Received: 25 April 2021 | Revised: 25 June 2021 | Accepted: 6 July 2021

DOI: 10.1111/ddi.13388

RESEARCH ARTICLE

Diversity and Distributions WILEY

Bridgehead effects distort global flows of alien species

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Funding information
canton Vaud; Swiss National Science Foundation; *Programme de la Famille Sandoz—Monique de Meuron pour la relève universitaire*; CNRS

Editor: Xuan Liu

Abstract

Aim: A major goal of invasion biology is to understand global species flows between donor and recipient regions. Our current view of such flows assumes that species are moved directly from their native to their introduced range. However, if introduced populations serve as bridgehead populations that generate additional introductions, tracing intercontinental flows between donor and recipient regions misrepresents the introduction history. Our aim was to assess to what extent bridgehead effects distort our view of global species flows.

Location: Global.

Methods: We separately mapped "flows" of 252 alien ant species established on one to six continents, representing a gradient of relatively certain to completely unreliable flows. To assess the importance of bridgehead effects in distorting our view of global species flows, we first quantified the proportion of cosmopolitan species per country. A high proportion of such species would indicate that exclusively mapped flows from the native range to these countries are unreliable. We then tested if the global flows obtained mapping species exotic in one continent to six continents differed and tested if these flows can be linked to global trade flows.

Results: In 83% of countries, more than 50% of alien ants were established on six continents, indicating that flows to these countries are unreliable. Flows of species established on a single continent were linked to global trade flows, while flows including cosmopolitan species were not linked to global trade.

Main conclusion: It is crucial to account for bridgehead effects when assessing the biogeography and intercontinental flows of alien species. This is urgent for improving our understanding of how species are moved around the planet.

KEYWORDS

alien species, ants, biogeography, biological invasions, invasion pathways, secondary introductions, trade

1 | INTRODUCTION

The intercontinental exchange of thousands of introduced species has become a hallmark of the Anthropocene (Capinha et al., 2015; Corlett, 2014), and the number of new species introductions has exploded with the increasing globalization of human activities (Seebens et al., 2017). Only a small subset of the countless plants, mammals, birds, invertebrates, bacteria, viruses and other taxa are able to establish in their introduced range given the necessary combination of abiotic conditions and resources required to sustain them (Blackburn et al., 2011; Simberloff et al., 2013). Yet, if they are able to proliferate and spread locally, alien species are a major environmental threat (Ricciardi et al., 2013). They have major impacts on biodiversity (Clavero & García-Berthou, 2005; McGeoch et al., 2010), agriculture (Paini et al., 2016), ecosystem functioning (Pyšek & Richardson, 2010) and human livelihood (Shackleton et al., 2019). Even though it has long been recognized that human activity is responsible for the vast majority of biological invasions, most research has focused on the role of habitat or species characteristics affecting invasion success, rather than on human-mediated dispersal (Catford et al., 2009; but see Chapman et al., 2017; Dawson et al., 2017; Seebens et al., 2020). A major goal of invasion science today is to quantify the global flows of alien species between their donor and recipient regions and to identify the socio-economic drivers of those intercontinental species exchanges. The growing availability of large databases containing data on the native and invaded ranges of alien species has made progress possible in mapping the global flows of plants (van Kleunen et al., 2015), amphibians and reptiles (Capinha et al., 2017). This research has shown that some donor regions were overrepresented relative to what would be expected based on the available source pools of these regions (i.e. the number of native species that could potentially be exported). These asymmetric exchanges of alien species among continents may be linked to different human activities, such as accidental transport, pet and horticultural trade or environmental factors.

Yet, a potential obstacle to finding relevant drivers of species flows is linked to the fact that our current view of such flows assumes implicitly that species are moved directly from their native to their introduced range. However, introduced populations can also serve as the source of additional introductions, which is referred to as bridgehead effect (Lombaert et al., 2010). If this occurs, tracing a flow between the native and each of the species' introduced populations misrepresents the true introduction history. Over the past few years, such secondary introductions have been demonstrated using population genetic surveys in a variety of organisms, in both terrestrial and marine habitats (Colautti & Lau, 2015; Geller et al., 2010; Krueger-Hadfield et al., 2017; Garnas et al., 2016). In general, such studies retrace the invasion history of individual well-studied species. Although evidence for complex invasion histories with recurrent bridgehead effects is accumulating, population genetic surveys are labour-intensive and require an extensive sampling effort and are therefore not suitable to assess whether secondary introductions are widespread in general. Using a dataset of ant interceptions at air and maritime ports, previous studies have found that the vast majority of introductions across all alien ant species arise via secondary transport (Bertelsmeier et al., 2018; Suhr et al., 2019). Given that the bridgehead effect is such a widespread phenomenon, we hypothesize that it has the potential to distort our view of global species exchanges between donor and recipient regions, which classically map flows as direct introductions from the native to the introduced range (e.g. Capinha et al., 2017; van Kleunen et al., 2015).

One possibility to test this hypothesis would be to retrace the actual invasion routes for each species individually before analysing the collective intercontinental flows of hundreds or thousands of species. Unfortunately, it is unrealistic to obtain detailed invasion routes for so many species. To still be able to address this question and assess whether secondary introductions distort our view of global species exchanges, we used the number of continents where a species has established as an approximation of the likelihood of being introduced secondarily. To confirm that this proxy is reasonable, we first tested the link between the frequency of secondary introductions and the number of continents where a species has established, using interception records from a previously published study on ants (Bertelsmeier et al., 2018). Intercontinental flows between the native and introduced region of species exotic in a single continent are very likely to reflect reality (i.e. the actual introduction route) while flows of species invasive to all continents are unlikely to reflect reality (as they could be introduced from any of these continents). In that way, we used species introduced in one to six continents as a gradient of relatively certain to completely uncertain flows to test if bridgehead effects change the relative importance of intercontinental flows.

We used the 252 known alien ant species for this study (i.e. ant species with established self-sustaining populations outside of their native range) because there is excellent and publicly available data on the distribution of ants (Janicki et al., 2016). Ants are an ecologically diverse group, present on all continents except Antarctica (Hölldobler & Wilson, 1990), and include infamous invasive species able to dominate a community quickly and displace numerous native species (Holway et al., 2002; Rabitsch, 2011; Sanders et al., 2003). Ants are mainly transported accidentally as hitch-hikers of traded commodities such as plants and fruits (Suarez et al., 2005, 2010), and their spread dynamics over the past two hundred years has mirrored the dynamics of the two globalization waves (Bertelsmeier et al., 2017). Because of the strong link with human-mediated transport through commodity trade, we expect global flows to be linked to international trade.

