Recurrent bridgehead effects accelerate global alien ant spread

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Biological invasions are a major threat to biological diversity, agriculture, and human health. To predict and prevent new invasions, it is crucial to develop a better understanding of the drivers of the invasion process. The analysis of 4,533 border interception events revealed that at least 51 different alien ant species were intercepted at US ports over a period of 70 years (1914–1984), and 45 alien species were intercepted entering New Zealand over a period of 68 years (1955–2013). Most of the interceptions did not originate from species' native ranges but instead came from invaded areas. In the United States, 75.7% of the interceptions came from a country where the intercepted ant species had been previously introduced. In New Zealand, this value was even higher, at 87.8%. There was an overrepresentation of interceptions from nearby locations (Latin America for species intercepted in the United States and Oceania for species intercepted in New Zealand). The probability of a species' successful establishment in both the United States and New Zealand was positively related to the number of interceptions of the species in these countries. Moreover, species that have spread to more continents are also more likely to be intercepted and to make secondary introductions. This creates a positive feedback loop between the introduction and establishment stages of the invasion process, in which initial establishments promote secondary introductions. Overall, these results reveal that secondary introductions act as a critical driver of increasing global rates of invasions.

biological invasions | globalization | propagule pressure | invasive ants | secondary introductions

The globalization of trade and travel is facilitating the accidental transport of animal and plant species around the world (1–3). Although many of these species fail to overcome biotic and abiotic barriers to establishment outside of their native range, those that do succeed are among the greatest threats to global biodiversity, agriculture, and human health (4, 5). A cross-taxonomic comparison has shown that there has been no saturation in the global accumulation of introduced species (6), and that the rates of new biological invasions may continue to rise in the future (7). In particular, the second wave of trade globalization after World War II provided opportunities for transport of a new set of species establishing ranges spanning transcontinental scales (8) and increased invasions to countries with historically low levels of trade (9).

It has been suggested that biological invasions are a self-reinforcing phenomenon ("invasion begets invasion") (10), via the so-called bridgehead effect (11). Under a bridgehead scenario, a successfully established invasive (Table 1) population serves as a source of colonists for new invasions and thereby gives rise to secondary introductions. A recent horizon scan of emerging challenges and opportunities in invasion science highlighted the bridgehead effect as one of the most important ecological issues likely to influence how biological invasions are studied and managed in the near future (12).

Previous studies have identified bridgehead effects in several well-studied invasive species (13–19). However, all of these studies reconstructed the invasion histories of individual species, and it remains unknown how frequent secondary introductions are compared with primary introductions overall. To quantify the frequency of secondary introductions, we analyzed border interceptions of ants at air and maritime ports in the United States and New Zealand, which we used as a proxy for accidental species introductions (20). Many introductions of species occur via air and maritime ports; the analysis of such data therefore constitutes a powerful means to investigate the first step of the invasion process and to determine the proportion of primary and secondary introductions (21). We focused on ants, which make up a particularly prominent group of widespread invasive species (22) that can rapidly disassemble native communities (23). The variety of their lifestyles, colony sizes, habitat requirements, and diets also allows them to colonize almost all terrestrial habitats on all continents except Antarctica (8, 22). Their complex social structure has contributed to them becoming highly successful invasive species. There are currently more than 200 known ant species that have established populations outside of their native range (hereafter referred to as alien species; Table 1), and 19 are classified as invasive by the International Union for the Conservation of Nature because of their effects on biodiversity,

Significance

Because of the globalization of trade and travel, worldwide invasion rates are high. A potential driver of the global acceleration of new invasions is the so-called bridgehead effect, in which initial invasive populations serve as the source of additional invasions via secondary introductions. However, the frequency and overall importance of secondary introductions remain largely unknown. Using a remarkable dataset, spanning nearly 100 years (1914–2013), of ant interceptions at air and maritime ports in the United States and New Zealand, we found that most ant introductions arise via secondary transport via intermediate regions. Our analyses also reveal positive feedback between the introduction and establishment stages of the invasion process via secondary introductions acting as a critical driver of increasing global invasion rates.

