

RESEARCH ARTICLE

Diversity and Distributions WILEY

Global flows of insect transport and establishment: The role of biogeography, trade and regulations

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Funding information

Canton de Vaud; Centre National de la Recherche Scientifique; Fondation Sandoz-Monique de Meuron pour la relève universitaire; National Science Foundation, Grant/Award Number: DBI-1639145; Swiss National Science Foundation, Grant/Award Number: 310030_192619; The Czech Operational Programme "Research, Development and Education, Grant/Award Number: CZ.02.1.01/0.0/0.0/16_019/0000803

Editor: Marco Túlio Pacheco Coelho

Abstract

Aim: Non-native species are part of almost every biological community worldwide, yet numbers of species establishments have an uneven global distribution. Asymmetrical exchanges of species between regions are likely influenced by a range of mechanisms, including propagule pressure, native species pools, environmental conditions and biosecurity. While the importance of different mechanisms is likely to vary among invasion stages, those occurring prior to establishment (transport and introduction) are difficult to account for. We used records of unintentional insect introductions to test (1) whether insects from some biogeographic regions are more likely to be successful invaders, (2) whether the intensity of trade flows between regions determines how many species are intercepted and how many successfully establish, and (3) whether the variables driving successful transport and successful establishment differ.

Location: Canada, mainland USA, Hawaii, Japan, Australia, New Zealand, Great Britain, South Korea, South Africa.

Methods: To disentangle processes occurring during the transport and establishment stages, we analysed border interceptions of 8199 insect species as a proxy for transported species flows, and lists of 2076 established non-native insect species in eight areas. We investigated the influence of biogeographic variables, socio-economic variables and biosecurity regulations on the size of species flows between regions.

Results: During transport, the largest species flows generally originated from the Nearctic, Panamanian and Neotropical regions. Insects native to 8 of 12 biogeographic regions were able to establish, with the largest flows of established species on average coming from the Western Palearctic, Neotropical and Australasian/Oceanian regions. Both the biogeographic region of origin and trade intensity significantly influenced the size of species flows between regions during transport and establishment. The transported species richness increased with Gross National Income in the source country, and decreased with geographic distance. More species were able to establish when introduced within their native biogeographic region.

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Main Conclusions: Our results suggest that accounting for processes occurring prior to establishment is crucial for understanding invasion asymmetry in insects, and for quantifying regional biosecurity risks.

KEYWORDS

establishment, globalization, human-mediated dispersal, insects, interceptions, invasion asymmetry, invasion stages

1 | INTRODUCTION

The globalization of trade and travel has led to an unprecedented acceleration of species introductions (Bonnamour et al., 2021; Seebens et al., 2017), which is increasingly impacting native ecosystems and human societies (Pagad et al., 2015). Mapping non-native species diversity and exchanges between world regions is therefore key to understanding large-scale drivers of invasions and identifying regionally specific biosecurity risks. Extensive and spatially explicit databases (e.g. CABI Invasive Species Compendium (CABI, 2022); DAISIE (Delivering Alien Invasive Species Inventories for Europe; Roy et al., 2020)) are increasingly available to document non-native species distributions, and there have been considerable advances in describing regional invasion patterns (e.g. Capinha et al., 2017; Casado et al., 2018; van Kleunen et al., 2015). Other studies have focused on the characteristics of trade and travel network topologies driving human-mediated dispersal (Banks et al., 2015; Tatem, 2009), or have identified socio-economic and biogeographic variables that are linked to non-native species richness (Baiocchi & Dalmazzone, 2000;

Capinha et al., 2017; Dawson et al., 2017; Lantschner et al., 2020). Yet while non-native species have been recorded in almost every biological community around the world (Convention on Biological Diversity, 2001), species establishments outside of their native range are not evenly distributed geographically. The imbalance in species exchanges, with some regions over- or under-represented as donors and recipients, is referred to as 'invasion asymmetry' (Torchin et al., 2021). For example, many non-native plants in the Southern hemisphere have originated in the Northern hemisphere, while the opposite trend is not observed (van Kleunen et al., 2015).