To assess the importance of bridgehead effect in distorting our view of global species flows, we first quantified the proportion of cosmopolitan species per country (i.e. species that are present on all six continents). A high proportion of such species would indicate that exclusively mapped flows from the native range to these countries are unreliable. We then tested whether the global flows estimated by mapping species exotic in one continent (hereafter "*Exo1* species") to six continents differed (hereafter "*Exo6* species") and tested whether these potential flows can be linked to global trade flows.

2 | MATERIAL AND METHODS

2.1 | Species distributions and flows

To determine the number of alien ant species that are established in each country, we used the geo-referenced database Antmaps (an authoritative database maintained and updated regularly by experts based on new records from the peer-reviewed scientific literature). The Antmaps database includes information on the native and alien ranges of 252 ant species. We did not consider occurrence records that may be dubious (needing taxonomic verification).

We kept both indoor and outdoor locations because all parts of the species' distribution are the consequence of human-mediated dispersal. Populations that occurred at indoor locations were also a possible source of new invasions, for example, if material such as potted plants and soil are moved from an indoor location to a different location. The aim of our analyses was not to distinguish between factors (climate, habitat) filtering out species at the establishment stage of the invasion process, but to understand what drives global species movements. As all species records are a reflection of global species flows, we kept all records for the analyses presented in the main part of the manuscript. However, for readers interested in the effects of indoor locations on the global biogeography of alien ants, we have added all figures excluding indoor locations as Appendix S1.

We delimited the countries and continents based on the administrative database GADM version 3.6. For mapping, we used the Mollweide projection. We defined a species "flow" as the number of species introduced from one region to another region, following previous research on global species exchanges (van Kleunen et al., 2015). To calculate the species flows from donor to recipient regions, we defined the species' native range as all countries containing native populations according to Antmaps (Janicki et al., 2016). For species whose native range covers more than one continent, we weighted the flow from each of the continents by the number of political regions where the species is native (i.e. non-overlapping country or sub-country polygons, representing states, counties or islands and which are more homogenous in size than entire countries (Janicki et al., 2016)).

2.2 | Countries

In total, 173 countries worldwide host alien ant species. To compare species flows, we focused on the 41 countries which had both species exotic in only one continent and species exotic in several continents. In that way, we were able to compare the different species flows for all alien species (hereafter *ALL* species) or species exotic in one continent (*Exo1*) or two (*Exo2*), three (*Exo3*), four (*Exo4*), five (*Exo5*) or all continents except Antarctica (*Exo6*).

2.3 | Interception data

We have sourced previously published interception records for the United States and New Zealand from 1914 to 2013 (described in detail in Bertelsmeier et al., 2018, the data are available online with the paper). In total, this dataset contains 69 alien ant species intercepted on cargo, goods, mail and baggage and has information on the country of origin for each interception and therefore allows calculating the proportion of secondary interceptions for each species (i.e. the proportion of all interceptions of a species which come from a country where the species is not native).

2.4 | Trade data

Most biological invasions arise via human-mediated transport, allowing species to establish in new geographic regions (Ruiz & Carlton, 2003). In particular, accidental transport with traded commodities is an important dispersal pathway for insects in general (Gippet et al., 2019) and especially ants (Suarez et al., 2010) as they are found directly associated with a variety of goods and as well as on wood-packaging material (Fenn-Moltu *et al.* in prep.). Previous research has shown that variations in general trade over time (Bertelsmeier et al., 2017; Chiron et al., 2010; Essl et al., 2011; Roques et al., 2016) and in space (Chapman et al., 2017; Costello et al., 2007; Dalmazzone & Giaccaria, 2014; Dawson et al., 2017; Westphal et al., 2008) are associated with differences in invasion risks. Therefore, we used general import flows to represent global flows of potential transport vectors. To calculate import flows to all countries, we used cumulative import data from 1998 to 2017 extracted from the UN Comtrade Database (United Nations Commodity Trade Statistics Database, http://comtrade.un.org/db/ (accessed May 2019)). This dataset contains dyadic trade flows between pairs of countries, given in US dollars per year. Such comprehensive data are not available for earlier periods; as most imports over the last two centuries have occurred during this recent period of globalization, we expect these relatively recent imports to have left their footprint on the flows of ants. Because no import data were available for four previously defined administrative units (Puerto Rico, Christmas Island, Norfolk Island and Marshall Islands), they were excluded from this analysis. The flows to each of the remaining 37 countries were standardized by dividing the flows by the total imports to each country in order to study variations in the proportions of geographic origins of the flows (and not the absolute quantities).

2.5 | Analyses

2.5.1 | Link between secondary introductions and number of continents

We used a linear model to test whether the number of continents where a species has established is associated with the proportion of secondary interceptions in the United States and New Zealand. This test confirmed that the number of colonized continents (*Exo1-Exo6*) can serve as a gradient of increasing likelihood that a species is introduced via bridgehead regions. However, we cannot exclude that some species may be present in a geographic area outside of their native range at a low enough density to have not yet been detected. Therefore, although *Exo1* flows are the most reliable flows, it is not possible to completely ascertain that the introduction of an *Exo1* species did not originate from a third continent where the species has not been recorded yet.

2.5.2 | Descriptive biogeography of alien ants

To quantify to what extent alien species assemblages are dominated by cosmopolitan species, we determined the proportion of *Exo1* to *Exo6* species in each country. We also determined the number of countries with a majority (>50%) of *Exo6* species, for which we have no information about the origin of donor regions. We also calculated the number of species established on one, two, three, four, five or six continents, and we determined the number of countries in which these species are established. We acknowledge the limitation of using the number of countries as a proxy of spread, yet distribution data for most species are only available at that scale.

2.5.3 | Comparing species flows to 41 countries

To standardize profiles of geographic origins for each country, we divided incoming flows arriving from each donor region by the total number of alien ant species in a country. This allowed representing the relative contribution of different parts of the world to each species flow while preventing more weight from going to countries with a high alien species richness.

To compare the most extreme species flows to the 41 focal countries, the most reliable (i.e. the most certain to reflect the true introduction route) *Exo1* flow, the least reliable *Exo6* and *ALL* species, we did a correspondence analysis (CA) on the "profiles" of geographic origins, after row standardization (Greenacre & Primicerio, 2013). Each row is a country, and each column is a continent. Therefore, each row contains the compositional data of species flows (for either *Exo1*, *Exo6* or *ALL* species) to one of the 41 countries. Differences among profiles of geographic origins are represented in the 2-D space of the factorial map. The two first axes represent 60% of the total inertia.