Table 1. Glossary

Status	Definition
Native species	Species with no established population outside of the native range.
Alien species	Species with at least one established (self-sustaining) population outside of the native range, at outdoor locations.
Invasive species	Alien species with documented effects on biodiversity, agriculture, health or ecosystem functioning; listed according to this criterion by the Invasive Species Specialist Group of the International Union for the Conservation of Nature

ecosystem functioning, agriculture, infrastructure, and human or animal health (8), causing important economic losses (24, 25). Five species are even among the "100 worst invasive species" (26).

We defined primary interceptions as those originating from any country within the native range of a given species, and secondary interceptions as those originating from any country outside the native range of a species. Our rich dataset of 4,533 ant

interception events provides an exceptional opportunity not only to quantify the relative importance of introductions arising from the native versus introduced range of intercepted species but also to identify potential sources of secondary transport and to test whether there is positive feedback among the introduction, establishment, and worldwide spread of species (i.e., if bridgehead effects have the potential to contribute to rising global invasion rates).
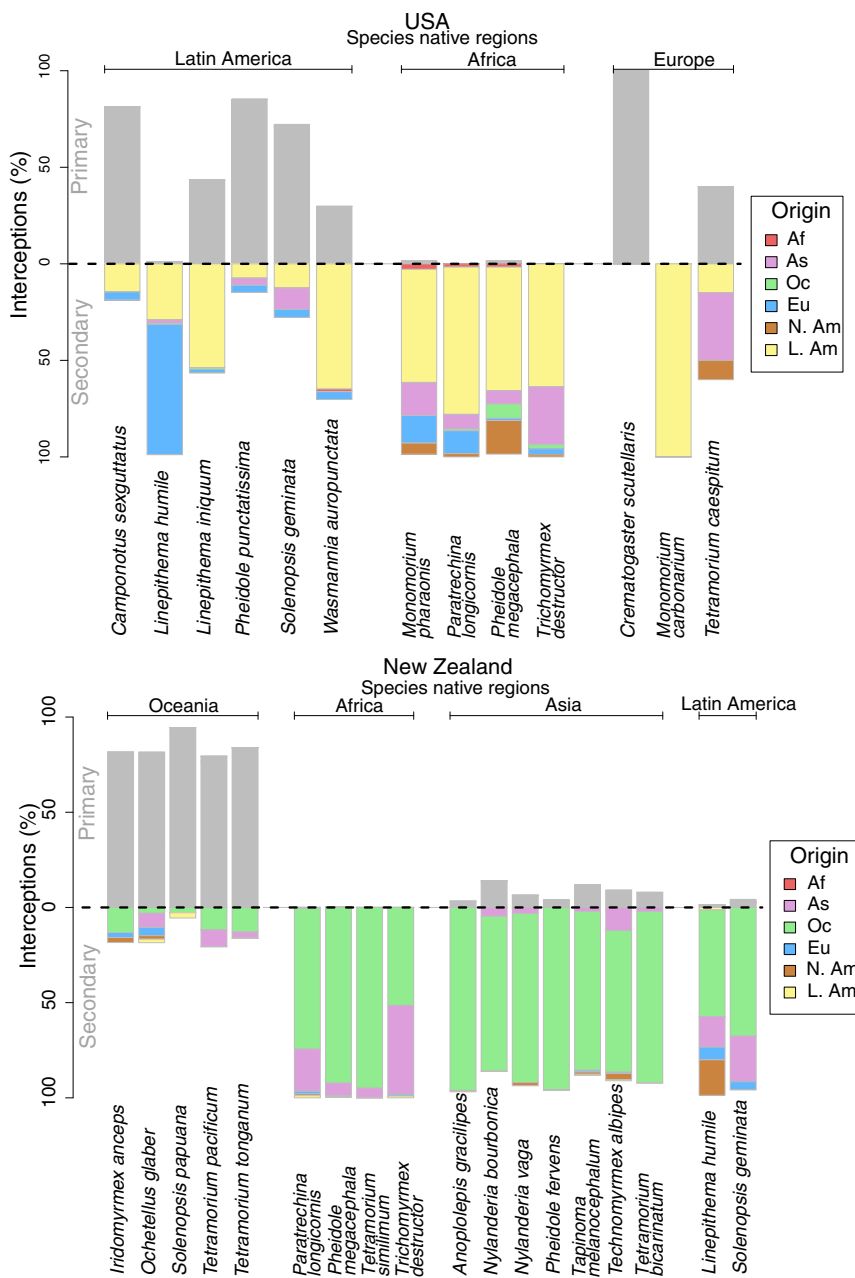
Fig. 1. Percentage of primary vs. secondary introductions of the most frequently intercepted species in the United States and New Zealand. The proportion of interceptions from the species' native countries is shown above the x-axis (in gray) and the proportion of interceptions from countries in the alien range below the x-axis (in color). The color code indicates the origin of the secondarily intercepted species. Species were visually grouped on the x-axis according to their native range (Dataset S1). Af, Africa; As, Asia; Eu, Europe; N. Am, North America; L. Am, Latin America; Oc, Oceania.

