Invasiveness is linked to greater commercial success in the global pet trade

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The pet trade has become a multibillion-dollar global business, with tens of millions of animals traded annually. Pets are sometimes released by their owners or escape, and can become introduced outside of their native range, threatening biodiversity, agriculture, and health. So far, a comprehensive analysis of invasive species traded as pets is lacking. Here, using a unique dataset of 7,522 traded vertebrate species, we show that invasive species are strongly overrepresented in trade across mammals, birds, reptiles, amphibians, and fish. However, it is unclear whether this occurs because, over time, pet species had more opportunities to become invasive, or because invasive species have a greater commercial success. To test this, we focused on the emergent pet trade in ants, which is too recent to be responsible for any invasions so far. Nevertheless, invasive ants were similarly overrepresented, demonstrating that the pet trade specifically favors invasive species. We show that ant species with the greatest commercial success tend to have larger spatial distributions and more generalist habitat requirements, both of which are also associated with invasiveness. Our findings call for an increased risk awareness regarding the international trade of wildlife species as pets.

biological invasions | exotic pets | human-mediated dispersal | internet trade | wildlife trade

The extraordinary movement of our own species through migration, colonization, and travel has driven the geographic expansion of countless other species since prehistoric times (1). Humans have deliberately introduced a diverse range of species, in particular domesticated crops and animals that have contributed to our success (1). Today, however, the trade in live organisms for nonutilitarian reasons has rocketed (2–4). In the last decade alone, billions of plants and animals comprising thousands of species were traded annually, fueling a multibillion-dollar global business (2, 3, 5, 6). In particular, the demand for nontraditional (also known as "exotic") ornamentals and pets, i.e., organisms without a long history of domestication, has grown (2). These species are sometimes released into the wild or escape and may survive and reproduce (2, 7–9). Species with populations that have established outside of their native range are referred to as invasive species hereafter (see Table 1 for terminology). Some invasive species can have severe impacts on global biodiversity (10–13) and impose tremendous costs on society by damaging physical infrastructure, agriculture, forestry, and human health (14, 15). However, even though it is undisputed that the trade in pets and ornamentals contributes to the global movement of invasive animals (16–19), it is still unclear whether this trade specifically favors invasive species.

Previous research has suggested that invasive plant species are overrepresented in the horticultural online trade (20), but it remains unknown whether this overrepresentation is a general phenomenon also found in animals. To address this, we compiled a dataset of 7,522 terrestrial and aquatic vertebrate species traded as pets [including mammals (3, 21), birds (3, 21, 22), reptiles (3, 17, 21), amphibians (3, 17, 23) and fish (24–26); see *SI Appendix*, Fig. S1 for details] and compared it to the global vertebrate species pool [totaling 67,181 species: 6,015 mammals, 10,327 birds, 10,603 reptiles, 7,385 amphibians, and 32,851 fish (27–31)]. Invasive species (see Table 1 for definition) represent 12.6% of all traded species. We found that across all taxa and datasets, invasive species were strongly overrepresented in trade (Fig. 1). On average, invasive species were 7.4 times more frequent in trade than in the global species pool (mammals, 4.2–7.2; birds, 2.5–7.4; reptiles, 4.0–12.7; amphibians, 8.0–9.0; and fish, 7.2–13.1; χ^2 tests for each of the 14 datasets, $P < 0.0001$; Fig. 1 and *SI Appendix*, Table S1).

This remarkably consistent overrepresentation may arise because the pet trade specifically favors invasive species. However, this idea would be extremely difficult to test in vertebrates because they have been traded as pets for decades to centuries (4), and according to recent estimates, 53% of invasive vertebrate species have been introduced by the pet trade (i.e., 957 out of 1,822 species) (16). Therefore, invasive vertebrates could also be overrepresented in the pet trade simply because, over time, pet species had more opportunities to become invasive. These two processes potentially generating an overrepresentation of invasive species in the pet trade are not mutually exclusive and may sometimes act in conjunction.