To test whether species flows including more cosmopolitan species are more similar among countries than flows of species exotic in a single continent, we assessed the homogeneity of countries' profiles of geographic origins of alien ants. To do this, we tested whether the variances of the coordinates in the CA space differed among *Exo1*, *Exo6* and *ALL* species flows, using Levene's test. We also tested if the profiles have a stronger regional signature for species exotic in one continent than for species more likely to be introduced via bridgehead effects (*Exo6* and *ALL* species flows). To do this, we performed a two-way ANOVA on the first four coordinates of the CA to analyse the effect of the species category (*Exo1*, *Exo6*, *ALL*) and the continent, as well as their interaction.

To visualize which species flows share the same geographic origins, we performed a classification of profiles using a hierarchical clustering analysis. To do this, we calculated Ward distances between the coordinates of the profiles in the CA space, keeping four axes (Greenacre & Primicerio, 2013).

2.5.4 | Intercontinental flows and link with trade

To assess whether cosmopolitan species also influence our view of species flows at a larger spatial scale, we calculated the species exchanges among continents for *Exo1*, *Exo6* and *ALL* species flows. We mapped these intercontinental flows using the now classical representation of chord diagrams (van Kleunen et al., 2015), which show all pairwise links between donor and recipient regions. To assess the link between these intercontinental exchanges and international trade for *Exo1*, *Exo6* and *ALL* species, we performed a co-inertia analysis (Dolédec & Chessel, 1994). Using the RV coefficient as a metric of this link (Josse & Holmes, 2016) and a Monte Carlo test with 999 permutations, we tested whether trade flows were associated with *Exo1*, *Exo6* or *ALL* species flows.

All analyses were carried out in R v.4.0.0. (R Core Team 2020). The R script, available with the manuscript, lists all R packages that were used.

3 | RESULTS

3.1 | Invasion biogeography

Among the 13,372 known ant species, 252 are currently listed as alien species; that is, 1.88% of all ant species have established populations outside of their native range in one or several of the 173 countries where alien ants occur. The majority of these species have established on a single continent ($n = 122$), followed by 41 which have established on two continents, 24 on three continents, 21 on four continents, 18 on five continents and 26 on all six continents (Figure 1a). Indoor locations represented 14% of our occurrence data, and 78% of indoor occurrences were located in Europe; in particular the Netherlands and the UK (see Appendix S1 for our analyses without indoor locations).

Species that were established on a higher number of continents were also more likely to be introduced via a bridgehead region ($F = 8.9$, $p = .04$). Among ant species intercepted in the United States and New Zealand, 90.3% of *Exo6* species came from areas outside of their native range, while only 17.3% of *Exo1* species were transported from a bridgehead region. These secondary introductions of *Exo1* species could stem from "silent populations" in the donor region (i.e. populations that have not yet been recorded). Alternatively, the commodity transporting these ants may have been moved through several ports before arriving in the United States or New Zealand, and the last port was potentially registered as "port of origin" of the interception without being the actual donor region of the species (i.e. the area containing the source population of the introduction). Our data do not allow distinguishing between these hypotheses. But it confirmed that the

