in population size (median population size = 2.3 million). Most sales happened in three of China's most populated areas: the Greater Bay area in the south, the Yangtze River Delta region in the east, and the Beijing-Tianjin-Hebei Economic Zone in the north (Fig. 2a, b). Among all traded species, the most popular ant species was *Camponotus turkestanus* with 8555 total sales, followed by *Carebara diversa* (6081 sales), *Camponotus japonicus* (6071 sales), *Camponotus nicobarensis* (4931 sales), and *Messor structor* (3988 sales). Among the 100 top-selling ant species, 10 % were not native to China (Fig. 3a).

3.2. Climate-based risk assessment

Out of 209 ant species, 119 species had >10 post-thinning native range distribution records and their MaxEnt models had higher than 0.8 AUC (see Supplementary Material 4 for model parameters, PC loadings, response curves and thresholds). The median number of post-thinning distribution records used for modelling was 70 points (s.d. = 299.3, spatial thinning removed 25.2 % of records). For PC-based models, the first two PCs accounted for 99.6 % of the total variance across 19 climatic variables and were used as MaxEnt inputs. The variables with the highest loadings on the first PC were "temperature seasonality", "minimum temperature of the coldest month" and "mean temperature of the driest quarter". Mean model AUC was 0.87 (s.d. = 0.06). In climate-based models, the variables that most frequently qualified for >5 % of model contributions were "precipitation of the driest month", "precipitation of the coldest quarter", "precipitation of the warmest quarter", "temperature seasonality" and "isothermality". Mean model AUC was 0.92 (s.d. = 0.05).

We generated species-city suitability values for 815 species-city pairs. The PC-based models estimated a higher percentage of species-city pairs that crossed suitability thresholds compared with climate-based models; 81.2 % of the threshold-crossing predictions from climate-based models agreed with those from PC-based models. Here we