Different mechanisms have been proposed to explain invasion asymmetry (Figure 1), often focussing on environmental factors and biotic acceptance or resistance during establishment (Jeschke & Genovesi, 2011). However, biological invasions are composed of a series of sequential stages: transport, introduction, establishment and subsequent spread (Blackburn et al., 2011; Gippet et al., 2019; Figure 1). Each stage constitutes a barrier that must be overcome for a species or population to successfully establish and proliferate. The overall invasion success of a species is accordingly determined

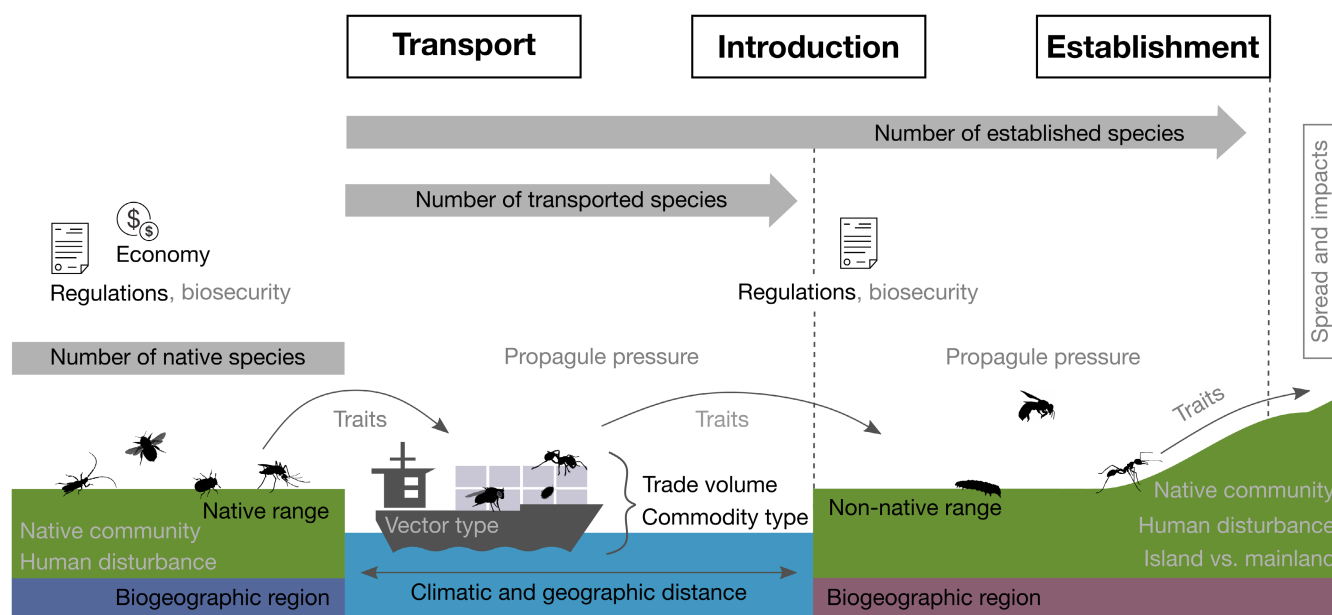


FIGURE 1 The invasion process for unintentional species introductions. The stages of transport, introduction and establishment are shown, along with key mechanisms affecting success/failure at each stage. Transport includes both maritime, aerial and overland introduction pathways. We have not included secondary, bridgehead introductions. Mechanisms and stages not explicitly included in our analyses are shown in grey. The dotted lines indicate the two points we analysed data from; border interceptions after transport, and lists of established insects. Adapted from Schulz et al. (2019).

by the extent to which its individuals or propagules can overcome these barriers (Blackburn et al., 2011). The number of individuals introduced or the number of introduction events (hereafter propagule pressure; Lockwood et al., 2005; Williamson, 1996) is a key element in species invasion success or failure. However, previous work has often not considered that the mechanisms responsible for differential invasion success, often linked to species traits, are likely to vary considerably throughout the invasion process (Blackburn et al., 2011; Gippet et al., 2019). While it has been possible to control for the introduction stage in rare cases where release attempts are well recorded (birds: Blackburn et al., 2008; Chiron et al., 2009; mammals: Jeschke & Genovesi, 2011), in most previous analyses of invasion patterns it has not been possible to isolate the factors responsible for invasion success at each stage (Puth & Post, 2005). Consequently, our understanding of species richness introduced from a source region to a destination region, hereafter referred to as species flows, is largely based on the distribution of already established non-natives (e.g. Capinha et al., 2015; Dawson et al., 2017; van Kleunen et al., 2015), hindering our ability to separate ecological factors from the influence of introduction pressure.