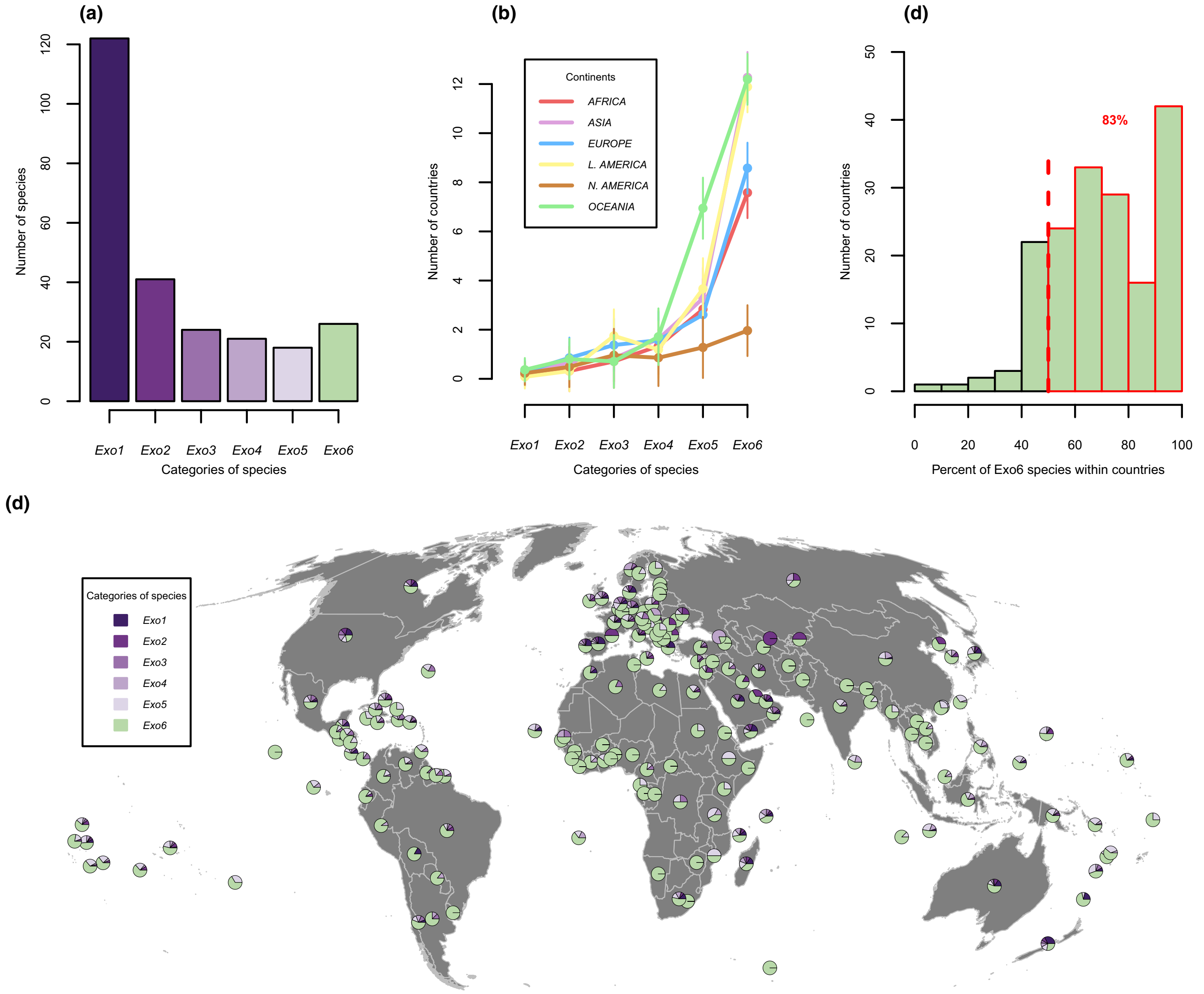

FIGURE 1 **Domination of cosmopolitan species.** a) Number of species exotic in one to six continents (*Exo1*-*Exo6*), b) number of countries within each continent where *Exo1*-*Exo6* species have established, c) percentage of cosmopolitan (*Exo6*) species per country, d) proportion of *Exo1*-*Exo6* species per country, showing that the majority of countries are dominated by *Exo6* species

proportion of secondary interceptions was higher for *Exo6* than *Exo1* species, enabling us to use them as a proxy for the relative reliability of species flows (*Exo1*=relatively certain, *Exo6*=relatively unreliable introduction route).

To assess how important "unreliable flows" (of species established on several continents which may be introduced from any of those) are in determining our global view of intercontinental species exchanges, we quantified the contribution of *Exo1-6* species to the composition of species assemblages within each country. We found that species exotic in several continents are disproportionally widespread within those continents (Figure 1b), as evidenced by a higher mean number of colonized countries within each continent (p <.001). Yet, the precise increase depended on the continent (interaction, p <.001). Even within the continent with the smallest number of countries (North America - 5 countries), *Exo6* species were on average established in more countries than *Exo1* species (p <.001).

As a consequence, most (83%) countries were dominated by alien species that were exotic in all six continents (*Exo6*), making up more than 50% of alien species established there (Figure 1c). No single country had a majority of species that were exotic in only one continent (Figure 1d) and only a few countries did not have a majority of extremely cosmopolitan species, such as New Zealand, Japan, Madagascar, the Seychelles and the United States (Figure 1d).

3.2 | Species flows

To compare potential flows of species from donor continents to recipient countries, we focused on 41 countries containing species exotic in a single continent (*Exo1*) and species exotic in several continents (*Exo2-6*) (Figure 2, see Appendix S2 for the same figure with the piecharts proportional to the number of alien species in each country). For most countries, the total species flow comprising all categories of alien species (*ALL*) closely resembled the *Exo6* flow, which had a large proportion of ant species native to Asia and Africa. The only exceptions where the *ALL* species flows were not closely linked to *Exo6* flows were the few countries not dominated by extremely cosmopolitan species such as New Zealand, Japan and the United States.

To compare flows of *Exo1*, *Exo6* and *ALL* species to the 41 focal countries, we did a correspondence analysis (CA) on the "profiles" of geographic origins for each country. A profile of geographic origins corresponds to the number of species introduced from each of the six continents to the focal country, standardized by the sum of the introduced species in that country. The variance of the coordinates in this CA space of the *Exo*1 flows was much greater than the variance of *Exo6* or *ALL* species flows (Levene's test, axis 1: *F* statistic 45.25, *p* <.0001, axis 2: statistic: 38.51, *p* <.0001) (Figure 3a). This demonstrates that the species flows including cosmopolitan species were much more homogenous in their geographic origins (Figure 2, Figure 3a).

We also found an effect of the interaction between the species' category (*Exo1*, *Exo6*, *ALL*) and the continent (ANOVA on coordinates of the 1st CA axis, interaction category: continent, *F* = 11.97, *p* <.0001, ANOVA on coordinates of the 2nd CA axis, interaction category: continent, *F* = 4.86, *p* <.0001) on the geographic origins of species flows. Flows of species exotic in all six continents did not differ from flows including all species (Tukey test; 1st CA axis: diff (*Exo6-ALL*)= 0.02, *p* =.97; 2nd CA axis, diff (*Exo*6-ALL)= 0.11, *p* =.54). However, flows of species exotic in a single continent differed from both *ALL* species flows (Tukey test; 1st CA axis: diff (*Exo6-Exo*1)= 0.26, *p* =.01; 2nd CA axis, diff (*Exo*6-*Exo*1)= 0.32, *p* <.01) and *Exo6* species flows (Tukey test; 1st CA axis: diff (*ALL-Exo1*)= 0.28, *p* <.01; 2nd CA axis, diff (*ALL-Exo1*)=0.43, *p* <.001). Hierarchical clustering confirmed that flows of *Exo6* species and *ALL* species were coherent groups, different from *Exo1* flows, which were distributed across three distinct groups (Figure 3b). Eight out of 15 pairwise continent comparisons of *Exo1* species flows were statistically different, as indicated by the Tukey test. This demonstrates that flows of species exotic in a single continent had strong regional differences (Figure 3c). Most species were introduced within the continent that they are native to (Figure 2).

3.3 | Species flows and trade

To assess whether cosmopolitan species also influence our view of species flows at a larger spatial scale, we also quantified intercontinental exchanges of *Exo1*, *Exo6* and *ALL* species (Figure 4), confirming that "reliable" flows of alien species exotic in one continent differed markedly from total flows of alien species present in a given country. To test whether this distortion of flows can blur the link with trade (known to transport ants), we performed separate co-inertia analyses between species flows and trade flows, for *Exo1*, *Exo6* and *ALL* species. We found that flows of species exotic in a single continent (*Exo1*) were associated with trade flows (RV=0.81, *p* =.014). These flows are the most reliable flows because the link between the donor region and the introduced region is certain, as there are no other continents that could have served as bridgehead regions generating secondary introductions. However, when considering species flows dominated by cosmopolitan species, we found that trade was no longer linked to species flows (*Exo6*: RV=0.35, *p* =.64, *ALL*: RV=0.64, *p* =.12).