To test whether the pet trade specifically favors species that are invasive, we chose ants (Formicidae) as a model system. More than 255 of the 15,377 described ant species have become invasive since the 1800s (32, 33). The spread of these invasive species can be attributed to accidental transport by humans, largely through the global commodities trade. However, following the commercial development of the internet (34) in the early 2000s, ants began to be sold as pets at global scale. It is unlikely that this pet trade has caused invasions so far, given that there is usually a time lag of one to several decades between the

Significance

The global pet trade may accelerate the spread of invasive species around the world, which threatens native biodiversity and impacts human economy and health. Here, using an extensive metaanalysis, we show that invasive species are strongly overrepresented across mammals, birds, reptiles, amphibians, and fish traded as pets. Even in the emergent trade of ants as pets, which is too recent to be responsible for any invasions yet, we found an overrepresentation of invasive species. This indicates that the pet trade not only creates opportunities for invasions, but that it favors specifically invasive species. These findings call for the rapid implementation of strict international regulations of the trade in animals as pets.

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Table 1. Glossary

Term	Definition
Invasive species	Species with at least one established population outside of the native range (regardless of any known impacts)
Noninvasive species	Species with no established population outside of the native range
Invasiveness	The property of an invasive species, defined here as a binary variable: Invasiveness is 0 for noninvasive and 1 for invasive species

initial introduction and the spread of a species (35–39). Therefore, observing an overrepresentation of invasive species among pet ant species would allow the conclusion that being invasive is linked to a greater commercial success. We do not assess differences among invasive species with and without impacts because impacts can vary temporally or spatially and may occur only after a considerable time lag (37, 40) and thus are not a good indicator of species invasiveness (41, 42).

To quantify the trade in ants as pets, we performed a standardized search of the internet, in 20 languages, for websites selling live ant colonies, revealing a global business that has increased steeply over the past 10 y (Fig. 2 *A* and *B* and *SI Appendix*, Tables S2–S4). In total, at least 520 ant species from 95 genera were sold online between 2002 and 2017, representing 3.4% of all 15,377 ant species and 28% of all 334 ant genera (33) (*SI Appendix*, Table S1 and Datasets S1–S3). As the pet trade in ants is extremely recent, it is not surprising that the number of traded species is lower than in more long-established pet trades such as mammals (506 species: ~8.4% of all mammal species), birds (3,749 species: ~36.3% of all bird species), reptiles (1,857 species: ~17.5% of all reptile species), and amphibians (591 species: ~8% of all amphibian species) (*SI Appendix*, Table S1 and Fig. S1). Among traded ant species, 57 were invasive, including 13 of the 19 worst global ant invaders listed by the International Union for Conservation of Nature (IUCN) (43) based on their high ecological and economic impacts (*Acromyrmex octospinosus*, *Anoplolepis gracilipes*, *Brachyponera chinensis*, *Monomorium floricola*, *Monomorium pharaonis*, *Myrmica rubra*, *Paratrechina longicornis*, *Pheidole megacephala*, *Solenopsis geminata*, *Solenopsis invicta*, *Tapinoma melanocephalum*, *Technomyrmex albipes*, and *Wasmannia auropunctata*). Invasive ant species were 6.6 times more common in trade than in the global species pool ($\chi^2 = 275.97$, $P < 0.0001$; Fig. 2*C* and *SI Appendix*, Table S1) and sold by 1.7 times more sellers than noninvasive species [likelihood ratio (LR) test for negative binomial generalized linear model (GLM): $n = 520$, LR = 21.6, $P < 0.0001$; Fig. 2*D*]. Thus, invasive species are specifically favored by the global pet trade. A potential explanation for this effect is that ecological traits linked to invasiveness could also increase commercial success.