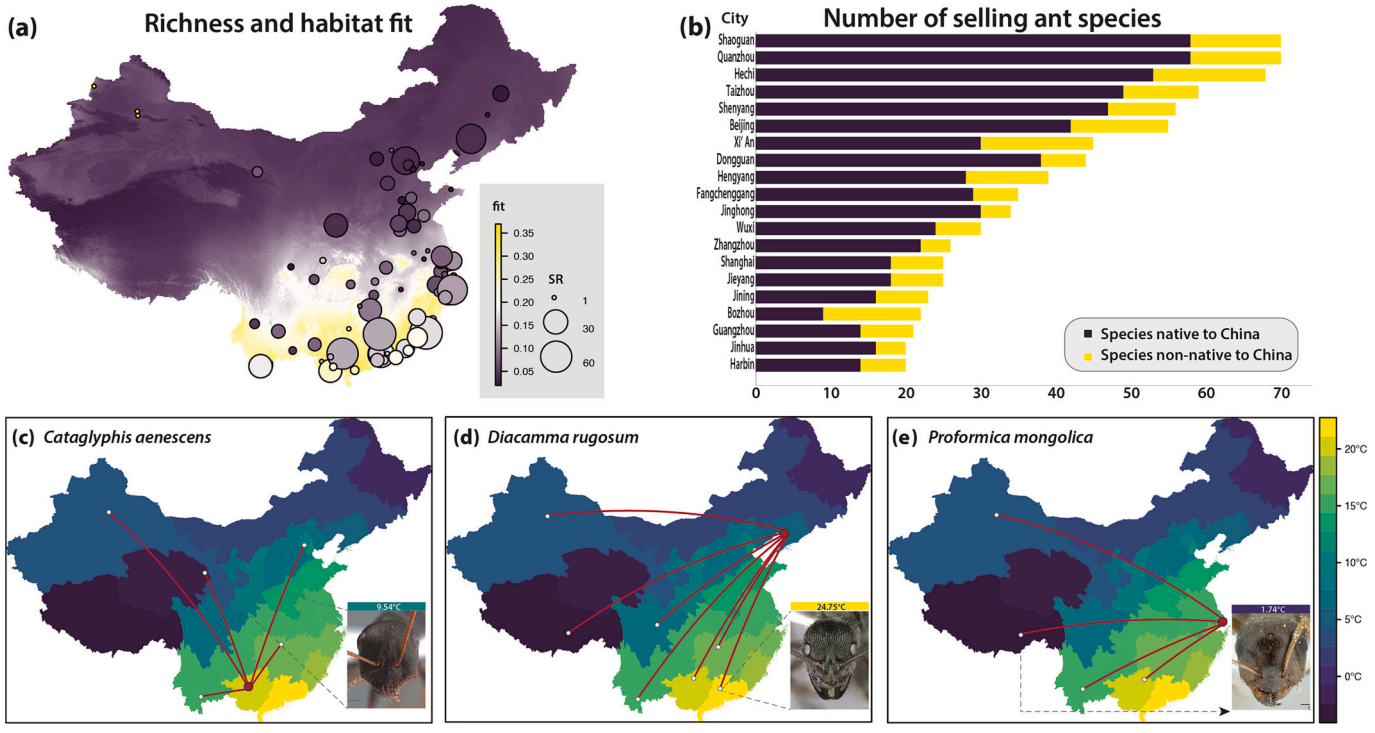

Fig. 2. Extensive ant transport across Chinese mainland. (a) Each ant-selling city in Chinese mainland is indicated as a circle, with the size of the circle proportional to the number of species sold (species richness, SR); the colour of each circle corresponds to the mean habitat suitability (fit) of a city's traded species for the city's climate. Background map of Chinese mainland is colored by the average habitat suitability of all traded species. (b) Top 20 cities with highest volume of ant sales in six months. (c-e) Examples of native species sold in cities outside their native distributions (photo credit: AntWiki). Lines connect distribution records (white dots) to seller location (red dot). Colors indicate the mean annual temperature of each province in Chinese mainland. Figures above the photo of each ant indicate the mean annual temperature of the distribution record with the highest temperature difference to its seller location. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