In this study, we address key mechanisms determining the number of non-native species exchanged between regions at the transport stage, and after establishment. Firstly, regions differ in the size of the native species pool potentially available for transport (Liebhold et al., 2017; Seebens et al., 2018). The pool of species in an area thereby sets an upper limit for the number of non-natives that area can supply. Furthermore, the environmental conditions species are adapted to also vary regionally, and likely play a role in establishment success outside their native range (Bomford et al., 2009; Cunze et al., 2018). Secondly, invasion asymmetry can arise from differences in propagule pressure, or the number of species introduced (colonization pressure; Blackburn et al., 2020; Lockwood et al., 2009). Propagule- and colonization pressure have been identified as key drivers of invasion success for several taxa (Blackburn et al., 2020; Lockwood et al., 2005), and are tightly linked to human activities (Pyšek et al., 2010). As most introductions occur via human-mediated dispersal (Hulme et al., 2008), the spatial and temporal heterogeneity of global trade and transport networks is likely a key contributor to invasion asymmetry (Banks et al., 2015; De Benedictis & Tajoli, 2011). Lastly, many countries put significant efforts into preventing invasions (Black & Bartlett, 2020; Saccaggi et al., 2016). Biosecurity measures that exclude new species introductions are generally considered more efficient than managing already established populations (Leung et al., 2002), and are coordinated through national policies and international conventions. Nonetheless, resources to regulate non-native species are also unevenly distributed, potentially exacerbating invasion asymmetry (Bacon et al., 2012; Early et al., 2016; McGeoch et al., 2010).

To disentangle the processes occurring during transport and establishment, we analysed insect border interception records (transport stage) and country-level lists of established non-native insects (establishment stage). Border interceptions generally represent live insects that have been successfully transported, and as such can be

considered as a proxy for introductions. Insects are among the most widespread and damaging non-native species in terrestrial habitats, costing at least 70 billion US \$ annually (Bradshaw et al., 2016; Lovett et al., 2016). Due to their small size, they are easily transported accidentally through human activities (Meurisse et al., 2019). While the introduction pathways of established species remain poorly known (National Research Council, 2002), insects are the focus of considerable biosecurity efforts globally (Lance et al., 2014; Leung et al., 2002; Nahrung et al., 2022). In addition to growing inventories of established non-native species, many countries record insect species detected during inspections of trade goods, mail and personal baggage at ports of entry (i.e. land borders, air- and sea ports and transitional facilities) as part of national biosecurity programmes (Black & Bartlett, 2020; Saccaggi et al., 2016). These border interceptions offer insight into the largely unobserved processes occurring prior to unintentional introductions (Turner, Bockerhoff, et al., 2021).

We quantified flows of transported species based on interceptions of 8199 insect species arriving in Canada, mainland USA, Hawaii, Japan, New Zealand, Great Britain and South Africa, from 227 countries around the world. Lists of 2076 established non-native insects, along with records of their native biogeographic region, allowed us to quantify flows of established species to the same destinations, plus Australia and South Korea. We modelled the effects of biogeography, trade intensity and biosecurity efforts on flows of insect species among regions, allowing us to test (1) whether insects from some biogeographic regions are more likely to be successful invaders, (2) whether the intensity of trade flows between regions determines how many insect species are intercepted and how many successfully establish, and (3) whether the variables driving successful transport and successful establishment differ.

2 | METHODS

2.1 | Flows of transported species

We analysed border interception records from Canada, mainland USA, Hawaii, Japan, New Zealand, Great Britain and South Africa to quantify the flows of insect species arriving from countries worldwide. See Table S1 for a description of the interception records available from each destination. The data consist of records of insect species detected during inspections of international cargo, mail, vessels and passenger baggage at air, land and maritime ports of entry. These border interceptions represent a fraction of the total insects being transported. While interceptions can be considered a proxy for species' undetected arrival, they do not directly represent introductions (Turner, Bockerhoff, et al., 2021). Furthermore, different types of organisms differ in the probability that they will be detected and recorded during inspection. We only include records with information on the source country and the associated commodity, and where the intercepted insect was identified to the species level (56%). We counted any

genera with no members identified to species level as representing one additional species. We standardized insect taxonomic names across years and recording regions according to the Global Biodiversity Information Facility (GBIF) backbone taxonomy (GBIF Secretariat, 2019) using the 'taxize' (Chamberlain & Szöcs, 2013) and 'rgbif' R packages (Chamberlain et al., 2021). This process was largely automated, but a small proportion of synonyms may still be present. We analysed interceptions between 1960 and 2019, depending on their availability per country (see Table S1). We carried out all analyses at a decadal scale to capture changing trade patterns while limiting the influence of random yearly fluctuations.

2.2 | Flows of established species

We used comprehensive lists of established non-native insect species in Australia, New Zealand, Great Britain, Japan, North America (continental USA and Canada), Hawaiian Islands, South Korea and South Africa. The native biogeographic region was recorded for each species using Holt's system (see below). The species lists and main source references are available from Turner, Blake, and Liebhold (2021). We did not include species that were intentionally introduced in our analyses. Furthermore, non-native populations often become the source of secondary introductions through a process termed the 'bridgehead effect' (Bertelsmeier & Ollier, 2021; Lombaert et al., 2010). To increase the likelihood that species arrived directly from their native region rather than via already invaded areas elsewhere, we excluded any species established in, or native to more than one biogeographic region. We restricted our analyses to first records of species establishment from 1960 onwards when detailed import values are available by commodity.