To test whether five ecological characteristics associated with invasiveness [measured as the binary invasive status: invasive (1) or noninvasive (0); see *SI Appendix*, Fig. S2 for details] in ants (32) are also linked to commercial success (measured as the number of sellers offering the species), we used a negative binomial GLM that accounted for the geographical origin of the species (*SI Appendix*, code). Two ecological characteristics associated with greater invasiveness also increase commercial success: large range size and a high degree of habitat generalism (according to the best-fitting negative binomial GLM with $n = 222$ species, pseudo-$R^2 = 0.46$; Fig. 3 and see *SI Appendix*, Table S5 and Fig. S3 for details). These two characteristics are linked to the species' spatial distribution. They are not specific to the biology of ants and have been associated with invasiveness in plants and animals (44, 45). Species with larger distributions and more generalist habitat requirements may also be favored in the pet trade more generally, as suggested for amphibians (23) and birds (22), because the most widespread species are more likely to be encountered, and thus harvested for the pet trade. Moreover, generalist habits can facilitate rearing and increase survival in captivity and thus species' attractiveness for pet owners, whereas species with a specialist lifestyle are more difficult to care for. We also found a trait that was negatively associated with invasiveness and positively associated with commercial success: large body size (32, 46) (Fig. 3 and *SI Appendix*, Table S2). Therefore, body size does not drive the overrepresentation of invasive species among traded ants. However, this might be different in other taxa: For example, in amphibians, large body size is positively linked to greater commercial success and to invasiveness (47), while in birds, small species are preferred as pets (22) but body size is not associated with invasiveness (48, 49). Many ecological characteristics linked to invasiveness are specific to each taxon, and it has been difficult to identify universal characteristics of invasiveness (50). Therefore, identifying the specific traits linking invasiveness and commercial success in different taxonomic groups would be extremely useful to predict which species pose the greatest threats; and thus, to recommend their regulation.

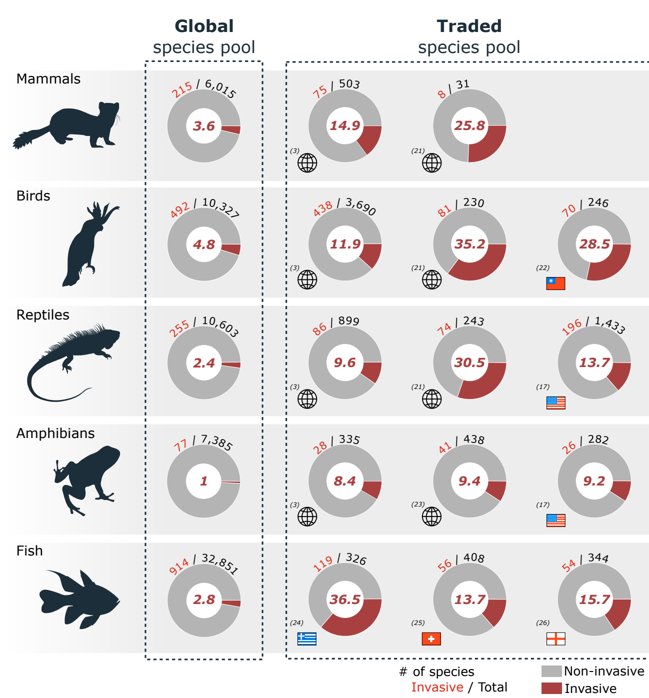

Fig. 1. Invasive species are overrepresented in the global pet trade. Patterns of overrepresentation of invasive species (i.e., species that have established outside of their natural range) in traded mammals (3, 21), birds (3, 21, 22), reptiles (3, 17, 21), amphibians (3, 17, 23), and fish (24–26). For each taxon, pie charts represent the proportion of invasive (red) and noninvasive (gray) species in the global and traded species pools. The exact percentage of invasive species is indicated in the center and the geographic origin of the data (and its reference) on the bottom left of each pie chart (see *SI Appendix*, Table S1 and Fig. S1 for details; silhouettes are from phylopic.org).