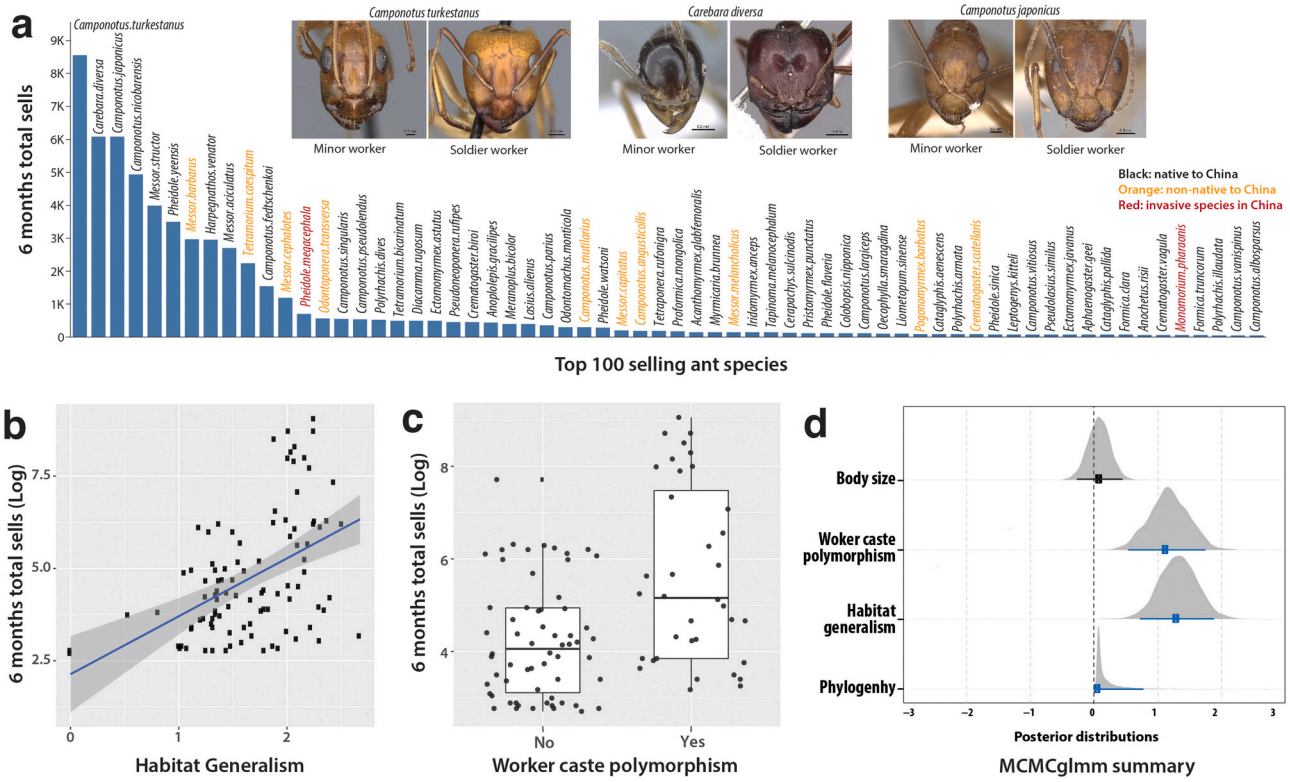

Fig. 3. More popular ants have traits that tend to make them more invasive. (a) The 100 best-selling ants on Taobao.com in 6 months. (b) Ants with more general habitat requirements have a significantly higher volume of sales compared with more specialized species ($p < 0.001$; GLM, points are jittered). (c) Species with worker caste polymorphism have a significantly higher volume of sales ($F = 17.54$, $p < 0.001$, One-way ANOVA). (d) Results of Bayesian phylogenetic generalized linear mixed models. Worker caste polymorphism, habitat generalism, and phylogeny are all significant predictors of the total volume of sales of a given ant species (in blue: their 95 % percentile confidence interval of estimate posterior are above zero). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

report the more conservative set of estimates from the climate-based models (Supplementary Material 4 lists current and future suitability predictions and thresholds for every species-city pair of all models): among 46 non-native ant species (251 species-city pairs), 24.7 % had suitable habitat in the city from which they were sold; among 73 native ant species (564 species-city pairs), 19.5 % had suitable habitat in the city from which they were sold. On average, southern and south-western China represented more suitable habitats for most of the traded species compared with northern China (Fig2A). Under a projection of an extreme climate warming scenario for 2070, 60 species-city pairs will cross the suitability threshold, while 45 pairs will recede below the threshold, with no clear geographical patterns.

3.3. Trait-based risk assessment

While most ants worldwide are monogynous (Bolton, 2003), nearly 70 % of all traded ants in our study were polygynous. GLM results, without accounting for phylogeny, are presented in Supplementary Material 5: all predictors were significantly correlated with either sale volume or number of sellers. A previous study used the number of sellers as a proxy for an ant species popularity and found a positive correlation between worker body size and the number of sellers (while also accounting for phylogeny, see Gippet and Bertelsmeier, 2021). We used both seller number and total sale volume as proxies for species popularity. Trade volume was significantly correlated with the number of sellers ($n = 98$, Pearson correlation $= 0.78$, $p < 0.01$) and both exhibited significant phylogenetic signals. Taking phylogeny into account, habitat generalism and worker caste polymorphism remained significantly correlated with a high sale volume and high number of sellers (Fig. 3b, d, see Supplementary Material 5 for compiled trait table and regression results, polygny was not included in the regression because of the high proportion of polygynous ants in our dataset). In other words, the better-selling ant species were more likely to possess traits that made them invasive compared with less popular species. We did not find a significant correlation between body size and sale volume, nor between body size and the number of sellers after taking phylogeny into account. While large-sized solitary hunters such as bulldog ants, *Myrmecia brevinoda,* were traded, small-sized *Carebara* ants were also popular.

4. Discussion

4.1. Methodological implication: online wildlife trade records

The pet ant trade (and wildlife trade in general) is a global conservation concern (Gippet and Bertelsmeier, 2021; Scheffers et al., 2019). Wildlife suppliers are especially concentrated in the economically disadvantaged Global South (Liew et al., 2021), where closely-guarded venues of transactions evade international scrutiny (although journalistic work provides a glimpse of the "black market": Laufer, 2010; Voigt, 2016; Nuwer, 2018). Our work shows that transactions leave online traces, but are only accessible to conservation practitioners cognizant of local languages and customs (Chowdhury et al., 2022). In the decentralized free market cyberspace, e-commerce information (such as trade volume, locality and species) can be useful in biosecurity risk assessment for avoiding future economic losses (Keller et al., 2007; Robertson et al., 2021). These information are often regional, and could be distilled from grassroots effort to compile web-based trade data (Chaber et al., 2021; Gippet and Bertelsmeier, 2021; Kubo et al., 2022; Marshall et al., 2022), or through mandatory reporting requirements imposed by regulatory bodies on e-commerce platforms and their participants. Similar web

scraping approaches applied to under-monitored, fast-developing economies can provide a bottom-up channel for gathering information crucial for guiding regional policy decisions.

4.2. Management implication: list of potentially invasive species

Since online ant sales in China operate without centralized documentation, web-scraped datasets offer the only way to tally species posing potential risks. Our six-month tally of 58,937 colonies from 209 species sold across Chinese mainland suggests previously unaccounted propagule pressure of non-native species, and warrants immediate attention due to its potential environmental toll. While individual species distribution models could be further fine-tuned through species-specific parameters (e.g. Fourcade, 2021; Feng et al., 2020; Pellissier et al., 2013), concurring predictive projections between PC-based and climate-based models used in our study point to many concerning habitat similarities among sold non-native species and their seller locations. For example, our models predicted high suitability in cities in southern China for the two traded invasive species, *Monomorium pharaonis* and *Pheidole megacephala*, based solely on their native distributions (outside China). These predictions were validated as these two species have already been reported to have established wild colonies in southern China (Wetterer, 2010, 2012, although involvement with the pet trade is unclear from these studies).