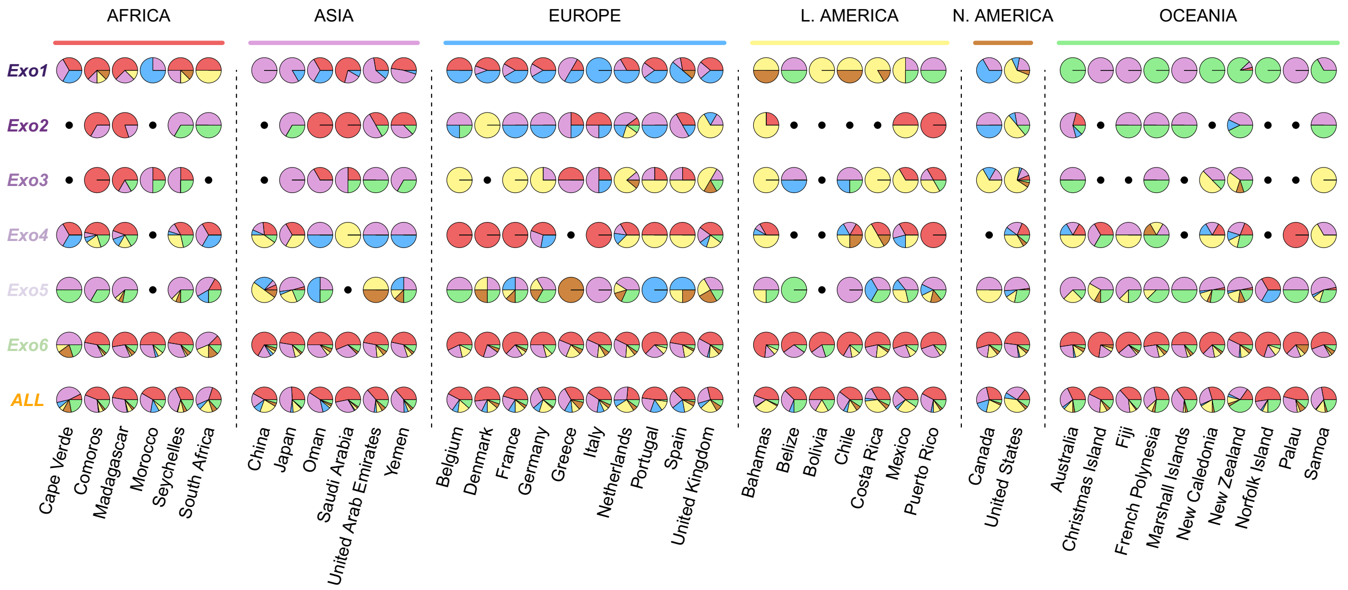

FIGURE 2 Species flows to 41 countries, depending on the number of exotic continents of each species. Countries are grouped by their continent. Each pie chart represents the proportions of geographic origins of each flow, and the colours indicate the native continent of a species. Species flows for species that are present on a higher number of continents are more similar across countries. The flow that includes all species (*ALL*) closely reassembles to species flows of cosmopolitan species (*Exo6*). See Appendix S2 for a representation with the size of the piecharts proportional to the number of species

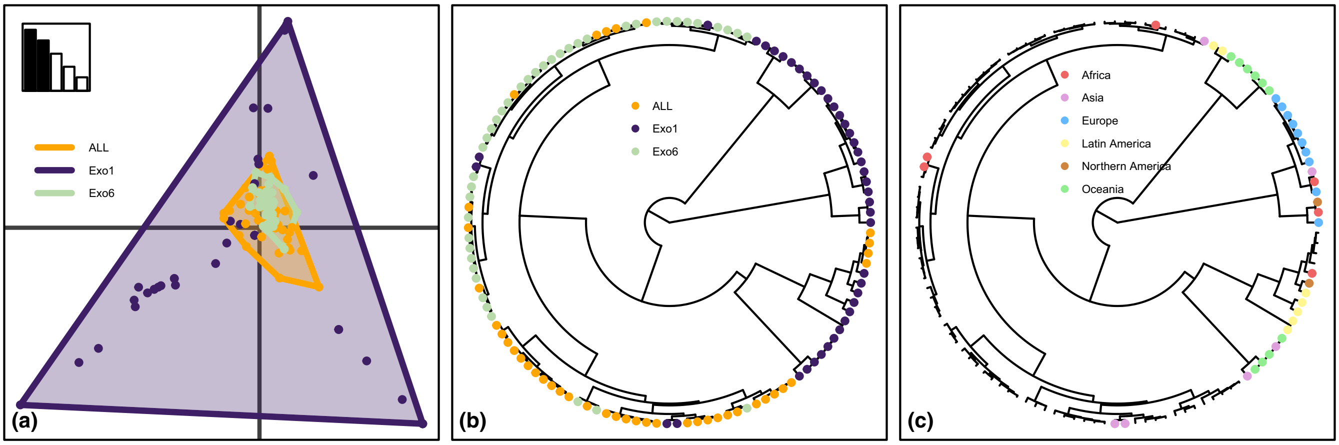

FIGURE 3 **Correspondence analysis of the geographic profiles of species flows for *Exo1*, *Exo6* and *ALL* species**. a) Flows of species exotic in six continents (green) and flows including all species (orange) are more homogenous than flows of species exotic in one continent (purple). b) Hierarchical clustering confirming that flows of *Exo6* species and *ALL* species are coherent groups, different from *Exo1* flows, which are distributed across three distinct groups; c) focusing on *Exo1 species* only, the flows were coloured according to the continent of the country. Flows of *ALL* and *Exo6* species are not highlighted here (displayed in white). *Exo1* flows tend to cluster together when belonging to countries on the same continent, revealing a regional signature of *Exo1* species flows