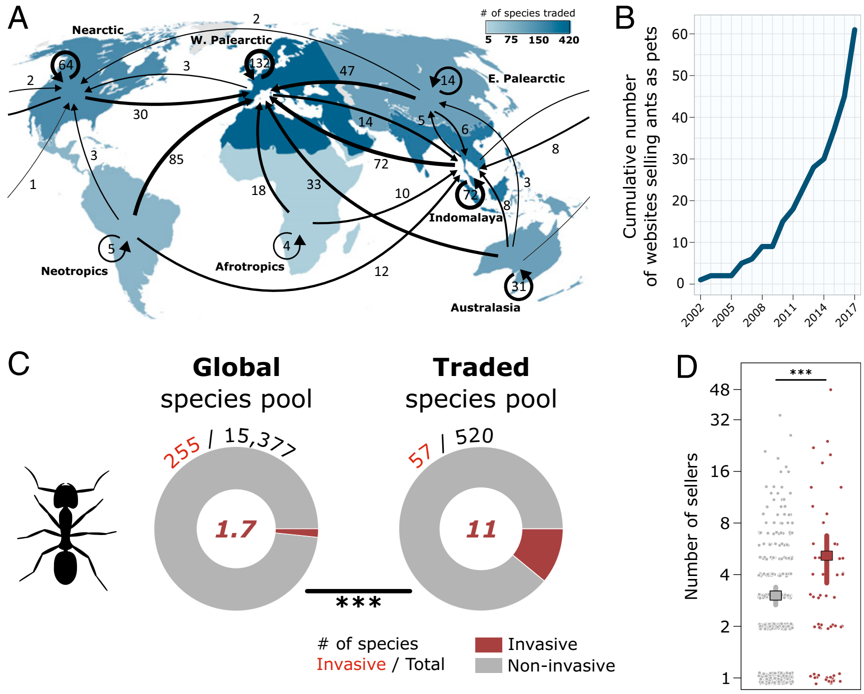

Fig. 2. The global trade in ants as pets. (*A*) Geographical flows. The arrows link the ecozones that source (species' native range) and receive (location of the online sellers) traded ant species; arrow width is proportional to the number of species traded (*SI Appendix*, Table S4). (*B*) Temporal trend in the number of websites selling ants. Sixty-five websites selling ant colonies were detected. Ninety-two percent of the detected websites went online during the last 10 y (i.e., 2007–2017). (*C*) Invasive species are overrepresented among traded ant species. (*D*) Invasive species are sold by 1.7 times more sellers than noninvasive species. Squares and vertical lines represent mean ± 99.5% CI estimations of the average number of sellers for each group. Each point represents a traded ant species.

The commercial success of ants was also linked to their geographical origin. Species' geographic origin is also important in the pet trade in vertebrates and is thought to be linked to species availability and societal demands (21, 22). In ants, Afrotropical species were offered by fewer sellers, and Western Palearctic species by more sellers (*SI Appendix*, Table S5). This is because the global ant trade is much more developed in the Palearctic region. Tropical areas, especially Afrotropics, have a rich and diverse ant fauna (33) but do not yet participate much in this pet trade (Fig. 2*A*). Therefore, there are important pools of commercially interesting species that are almost unexploited by ant sellers. These species may have lacked the opportunity to invade new habitats so far but are likely to become threats in the future if the demand for pet ants further increases, following the trend of the last 10 y (Fig. 2*B*).

Our analyses reveal an emergent and fast-growing invasion pathway for ants. Ants are especially easy to sell globally compared to other pets because a colony consisting of a queen, a few workers, and some brood can easily be delivered through standard mail. Moreover, there is no international legal framework regulating the trade in ants (34), despite the well-documented threat they pose for native biodiversity and ecosystem functioning when they establish outside of their natural range (51, 52). Given that pet owners of any taxon are known to release a certain proportion of individuals into the wild (2, 17, 18, 53), we expect the ant pet trade to contribute to the spread of invasive species in the future. Strikingly, our analyses showed that the pet trade is not simply an additional mode of human-mediated transport but that it favors species that are already invasive. This may generate a positive-feedback loop where invasion begets invasion, known in the literature as "bridgehead effect" (54). Indeed, traded species may get introduced outside of their native range (i.e., by escaping captivity or by being released intentionally) and these newly created populations can in turn serve as sources of accidental human-mediated dispersal events or even be collected to be sold as pets again, given that invasive species are preferentially traded. Remarkably, the size of a species' invaded range was positively linked to its commercial success, even when controlling for the size of its native range (negative binomial GLM: estimate ± SE = 0.09 ± 0.03, $z = 2.74$, $P = 0.006$; *SI Appendix*, Table S5 and Fig. S3), supporting the idea that an accelerating process may have already begun.

In addition to transporting species that are already known invaders, the pet trade may also provide dispersal opportunities for species that are not yet invasive but have a great potential to become invasive in the future, given that many share ecological traits associated with invasiveness and commercial success, such as a generalist lifestyle and large spatial distribution. Our findings stress the urgency to put in place international policies regulating the global trade of live animals (including invertebrates). Existing international regulation systems such as the Convention of International Trade in Endangered Species of Wild Fauna and Flora (CITES) (55) do not cover a majority of species (56) and focus on protecting threatened plants and animals from overexploitation and poaching, and thus are not well designed to prevent the global spread of invasive species (57). Only 30 animal species, including 22 vertebrate and 8 invertebrate species, are currently prohibited from being traded by the European Union due to potential invasion risks (58). In addition to strengthening international regulations, it is also important to inform clients about the potential risks of buying invasive species (59) and encourage them to purchase species that are native in their area (60). More initiatives are needed to prevent or at least decrease the spread of invasive species through the pet and ornamental trade.