Other non-native ants on sale highlight a suite of potential ecological problems. For example, *Messor cephalotes*, an east African native, is among the largest seed harvesters in the world and could potentially disrupt predominantly grain-based agriculture in south-eastern China (Paolini et al., 2020, but see Martínez-Duro et al., 2010); *Acromyrmex octospinosus*, a New World leaf-cutter, is capable of sweeping defoliation and enormous agricultural damage even in its native range (Boulogne et al., 2014); the Australian bulldog ant *Myrmecia brevinoda* is aggressive and capable of delivering powerful stings (Lester and Keall, 2005). Aggravating the threat of an invasive spill-over is our finding that the popularity of a species positively correlates with its possession of traits that facilitate invasiveness (i.e. polygyny, worker caste polymorphism, high degree of habitat generalism), a theme corroborated across studies of a wide range of traded plants and animals (Gippet and Bertelsmeier, 2021; Beaury et al., 2021). It is understandable that sellers prefer hardy species and new hobbyist buyers prefer species that do not require extensive care; such market-driven selection amplifies the severity of potential species introduction events.

4.3. Management implication: high risk regions

Our risk assessment suggests that the Greater Bay area of subtropical southern China faces the highest risk of a non-native ant introduction (Fig. 2a). The threat results from a confluence of high transaction rates and suitable climate: 35.8 % of the total trade in Chinese mainland was conducted by sellers in the Greater Bay area, making intentional or unintentional release most likely to occur in this region; simultaneously, our climate-based assessment found that the region's wet subtropical climate is suitable for many popularly traded ant species, both southern natives (*Acanthomyrmex glabfemoralis*) and non-natives from the tropical Andes (*Acromyrmex octospinosus*), Southeast Asia (*Dinomyrmex gigas*) and eastern Africa (*Messor cephalotes*). The same combination of vibrant commerce and wet subtropical climate likely explains why the most recently reported invasives, the red imported fire ants (*Solenopsis invicta*) and the little fire ant (*Wasmannia auropunctata*), both first established wild colonies in the Greater Bay area of China (Chen et al., 2020, 2022), although there is no indication that these introductions resulted from pet trade. If released, pet ants could survive in niches within the diverse urban ecosystems that are particularly suitable for insects (Kantsa et al., 2013; Theodorou et al., 2020). They could compete with native insects, disrupt urban habitat connectivity (corridors) and decimate urban biodiversity (Rajesh et al., 2022; Ives et al., 2011).From their origin of release they could eventually spill over to disturb rural agriculture (Liu et al., 2021) and the highly biodiverse hilly forests of southern China (Zhu, 2017).

4.4. Management implication: need for region-specific policy

Our habitat suitability assessment focuses on seller localities, but any buyer within China could purchase these ants. This means that our assessment is an underestimate of the real invasive risk of the ant trade. There is no permitting requirement for cross-provincial transport of biological material in China (e.g. the equivalent of the USDA 526 permit in the USA, the "mobilization permit" in Ecuador, and NBA form IV in India to move biological material across state/provincial borders). Chinese ant enthusiasts from the northern city of Harbin (mean annual temperature: 4.8 °C) can purchase subtropical ants from Guangzhou (mean annual temperature: 22.6 °C, 2600 km away) without having to apply for a permit. A worrisome example from our study is that 431 colonies of yellow crazy ants *Anoplolepis gracilipes*, a native of southern China but invasive pest worldwide (Hoffmann and Saul, 2010; Lester and Tavite, 2004) had been legally transported across China. Such tropical/sub-tropical species could easily establish colonies in temperate northern China (see Fitzpatrick et al., 2007 on how tropical ants' native occurrence range under-predicts their invasive potential into temperate regions). In other words, without cross-provincial transport regulation, even transport of "native" ant species (defined as recorded in the country) poses severe invasive risks.

Similar dynamic shifts of each species' distribution range in response to future climatic changes further complicate our habitat suitability assessments (Battisti and Larsson, 2015). Selling subtropical ants in temperate northern China might pose increasing danger in the future due to "tropicalization" of temperate ecosystems (Osland et al., 2021; Walther et al., 2009): we predicted 60 species-city pairs crossing their suitability threshold in a drastic global warming scenario. However, we have no evidence of northern cities becoming, on average, more suitable for traded ants. This is because northern cities also currently house temperate-climate adapted ants, which might be less likely to survive projected warmer climates. These biological intricacies suggest that biological invasions risk assessment and resulting policies need to be fine-tuned and region-specific: in each city, any seller could be selling an assortment of native or non-native species—each may or may not survive the changing local climate following their release. The roster of potential invasive species changes over time and space. Transparent aggregation of trade information would be a welcome step toward formulating appropriate regional policy responses to the burgeoning pet ant trade.