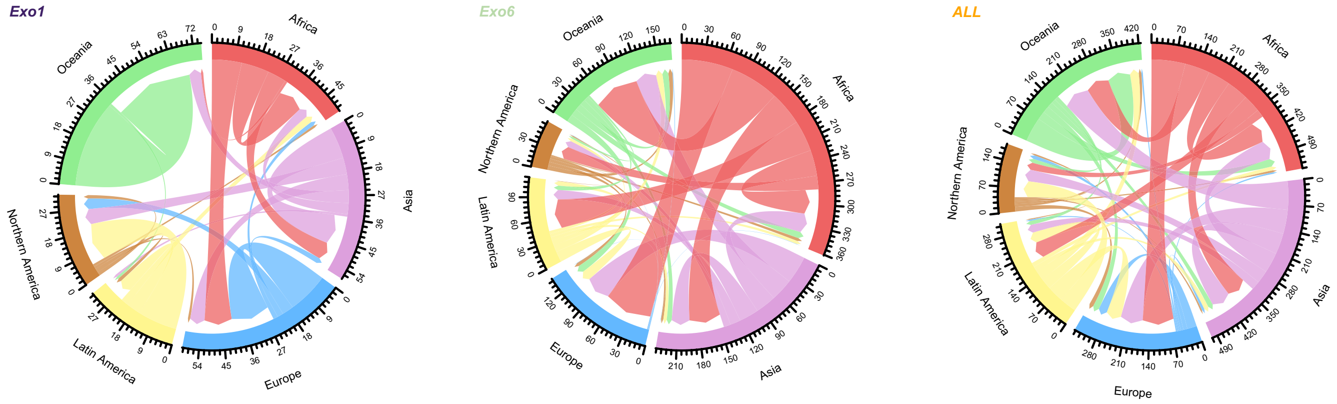

FIGURE 4 **Intercontinental species flows**. The white part of the bar on the outer circle represents incoming species; the filled part of the bar on the outer circle indicates outgoing species: species exotic in one continent (*Exo1*), species exotic in six continents (*Exo6*) and all alien species (*ALL*)

4 | DISCUSSION

We found that our view of alien species flows changed dramatically when we only considered species for which the "flow" between their native and their recipient region represented the actual introduction pathway with a higher degree of certainty. The more continents a species has colonized, the greater the uncertainty where it was introduced from. Even species exotic on a single continent (*Exo1*) may occasionally be introduced secondarily, for example, if they have established a bridgehead population which is not yet known to science. Yet, *Exo1* species have a lower chance of being secondarily introduced than species established on several continents. Therefore, species introduced in one to six continents can serve as a gradient of relative certainty to great uncertainty about the actual introduction pathways.

The invasion biogeography of ants was dominated by the 26 most extreme cosmopolitan species which had established on all six continents and could potentially arrive from any continent, via bridgehead effects. These few cosmopolitan species constituted the majority of non-cosmopolitan alien species in ant assemblages of most countries worldwide, while most alien species had restrictive distributions. Although there are 252 alien ant species worldwide, more than half of the established species in 83% of countries were established on all six continents. This implies that the global homogenization of alien species was due to a minority of widespread alien species, which has been observed in other taxa (Baiser et al., 2012; Capinha et al., 2020; Weigelt et al., 2016; Winter et al., 2009),. Yet, these taxa dominated intercontinental exchanges and blurred the links between actual donor and recipient regions. This may be problematic for the view of global species exchanges represented in such studies which draw direct links between the native and introduced regions. Indeed, these global assessments do not distinguish between species exotic in one or more continents.

Recent advances in building large datasets of species distributions have enabled researchers to make quantitative assessments of intercontinental species exchanges (Capinha et al., 2017; van Kleunen et al., 2015). Although it is interesting to map hotspots of alien species and the regions where these alien species are native (Dawson et al., 2017), labelling the links between native regions and exotic ranges of species as "flows" may suggest that the native regions have indeed acted as direct donors of these alien species. Here, we show that potential flows of species exotic in a single continent were coherent with global trade flows. This coherence between an important invasion pathway of ants and potential global species flows was lost when flows of cosmopolitan species were included. Our results demonstrate that the coherence between trade and invasion flows was contingent on using species for which the "flow" between their donor and recipient continents was relatively reliable, meaning that it reflects their true invasion route. Suppressing indoor locations did not affect these conclusions but it slightly changed our view of Europe (Appendix S1), which was less dominated by *Exo6* species and contained much fewer alien ant species in general—probably due to the fact that Europe does not possess the tropical climate that is necessary for the outdoor establishment of many alien ant species.

We acknowledge that species flows are likely to be driven by a combination of environmental and human factors, including trade. We have used trade here because the international trade is thought to be the main introduction pathway for ants (Suarez et al., 2010) and has been linked to their spread dynamics over the past two waves of globalization (Bertelsmeier et al., 2017). In this way, we have illustrated that the link between a known relevant driver of ant invasions, trade and flows of alien ants can be obscured when including more cosmopolitan species in the analysis.

It is beyond the scope of this study to assess the relative importance of trade and other biotic and abiotic variables in determining species flows. We hope that our findings stimulate future research into disentangling these factors by using a pool of species for which such an analysis is pertinent, that is, only species that are exotic ideally to a single continent only or a few continents because flows of these species are more likely to reflect the actual introduction pathways. We believe that this will help address the long-standing question in invasion science: Why are some regions overrepresented as donors of invasive species? Since Darwin (Darwin, 1859), many biologists have found that "flows" of species do not simply represent the relative species richness on different continents (Capinha et al., 2017; Lonsdale, 1999; Rejmanek, 2015; van Kleunen et al., 2015). Yet, tests of this question have been lacking, perhaps because secondary introductions from previously invaded continents blur the relationships between human trade and travel and the spread of invasive species. Future research is needed which undertakes such assessments, comparing different taxonomic groups with different introduction pathways.

In conclusion, our results show that it is crucial to account for bridgehead effects when assessing the biogeography and intercontinental flows of alien species. This is urgent for improving our understanding of how species are moved around the planet.

ACKNOWLEDGEMENTS

We thank Xuan Liu and two anonymous referees for their helpful comments. CB was supported by funding from the canton Vaud and grants from the Swiss National Science Foundation and the *Programme de la Famille Sandoz—Monique de Meuron pour la relève universitaire*. SO and CB were supported by an International Emerging Action entitled "Globalization and insect invasions (GLOBINV)" and funded by the CNRS.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORSHIP STATEMENT

Both authors conceived the project, formatted, analysed and interpreted the data and wrote the manuscript.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13388.

DATA AVAILABILITY STATEMENT

All analyses were carried out in R v.4.0.0. (R Core Team 2020). The script and workspace containing all data are supplied to generate figures. Both are available on Dryad: https://doi.org/10.5061/dryad.34tmpg4kr.