This study provides a quantitative assessment of the proportion of invasive species in the global pet trade and reveals that

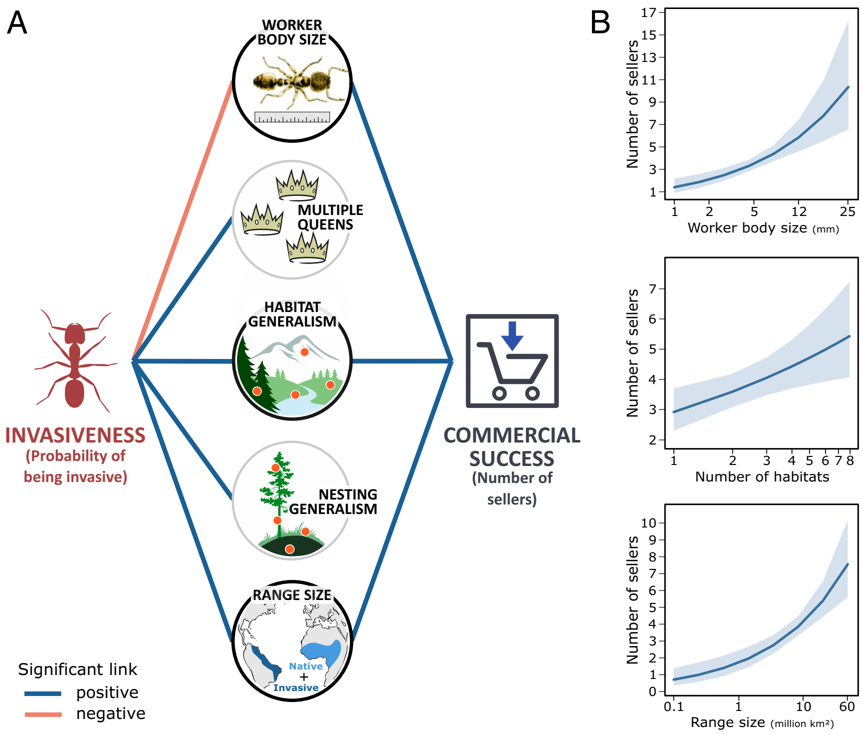

Fig. 3. Three ecological characteristics associated with greater invasiveness also increase commercial success. (*A*) Habitat generalism and range size are positively linked to both commercial success and invasiveness. Worker body size is also positively linked to commercial success but is negatively linked to invasiveness (invasive ant species are smaller than noninvasive species). (*B*) Marginal effects (mean ± 95% CI) of each ecological characteristic linked to both invasiveness and commercial success according to the best-fitting negative binomial model explaining ant species commercial success (see *SI Appendix*, Table S5 for statistical details).

invasive species are strongly overrepresented in trade across all vertebrates and ants. Importantly, using ants as model system, we showed that the pet trade is not simply a passive means of transport, but specifically favors generalist species with large range sizes, two ecological characteristics associated with invasiveness. Given the ever-increasing demand for exotic animals (2) and the growing use of the internet to purchase them, this phenomenon could result in an acceleration of current invasions and an emergence of new invaders. This further strengthens the call for a ban on, or at least increased risk awareness with, the international trade of wildlife species for pet or ornamental reasons.

Materials and Methods

Metaanalysis of Invasive Species Overrepresentation in the Pet Trade.