4.5. Unanswered questions and potential opportunities

In the earliest warning of the online ant trade, Buschinger (2004) urged for an unequivocal trade ban of "exotic ant species, for commercial and non-scientific purposes". However, conservationists have since gathered evidence that such blanket-bans do not reduce wildlife consumption of either vertebrates or invertebrates (Di Minin et al., 2016; Kubo et al., 2022). In China, selling non-native ants is illegal and intercepted smuggled ant colonies frequently make national headlines (e.g. finance.china.com.cn, 2017; china.huanqiu.com, 2015; china.qianlong.com, 2022). The profusion of illegal ant sales revealed in our study attests to the difficulty of online law-enforcement; more importantly these transgressions require an explanation for the buyers' high demand for pet ants.

Most tellingly, our study period coincided with the onset of a nationwide campaign to denounce the "pet ant business" in China (Zhang and Fang, 2021). The campaign was part of the central government's initiative to halt the spread of the red imported fire ant (*Solenopsis invicta*), a South American native that had spread to 12 provinces across China in the past fifteen years (Song et al., 2021). *Solenopsis invicta* is not

sold online, but a media campaign portrayed all ant trading as harmful and reckless. During our study period, negative media portrayal of the online pet ant trade was correlated with a reduction in the volume of online ant sales, but a slight increase in the number of sellers (comparing April 2021 with April 2022, monthly sale volume dropped from 8221 to 4820, but the number of sellers increased from 118 to 128). Prevalent sales in the middle of a sweeping anti-trade campaign indicates high demand from buyers: their motivation needs to be understood in order to more effectively regulate trade.

Consumer demand reduction campaigns have increasingly been used alongside law enforcement to control wildlife trade (Holden et al., 2019; Veríssimo and Wan, 2019). In particular, presenting species-specific information regarding the consequences of buying an animal could significantly reduce consumers' likelihood to make purchases (Moorhouse et al., 2017). While the afore-mentioned Chinese media campaign focused only on *S. invicta* and the illegality of importing ants, we suspect that most consumers are simply not be aware that all non-native ants could become serious biosecurity hazards (Lach and Hooper-Bùi, 2009; Angulo et al., 2022). Proper dissemination of information regarding ant invasiveness ecology could facilitate demand reduction, or at least reduce propagule pressure from owners intentionally releasing their pet ants (Lockwood et al., 2005).

From an insect conservation perspective (Cardoso et al., 2011; Samways et al., 2020), persistent high demand for pet ants might reflect genuine public interest in learning about "the little things that run the world" (Wilson, 1987) in the context of a global insect apocalypse—many pet ant sellers advertised their products as natural history education tools. Since the public's conservation awareness increases with their exposure to insects (Leandro and Jay-Robert, 2019; Wang et al., 2021), well-designed educational campaigns could even channel consumer desire for rearing ants to promote environmental protection. For instance, since ants are everywhere (Kass et al., 2022), and culturally significant (Wilson, 2010), demand reduction campaigns could emphasize formicarium construction for only native species (while heeding that even native species could be disease vectors in urban settings, e.g. Máximo et al., 2014), or promote natural history observations of local ants' natural habitats. Invasive ants are undoubtedly biohazards, but demand reduction campaigns should not demonize all ants. We urge scientists, conservation practitioners, e-commerce managers and policy makers to engage in conversations regarding these issues, while taking into account the motivation and financial drive behind hundreds of thousands of ant sellers and buyers.

CRediT authorship contribution statement

Zhengyang Wang: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Jimmy Zeng:** Methodology, Writing – review & editing. **Hao Ran:** Data curation, Resources, Writing – review & editing. **Weilin Meng:** Methodology, Writing – review & editing. **Shanyi Zhou:** Supervision, Resources, Writing – review & editing. **Andrew B. Davies:** Funding acquisition, Writing – review & editing. **Cong Liu:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare no competing interests.

Data availability

Supplementary Material including (1) code used for web-scraping, (2) raw sales data (seller information anonymized), (3) maps for species distribution and seller distribution, (4) results for species distribution models, (5) ecological traits for each species and results for generalized linear models, (6) sample scripts for running species distribution modelling and generalized linear models are deposited at Zenodo: https://doi.org/10.5281/zenodo.7796558.

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