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REFERENCES

Baiser, B., Olden, J. D., Record, S., Lockwood, J. L., & McKinney, M. L. (2012). Pattern and process of biotic homogenization in the New Pangaea. *Proceedings of the Royal Society B-Biological Sciences*, *279*, 4772–4777. https://doi.org/10.1098/rspb.2012.1651

Bertelsmeier, C., Ollier, S., Liebhold, A. M., Brockerhoff, E. G., Ward, D., & Keller, L. (2018). Recurrent bridgehead effects accelerate global alien ant spread. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 5486–5491. https://doi.org/10.1073/pnas.1801990115

Bertelsmeier, C., Ollier, S., Liebhold, A., & Keller, L. (2017). Recent human history governs global ant invasion dynamics. *Nature Ecology & Evolution*, *1*, 0184. https://doi.org/10.1038/s41559-017-0184

Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., Wilson, J. R. U., & Richardson, D. M. (2011). A proposed unified framework for biological invasions. *Trends in Ecology & Evolution*, *26*, 333–339. https://doi.org/10.1016/j.tree.2011.03.023

Capinha, C., Essl, F., Seebens, H., Moser, D., & Pereira, H. M. (2015). The dispersal of alien species redefines biogeography in the Anthropocene. *Science*, *348*, 1248–1251. https://doi.org/10.1126/science.aaa8913

Capinha, C., Marcolin, F., & Reino, L. (2020). Human-induced globalization of insular herpetofaunas. *Global Ecology and Biogeography*, *29*, 1328–1349. https://doi.org/10.1111/geb.13109

Capinha, C., Seebens, H., Cassey, P., García-Díaz, P., Lenzner, B., Mang, T., Moser, D., Pyšek, P., Rödder, D., Scalera, R., Winter, M., Dullinger, S., & Essl, F. (2017). Diversity, biogeography and the global flows of alien amphibians and reptiles. *Diversity and Distributions*, *23*, 1313–1322. https://doi.org/10.1111/ddi.12617

Catford, J. A., Jansson, R., & Nilsson, C. (2009). Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, *15*, 22–40. https://doi.org/10.1111/j.1472-4642.2008.00521.x

Chapman, D., Purse, B. V., Roy, H. E., & Bullock, J. M. (2017). Global trade networks determine the distribution of invasive non-native species. *Global Ecology and Biogeography*, *26*, 907–917. https://doi.org/10.1111/geb.12599

Chiron, F., Shirley, S. M., & Kark, S. (2010). Behind the Iron Curtain: Socio-economic and political factors shaped exotic bird introductions into Europe. *Biological Conservation*, *143*, 351–356. https://doi.org/10.1016/j.biocon.2009.10.021

Clavero, M., & García-Berthou, E. (2005). Invasive species are a leading cause of animal extinctions. *Trends in Ecology & Evolution*, *20*, 110. https://doi.org/10.1016/j.tree.2005.01.003

Colautti, R. I., & Lau, J. A. (2015). Contemporary evolution during invasion: Evidence for differentiation, natural selection, and local adaptation. *Molecular Ecology*, *24*, 1999–2017. https://doi.org/10.1111/mec.13162

Corlett, R. T. (2014). The Anthropocene concept in ecology and conservation. *Trends in Ecology & Evolution*, *30*, 36–41. https://doi.org/10.1016/j.tree.2014.10.007

Costello, C., Springborn, M., McAusland, C., & Solow, A. (2007). Unintended biological invasions: Does risk vary by trading partner? *Journal of Environmental Economics and Management*, *54*, 262–276. https://doi.org/10.1016/j.jeem.2007.06.001

Dalmazzone, S., & Giaccaria, S. (2014). Economic drivers of biological invasions: A worldwide, bio-geographic analysis. *Ecological Economics*, *105*, 154–165. https://doi.org/10.1016/j.ecolecon.2014.05.008

Darwin, C. (1859). *On the origin of species by means of natural selection*. John Murray.

Dawson, W., Moser, D., van Kleunen, M., Kreft, H., Pergl, J., Pyšek, P., Weigelt, P., Winter, M., Lenzner, B., Blackburn, T. M., Dyer, E. E., Cassey, P., Scrivens, S. L., Economo, E. P., Guénard, B., Capinha, C., Seebens, H., García-Díaz, P., Nentwig, W., … Essl, F. (2017). Global hotspots and correlates of alien species richness across taxonomic groups. *Nature Ecology & Evolution*, *1*, 1–7. https://doi.org/10.1038/s41559-017-0186

Dolédec, S., & Chessel, D. (1994). Co-inertia analysis: An alternative method for studying species-environment relationships. *Freshwater Biology*, *31*, 277–294. https://doi.org/10.1111/j.1365-2427.1994.tb01741.x

Essl, F., Dullinger, S., Rabitsch, W., Hulme, P. E., Hülber, K., Jarošík, V., Kleinbauer, I., Krausmann, F., Kühn, I., Nentwig, W., Vilà, M., Genovesi, P., Gherardi, F., Desprez-Loustau, M.-L., Roques, A., & Pyšek, P. (2011). Socioeconomic legacy yields an invasion debt. *Proceedings of the National Academy of Sciences United States of America*, *108*, 203–207. https://doi.org/10.1073/pnas.1011728108

Geller, J. B., Darling, J. A., & Carlton, J. T. (2010). Genetic perspectives on marine biological invasions. *Annual Review of Marine Science*, *2*, 367–393. https://doi.org/10.1146/annurev.marine.010908.163745

Gippet, J. M., Liebhold, A. M., Fenn-Moltu, G., & Bertelsmeier, C. (2019). Human-mediated dispersal in insects. *Current Opinion in Insect Science*, *35*, 96–102. https://doi.org/10.1016/j.cois.2019.07.005

Greenacre, M., & Primicerio, R. (2013). *Multivariate analysis of ecological data*. BBVA.

Hölldobler, B., & Wilson, E. O. (1990). *The ants*. Harvard University Press.

Holway, D. A., Lach, L., Suarez, A. V., Tsutsui, N. D., Case, T. J., Suarez, A. V. et al (2002). The causes and consequences of ant invasions. *Annual Review of Ecology and Systematics*, *33*, 181–233. https://doi.org/10.1146/annurev.ecolsys.33.010802.150444

Janicki, J., Narula, N., Ziegler, M., Guénard, B., & Economo, E. P. (2016). Visualizing and interacting with large-volume biodiversity data using client-server web-mapping applications: The design and implementation of antmaps.org. *Ecological Informatics*, *32*, 185–193. https://doi.org/10.1016/j.ecoinf.2016.02.006

Josse, J., & Holmes, S. (2016). Measuring multivariate association and beyond. *Statistics Surveys*, *10*, 132–167. https://doi.org/10.1214/16-SS116

Krueger-Hadfield, S. A., Kollars, N. M., Strand, A. E., Byers, J. E., Shainker, S. J., Terada, R., Greig, T. W., Hammann, M., Murray, D. C., Weinberger, F., & Sotka, E. E. (2017). Genetic identification of source and likely vector of a widespread marine invader. *Ecology and Evolution*, *7*, 4432–4447. https://doi.org/10.1002/ece3.3001

Lombaert, E., Guillemaud, T., Cornuet, J. M., Malausa, T., Facon, B., & Estoup, A. (2010). Bridgehead effect in the worldwide invasion of the biocontrol harlequin ladybird. *PLoS One*, *5*, e9743. https://doi.org/10.1371/journal.pone.0009743

Lonsdale, W. (1999). Concepts & Synthesis Global Patterns of Plant Invasions and the Concept of. *Ecology*, *80*, 8–11.