Data collection. We compiled 14 published lists of vertebrate species traded as pets from eight publications: two for mammals (3, 21), three for birds (3, 21, 22), three for reptiles (3, 17, 21), three for amphibians (3, 17, 23), and three for fish (24–26). These lists of traded species were compiled using different sources and methodologies. Four global wildlife trade lists (mammals, birds, reptiles, and amphibians) (3) were compiled using two sources: the Convention on International Trade in Endangered Species of Wild Fauna and Flora (55) and the IUCN Red List of Threatened Species (www.iucnredlist.org/). We refined these four species lists by considering only species traded as pets and excluded species traded as dead products. Three global pet trade lists (for mammals, birds, and reptiles) (21) were compiled by combining a systematic review of scientific and gray literature (154 papers and 49 reports published between 2006 and 2012) and reports from CITES. One global amphibians pet trade list (23) was compiled by combining a literature review (25 papers published between 1971 and 2018) and 2013–2018 import data from the United States Fish and Wildlife Service's Law Enforcement and Management Information System (LEMIS) (www.fws.gov/le). Two pet trade lists (for reptiles and amphibians) from the United States (17) were compiled by combining 1999–2016 import data from the LEMIS and an internet survey (of the top three internet-based reptiles and amphibians pet stores in the United States). One list of ornamental marine fish imported in Switzerland in 2009 (25), was compiled by the Swiss Federal Food Safety and Veterinary Office. Three additional lists of traded species were obtained from national case studies that have recorded species sold in pet shops and aquarium shops selling freshwater and marine fish in Greece in 2011 (24), pet shops selling birds in Taiwan in 2012 (22), and aquarium shops selling marine fish in eastern England in 2011 (26). The composition of global species pool, for each taxon (i.e., mammals, birds, reptiles, amphibians and fish), was obtained from five comprehensive databases: FishBase (27), Mammal Diversity Database (28), Clements Checklist of Birds of the World (29), The Reptile Database (30), and AmphibiaWeb (31) (*SI Appendix*, Table S1). We used the Global Register of Introduced and Invasive Species (9) (GRIIS) to determine which mammal, bird, reptile, amphibian, and fish species were invasive. A species was considered invasive if it was listed in the GRIIS database. Invasive species are species that have established somewhere outside of their natural range, regardless of their impacts on ecosystems or humans (8, 9).

Taxonomic verification. We checked all species names using Open Tree of Life (opentreeoflife.github.io), National Center for Biotechnology Information (https://www.ncbi.nlm.nih.gov/), and Integrated Taxonomic Information System (https://www.itis.gov/) databases using the R package *taxize* (61). Species records for which no valid species name was found were removed from the dataset. This concerned 1.68% of the GRIIS database, 0.13% of fish global species pool, 2.58% of mammals' global species pool, 2.15% of birds' global species pool, 1.62% of reptiles' global species pool, 6.29% of amphibians' global species pool, and 1.44% of all traded species recorded in the 14 compiled pet trade lists. Overall, our final dataset contains 67,181 species (32,851 fish species, 6,015 mammal species, 10,327 bird species, 10,603 reptile species, and 7,385 amphibian species), including 1,953 invasive species [i.e., 2.91% of all vertebrate species are listed in the GRIIS databases (9)] and 7,522 traded species (i.e., 11.2% of all vertebrate species were recorded as traded based on our metaanalysis) (Datasets S1–S3 and see *SI Appendix*, Fig. S1 for more detailed information about the overlaps between species lists). In total, 951 (i.e., 12.6%) of traded vertebrate species were listed in the Global Register of Introduced and Invasive Species (9) (Fig. 1 and Datasets S1–S3).

Global Internet Trade in Ants as Pets.

Ant trade dataset. Ants are traded online and delivered via postal services in tests tubes or artificial nests containing a founding queen or entire colonies. We compiled a dataset of the global internet trade in ants as pets. Between

July and December 2017, we systematically searched for websites specialized in selling ant colonies. We used the following keywords in Google search: "Buy living ants," "Buy queen ant," "Buy ant colony," "Living ants for sale," "Queen ant for sale," and "Ant colony for sale" in 20 languages (Arabic, simplified Chinese, Dutch, English, Finnish, French, German, Hindi, Italian, Japanese, Korean, Malay, Persian, Polish, Portuguese, Russian, Spanish, Swedish, Turkish and Vietnamese; *SI Appendix*, Table S2). Nonspecialized websites (e.g., Amazon, eBay) and websites selling only ant workers (without queen) were ignored. We found 65 websites specialized in selling ants as pets. Among them, 49 were located in the Western Palearctic region, six in Indomalaya, four in Australasia, three in the Eastern Palearctic, one in the Afrotropics, one in the Nearctic region, and one (https://www.antscanada.com/; see *SI Appendix*, Table S3) was an international platform regrouping sellers from the Nearctic region (27 sellers), the Neotropics (2 sellers), Indomalaya (5 sellers), Western Palearctic (9 sellers), and Australasia (including New Zealand; 2 sellers). We thus considered 109 sellers selling living ants on the internet (*SI Appendix*, Table S3). We searched each of the 65 websites and recorded all sold species. Species identified only to the genera were ignored. Using the AntWeb database (62), species names were checked for synonyms and misspellings. Records with invalid or nonexistent species names were removed from the dataset. Our final dataset consisted of a list of 520 traded ant species and the number of sellers offering them (Datasets S1–S3). This is a conservative estimate of the actual number of ant species sold worldwide because our online search was a snapshot in time (July to December 2017) and excluded specimens not identified to the species level and websites that are not explicit shops (e.g., forums, social media). The number of sellers is a good proxy of commercial success because it is strongly positively correlated to the number of individual animals offered in pet shops (26, 63, 64). Finally, the year since websites went active online was obtained from the digital library Internet Archive (web.archive.org/; information was available for 61 out of 65 detected websites; *SI Appendix*, Table S3).