Fig. 2. Origin of all interceptions in the United States and New Zealand, (*A*) the log of the number of interceptions, weighted by the log land area of the country. (*B*) The raw number of interceptions arriving from each country is shown as a bar chart.

Results and Discussion

During a period of 70 y (1914–1984), a total of 51 alien ant species were identified from 1,428 interceptions made by inspectors at ports of entry in the United States (Datasets S1 and S2). In New Zealand, a total of 45 alien ant species were identified from 3,105 interceptions over a period of 68 y (1955–2013) (Dataset S1). In the United States, a surprisingly large percentage (75.7%) of the intercepted alien ants came from a country outside the native range. This percentage was even higher in New Zealand (87.8%). Invasive species exhibited a higher proportion of secondary interceptions than noninvasive alien species in both the United States (88.4% vs. 43.2%; $\chi^2 = 317$; df = 1; $P <$ 0.001) and New Zealand (95.2% vs. 73.6%; $\chi^2 = 300$; df = 1; $P <$

0.001). Among the most frequently (>20 times) intercepted species, the rate of secondary interceptions was 79.7% in the United States and 88.1% in New Zealand (Fig. 1). There were strong differences among species in the proportion of primary versus secondary interceptions in both the United States ($\chi^2 =$ 719; df = 12; $P < 0.001$; Fig. 1*A*) and New Zealand ($\chi^2 = 1,673$; df = 17; $P < 0.001$; Fig. 1*B*). Some of the species were introduced from a wide range of introduced populations. For example, the big-headed ant *Pheidole megacephala* and the longhorn crazy ant *Paratrechina longicornis* were intercepted from all continents at both the US and New Zealand ports (Fig. 1).

The finding of a very high proportion of secondary interceptions has important implications for the understanding of global

Fig. 3. Worldwide flows of intercepted ants in the United States and New Zealand. The pie charts represent the proportion of primary (in gray) and secondary interceptions (in color) coming from each country. The color code indicates the native range of secondarily intercepted species, and the size of the pie charts is proportional to the number of interceptions from each country.