McGeoch, M. A., Butchart, S. H. M., Spear, D., Marais, E., Kleynhans, E. J., Symes, A., Chanson, J., & Hoffmann, M. (2010). Global indicators of biological invasion: Species numbers, biodiversity impact and policy responses. *Diversity and Distributions*, *16*, 95–108. https://doi.org/10.1111/j.1472-4642.2009.00633.x

Paini, D. R., Sheppard, A. W., Cook, D. C., Barro, P. J. D., Worner, S. P., & Thomas, M. B. (2016). Global threat to agriculture from invasive species. *Proceedings of the National Academy of Sciences*, *113*, 7575–7579. https://doi.org/10.1073/pnas.1602205113

Pyšek, P., & Richardson, D. M. (2010). Invasive species, environmental change and management, and health. *Annual Review of Environment and Resources*, *35*, 25–55. https://doi.org/10.1146/annurev-environ-033009-095548

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

R. Garnas, J., Auger-Rozenberg, M.-A., Roques, A., Bertelsmeier, C., Wingfield, M. J., Saccaggi, D. L., Roy, H. E., & Slippers, B. (2016). Complex patterns of global spread in invasive insects: Eco-evolutionary and management consequences. *Biological Invasions*, *18*, 935–952. https://doi.org/10.1007/s10530-016-1082-9

Rabitsch, W. (2011). The hitchhiker's guide to alien ant invasions. *BioControl*, *56*, 551–572. https://doi.org/10.1007/s10526-011-9370-x

Rejmanek, M. (2015). Global trends in plant naturalization. *Nature*, *525*, 39–40. https://doi.org/10.1038/nature15206

Ricciardi, A., Hoopes, M. F., Marchetti, M. P., & Lockwood, J. L. (2013). Progress toward understanding the ecological impacts of non-native species. *Ecological Monographs*, *83*, 263–282. https://doi.org/10.1890/13-0183.1

Roques, A., Auger-Rozenberg, M.-A., Blackburn, T. M., Garnas, J., Pyšek, P., Rabitsch, W. et al (2016). Temporal and interspecific variation in rates of spread for insect species invading Europe during the last 200 years. *Biological Invasions*, *18*, 907–920.

Ruiz, G. M., & Carlton, J. T. (2003). *Invasive species - Vectors and management strategies*. Island Press.

Sanders, N. J., Gotelli, N. J., Heller, N. E., & Gordon, D. M. (2003). Community disassembly by an invasive species. *Proceedings of the National Academy of Sciences United States of America*, *100*, 2474–2477. https://doi.org/10.1073/pnas.0437913100

Seebens, H., Bacher, S., Blackburn, T. M., Capinha, C., Dawson, W., Dullinger, S., Genovesi, P., Hulme, P. E., Kleunen, M., Kühn, I., Jeschke, J. M., Lenzner, B., Liebhold, A. M., Pattison, Z., Pergl, J., Pyšek, P., Winter, M., & Essl, F. (2020). Projecting the continental accumulation of alien species through to 2050. *Global Change Biology*. https://doi.org/10.1111/gcb.15333.

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu, G., Capinha, C., Celesti-Grapow, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger, H., … Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, *8*, 14435. https://doi.org/10.1038/ncomms14435

Shackleton, R. T., Shackleton, C. M., & Kull, C. A. (2019). The role of invasive alien species in shaping local livelihoods and human well-being: A review. *Journal of Environmental Management*, *229*, 145–157. https://doi.org/10.1016/j.jenvman.2018.05.007

Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., & Vilà, M. (2013). Impacts of biological invasions - What's what and the way forward. *Trends in Ecology & Evolution*, *28*, 58–66. https://doi.org/10.1016/j.tree.2012.07.013

Suarez, A. V., Holway, D. A., & Ward, P. S. (2005). The role of opportunity in the unintentional introduction of nonnative ants. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 17032–17035.

Suarez, A. V., McGlynn, T., & Tsutsui, N. D. (2010). Biogeographic and taxonomic patterns of introduced ants. In L. Lach, C. L. Parr, & K. L. Abbott (Eds.), *Ant ecology*. Oxford University Press.

Suhr, E. L., O'Dowd, D. J., Suarez, A. V., Cassey, P., Wittmann, T. A., Ross, J. V., & Cope, R. C. (2019). Ant interceptions reveal roles of transport and commodity in identifying biosecurity risk pathways into Australia. *NeoBiota*, *53*, 1–24. https://doi.org/10.3897/neobiota.53.39463

van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E., Kreft, H., Weigelt, P., Kartesz, J., Nishino, M., Antonova, L. A., Barcelona, J. F., Cabezas, F. J., Cárdenas, D., Cárdenas-Toro, J., Castaño, N., Chacón, E., Chatelain, C., Ebel, A. L., … Pyšek, P. (2015). Global exchange and accumulation of non-native plants. *Nature*, *525*, 100–103. https://doi.org/10.1038/nature14910

Weigelt, P., Kreft, H., & Christian, K. (2016). Dissecting global turnover in vascular plants. *Global Ecology and Biogeography*, 1–15.

Westphal, M. I., Browne, M., MacKinnon, K., & Noble, I. (2008). The link between international trade and the global distribution of invasive alien species. *Biological Invasions*, *10*, 391–398. https://doi.org/10.1007/s10530-007-9138-5

Winter, M., Schweiger, O., Klotz, S., Nentwig, W., Andriopoulos, P., Arianoutsou, M., Basnou, C., Delipetrou, P., Didziulis, V., Hejda, M., Hulme, P. E., Lambdon, P. W., Pergl, J., Pysek, P., Roy, D. B., & Kuhn, I. (2009). Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 21721–21725. https://doi.org/10.1073/pnas.0907088106

BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Bertelsmeier, C., & Ollier, S. (2021). Bridgehead effects distort global flows of alien species. *Diversity and Distributions*, 00, 1–10. https://doi.org/10.1111/ddi.13388