Invasive status and geographical origin of ant species. Based on the Antmaps database (33), ant species were classified as invasive if they have established populations outside of their native range (at outdoor locations) and as noninvasive otherwise. We also recorded, for each traded ant species, in which ecozones it occurs (among seven ecozones: Afrotropics, Australasia, Indomalaya, the Nearctic, the Neotropics, the Eastern Palearctic, the Western Palearctic; Fig. 2*A*).

Ecological characteristics linked to invasiveness. Using the databases Antmaps (33) and Antprofiler (65), we compiled five ecological characteristics that are linked to invasiveness in ants (32, 51, 52) (*SI Appendix*, Fig. S2). These characteristics were as follows: 1) queen number, that is, if species can have multiple queens within the same nest (polygynous) or if they always have a single queen (monogynous); 2) mean worker size, that is, the log-transformed average body length of the ant workers; 3) 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]; 4) 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)]; and 5) range size, that is, the log-transformed surface area of species whole range (i.e., native and invasive part of the range) (Datasets S1–S3).

Statistical Analyses.

Overrepresentation of invasive vertebrate species in the pet trade. We tested whether invasive species were overrepresented in the pet trade across mammals, birds, reptiles, amphibians, fish, and ants using χ^2 tests with Bonferroni correction for multiple tests [*chisq.test* function in R package stats (66); see *SI Appendix*, Table S1 for details on species pools' composition and statistical tests].

Commercial success of invasive ant species. In traded ants, we tested whether invasive species were traded by more sellers than noninvasive species using a negative binomial generalized linear model (GLM) and a LR test (*SI Appendix*, code). We modeled the number of sellers by species using a negative binomial model [*glm.nb* function in R package MASS (67)] to account for overdispersion in the data [overdispersion test (68): dispersion = 4.55, $z = 3.62$, $P < 0.001$].

Testing for traits linked to commercial success. We used a negative binomial generalized linear mixed model [*glmmTMB* function in R package glmmTMB (69)] to test whether commercial success (i.e., number of sellers by species) was linked to five ecological characteristics associated with invasiveness in ants (polygyny, worker body size, habitat generalism, nesting generalism, and total range size; *SI Appendix*, Fig. S2), while accounting for species' geographical origin (i.e., in which ecozone species occur) and controlling for phylogenetic effects by using ants' superfamily and genus as nested random effects. This analysis included 222 traded ant species (out of 520) for which all predictor information was available. We determined the best-fitting model using stepwise model selection by AIC (Akaike information criteria) (70) (*stepAIC* function in R package MASS). We calculated the coefficient of determination of the best-fitting model using Nakagawa's pseudo–R-squared [*r2_nakagawa* function in R package performance (71)]. Finally, to test whether the size of the invaded range has an impact on the commercial success of ants, we performed the same analysis and model selection procedure, while separating the total range size into two different variables: native range size (that is, the log-transformed surface area of species range where the species is native) and invasive range size (that is, the log-transformed surface area of species range where the species is invasive) using the Antmaps database (33) (*SI Appendix*, Table S5 and Fig. 2).

Data Availability. All data generated or analyzed during this study are included with the paper and *SI Appendix*, S1. Code used to perform statistical analyses is included in *SI Appendix*, S2. All other study data are included in the article and/or supporting information.

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