invasion dynamics. Secondary spread from invasive population has been demonstrated in different taxa, including invertebrates, plants, and microorganisms (e.g., refs. 15–19, 27, and 28). Our results showing that introduced ant populations frequently serve as the source of secondary introductions are consistent with the available genetic data documenting the invasion histories of five alien ants. These studies showed that at least half of alien populations (14), or even higher proportions (13, 29–31), had been introduced secondarily (*SI Appendix*, Table S1). A potential explanation for this is that many invasive species become far more abundant in the invaded range than in their native range, where they typically have more competitors and natural enemies. Hence, subsequent transport might be more likely from the invaded range than from the native range. To explain recurrent secondary spread, it has also been suggested that introduced populations may evolve greater invasiveness compared with native populations, thereby acting as operative bridgeheads for secondary introductions (11). However, there is currently little evidence for adaptive evolution in invasive populations (32, 33) and no empirical support for the evolution of greater invasiveness in bridgehead populations, preadapting them for further spread. An alternative explanation is that the observed introduction patterns simply reflect the topology of human transport networks. Maritime, air, train, and road networks are generally scale-free, implying that most nodes (cities, ports, countries) have few connections, whereas few nodes have many connections (34). In addition, these networks also have small-world properties, meaning that any node in the network can be reached from any other node in a few steps (34). In terms of

biological invasions, this implies that organisms should be more likely to be introduced in high-volume transport hubs (where there are more ships, trucks, and aircraft arriving), from which they will similarly have increased chance to further disperse because of the high connectivity of these hubs (34, 35), which are not necessarily geographically close to other nodes in the network. A species entering one major port system would thus be likely to interface with multiple global transportation routes; this has previously been called the hub and spoke model (36).

The hypothesis that a high frequency of secondary introduction reflects the topology of human transport leads to two predictions. The first is that secondary introductions should preferentially occur from specific regions and that these regions should not be the same for the United States and New Zealand, which import goods from a different but overlapping set of countries. We found strong support for this prediction. There was not only a significant variation among continents in their contribution to secondary interceptions into the United States ($\chi^2 = 47.1$; df = 5; $P < 0.001$) and New Zealand ($\chi^2 = 313$; df = 5; $P < 0.001$) but also a significant difference between the United States and New Zealand regarding which continent contributed the highest number of interceptions ($\chi^2 = 3,482$; df = 5; $P < 0.001$). The principal source of ants intercepted at US borders was Latin America (Fig. 2*A*), with Cuba, Jamaica, Bermuda, and Guatemala contributing (in descending order) to the highest number of interceptions (Fig. 2*C*). In contrast, the main source of ants intercepted at New Zealand ports was Oceania (Fig. 2*B*), with Fiji, Tonga, Samoa, and Australia contributing (in descending order) to the highest numbers of interceptions (Fig.
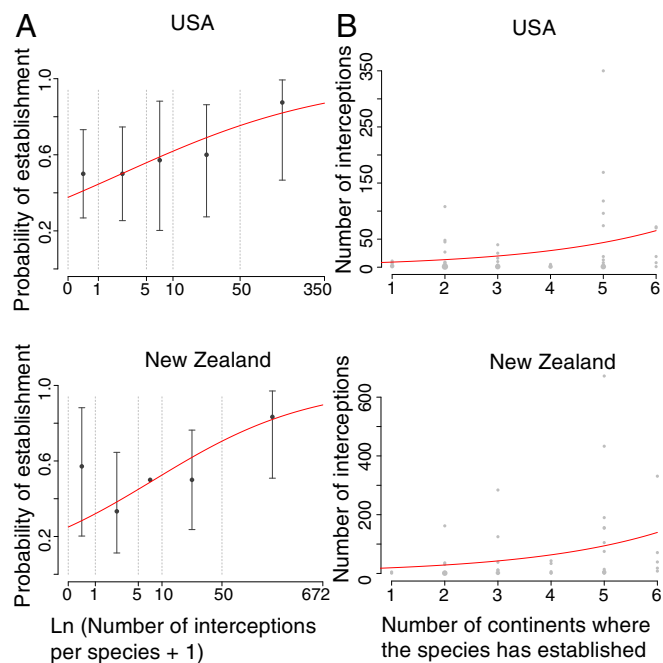
Fig. 4. Feedback loop between interceptions and successful establishment. (*A*) Link between the number of border interceptions per species and establishment probability ±SD, modeled using a binomial GLM (red line). (*B*) Link between the number of continents where a species has established and the number of times it has been intercepted, modeled using a GLM with Poisson link function (red line). The size of the gray points is proportional to the number of cases.

2*D*). Thus, Latin America acted as a bridgehead to the United States, and Oceania as a bridgehead to New Zealand (Fig. 3). Our findings that a high frequency of secondary introduction reflects the topology of human transport does not exclude that some species evolved a greater invasiveness in some introduced populations.

The second prediction is that secondary introductions should generate a positive feedback loop whereby invasion begets invasion, similar to the way in which an infectious disease can increase the rate of spread when the number of infected hosts increases (35). To test this prediction, we first investigated whether the probability of establishment (i.e., attaining a self-sustaining population) was positively associated with the number of interceptions and, second, if successful establishments on a higher number of continents lead, in turn, to a higher number of interceptions. In line with these predictions, species that were more frequently intercepted at ports of entry were also more likely to become established in both the United States [generalized linear model (GLM), $\chi^2 = 4.6$; $P = 0.047$] and New Zealand (GLM, $\chi^2 = 7.1$; $P < 0.01$; Fig. 4*A*). Conversely, species that were successfully established in a greater number of continents were more likely to be intercepted at ports of entry in both the United States (GLM, $\chi^2 = 539$; $P < 0.0001$) and New Zealand (GLM, $\chi^2 = 879$; $P < 0.0001$; Fig. 4*B*). Species established in a greater number of continents also had a greater proportion of secondary interceptions in both the United States (GLM, $\chi^2 = 320$; $P < 0.0001$) and New Zealand (GLM, $\chi^2 = 618$; $P < 0.0001$). These data thus confirmed a positive effect of propagule pressure on invasion success (20, 37, 38) and demonstrated a positive feedback of the rate of successful establishment on the rate of interceptions. Moreover, some species-level morphological and life-history traits can also influence the probability that a species is transported, is established successfully, and will be transported further (20). It has been shown that nesting habits can interact with the effect of propagule

pressure on establishment probability (20). Additional traits such as the type of colony founding, queen number, and habitat generalism also influence colonization ability after transcontinental transport (8). Therefore, species with these life-history traits may be particularly likely to benefit from the positive feedback loop between introductions and new establishments once they have started to spread through human transport.

This study provides a quantitative global assessment of secondary introductions and reveals that a surprisingly large number of interceptions of alien ant species comes from invaded ranges. This has important implications for our understanding of invasion processes because bridgeheads appear to play a key role in increasing invasion rates when species reach regions that are highly connected. Our analyses also reveal a positive feedback among global introduction, spread, and subsequent invasion, which is likely to lead to further acceleration of the worldwide spread of invasive species in the future.

Materials and Methods

Interceptions. For the United States, we used records of ant interceptions made by inspectors of the US Department of Agriculture (USDA) and the Department of Homeland Security at ports of entry (maritime, land, and air) from 1914 to 1984, published by the US Department of Agriculture (39). For New Zealand, we used ant interceptions compiled by the New Zealand Ministry for Primary Industries (or predecessors to this ministry previously recorded under different names) responsible for examining cargo, goods, mail, and baggage that arrived from 1955 to 2013. Parts of these data have been described in an earlier paper on New Zealand interception records (40). Data in both interception databases included ant species names and the country of origin. Species names were checked for synonymy using the authoritative AntWeb v. 6.0.13. (antweb.org), which contains 15,961 valid species names based on the Bolton World catalog (41) and the taxonomic history of senior synonyms that have become outdated because of taxonomic revisions. Because countries have also changed names over the course of the last century, we revised the list of origins using ISO code 3166, which provides an international standard for country codes and their subdivisions.

We used the Antmaps database, a web interface of the Global Ant Biodiversity Informatics project (42), to obtain a list of alien species. To be conservative and consider only species with known established populations outdoors, we excluded all species listed as "needing verification," "dubious," or "indoors" (see Dataset S1 for interceptions of alien ants and Dataset S2 for other intercepted ant species without documented alien populations). The US dataset contained 1,428 alien ant interceptions with information on the country of origin and a specimen identified at the species level (51 species from 29 genera were recorded). The New Zealand dataset contained 3,105 alien ant interceptions with information on the country of origin and a specimen identified at the species level (45 species from 26 genera). In total, our dataset contains 69 alien ant species, 27 of which were intercepted in both countries. To test whether species classified as invasive exhibit a higher rate of secondary introductions than other alien species, we distinguished between alien and invasive alien species, according to the Invasive Species Specialist Group of the International Union for the Conservation of Nature, which lists as invasive species those with documented effects on biological diversity and/or human activities (www.iucngisd.org/gisd/).

Distribution and Establishment. To determine the global country-level distribution of species and to confirm the presence/absence of all intercepted species in the United States and New Zealand, we used georeferenced AntWeb v. 6.0.13 specimen data; species lists from the literature assembled by AntWiki (an authoritative database maintained by ant experts, which contains regional ant fauna lists from different countries over the world and is interlinked with the Encyclopedia of Life); the New Zealand Landcare Research database (43), which provides occurrence data of alien and invasive ant species; a dataset of recorded alien ants in the United States (44, 45); and a dataset of alien ant species worldwide (46). To determine the native and introduced range of the alien ant species, we combined information on the introduced ranges of alien ant species from the literature (46) and the Antmaps database. The alien range of a species was defined as all the countries comprising at least one introduced population (recorded by one or both of these datasets). Conversely, the native range was defined as all countries containing native but no introduced populations.

Secondary Introductions. For all species intercepted more than 20 times in the United States or New Zealand, we calculated the proportion of primary

introductions (interceptions originating from countries within the native range) and secondary introductions (interceptions originating from countries where the species has established an introduced population). To test whether the proportion of secondary introductions varied across species, we used a chi-square test. To visually represent the origin of secondary interceptions for the most frequently intercepted species (Fig. 1), we grouped species according to their native range (Asia, Africa, Europe, Oceania, Latin America, and North America; hereafter called continents). When the native range covered several continents, we selected the continent containing the larger number of native countries (Dataset S1).

To identify countries and regions acting as major source of interceptions in the United States and New Zealand, we analyzed the total number of ant interceptions originating from each country. We mapped these export countries, calculating an interception index, based on the log number of interceptions. To visually identify countries that are important exporters, we divided the number of interceptions by the log of land area of each country because the number of interceptions should be influenced by the size of the countries (Fig. 2). To map global flows of ant interceptions, we calculated the proportion of primary and secondary interceptions from each country, represented as a pie chart, where we subdivided secondary interceptions according to the native range of the species, using a color code (Fig. 3). When a species was native from more than one continent, we allocated the number of secondary interceptions to the respective continents proportional to the number of countries comprising native populations.

Propagule Pressure and Positive Feedback. To test for an association between propagule pressure and establishment likelihood, we modeled the estab-

lishment probability at the species-level with a binomial GLM (logit-link), including all alien ant species intercepted at least once. The interception counts for each species were log-transformed. To test for a positive feedback (i.e., if the establishment in a higher number of continents elsewhere is linked to a higher number of interceptions in the United States and New Zealand), we used a GLM (Poisson link) of the number of interceptions per species against the number of continents where it has established. To test whether the number of continents in which a species has established was linked to the proportion of secondary introductions in the United States and New Zealand, we used a GLM (binomial link), where we used the total number of interceptions per species as weights. This GLM parameter is used to specify the number of cases when the response variable is a proportion.

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