2.3 | Socio-economic factors

There is ample evidence linking biological invasions to trade, and broad metrics of economic activity such as Gross Domestic Product (GDP) have been used to predict invasion success in several previous studies (e.g. Baiocchi & Dalmazzone, 2000; Dawson et al., 2017; Sharma et al., 2010). However, Gross National Income (GNI) represents total income, whether earned within a country's borders or derived from foreign investments, and may provide a better measure of countries' economic condition (Maverick, 2022). Measures of GDP (constant 2015 USD) and GNI (constant 2015 USD) from World Bank and OECD National Accounts data were highly correlated, so we used yearly GNI per capita (The World Bank Group, 2022), summed per decade to quantify the economic status of each source country.

We standardized commodity descriptions in the interception records using the international Harmonized Commodity Description and Coding Systems (HS) for classifying traded goods (World Customs Organization, 2021), and subsequently grouped commodities

into broad classes based on the type of product (see Table S2). To provide a precise measure of relevant trade flows, we used the 'tradedata' R package (Vargas, 2022) to access historical import values per commodity based on UN Comtrade data (United Nations, 2022). Additional import records for Hawaii were obtained from the US Census Bureau as imports to the district of Honolulu (United States Census Bureau, 2022). We summed yearly import values in US dollars for each combination of commodity class, source country and destination, per decade. The dollar value of imports was corrected for inflation using the `ots_gdp_deflator_adjustment()` function in the 'tradedata' package with 2018 as the reference year.

While we know the exact year when species were intercepted, there is commonly a lag time between a species' establishment and its detection (Kowarick, 1995; Sakai et al., 2001). Such discovery lags for plant invasions sometimes exceed 50 years (Aikio et al., 2010; Kowarick, 1995; Larkin, 2012), but may be shorter for animals (Aagaard & Lockwood, 2014; Essl et al., 2011). In Japan, non-native insects generally have a lag time of 4–10 years before detection (Kiritani & Yamamura, 2003). Consequently, we used import values in the same decade as establishment to predict variation in species richness.

2.4 | Biogeographic regions

To describe insect invasion asymmetry between regions, we assigned all source countries and destinations to biogeographic regions. The regions were classified as per Holt et al. (2013), with the large Palearctic region divided into the Eastern and the Western Palearctic (Figure S1). Due to the low sample size, we excluded flows from the Antarctic and Madagascan biogeographic regions and combined the Australasian and Oceanian regions in our analyses.

2.5 | Climatic and geographic distance

While environmental similarity between the source and destination may be of limited importance during the early stages of the invasion process, it is likely to have a strong impact on establishment success (Bomford et al., 2009; Cunze et al., 2018). We quantified the climatic similarity between countries using the 19 bioclimatic variables from the WorldClim Global Climate Database at a resolution of 5 arc-minutes (Hijmans et al., 2005). The bioclimatic variables were reduced to eight axes using Principal Components Analysis (PCA) using the `dudi.pca()` function from the 'ade4' package (Dray & Dufour, 2007), then grouped based on the 32 Köppen-Geiger climate categories (Kottek et al., 2006). For each Köppen-Geiger climate, the eight PCA axes representing bioclimatic conditions were projected into hypervolume space using the Gaussian method, with a chunk size of 500 in the 'hypervolume' package (Blonder et al., 2014). We calculated the Euclidean

distance between the centroids of each climate in hypervolume space using the `dis_centroid()` function (Blonder et al., 2014). We then used a double PCA to create a dissimilarity matrix of how frequently each Köppen-Geiger climate occurs per country based on these distances. The values were normalized so that 0 represents no dissimilarity between regions, and 1 represents complete dissimilarity.

In addition to climatic distance, the geographic distance transported may have an impact on introduction success if species more easily survive transport across short distances (Chapman et al., 2017; Seebens et al., 2013). We used a vector map of country boundaries from the 'rworldmap' package with the WGS 84 coordinate reference system (South, 2011), and calculated the geographic distance transported as the distance in kilometres between country centroids. We calculated country centroids using the `gCentroid()` function in the 'rgeos' package (Bivand & Rundel, 2021) and the great circle distances between them using the `st_distance()` function in the 'sf' package (Pebesma, 2018).

2.6 | Native insect richness

Species that are transported from an area are necessarily a subset of the pool of species present there. While regional variation in species richness and diversity is therefore likely important for invasion asymmetry, insect biodiversity remains poorly quantified in many parts of the world. Stork et al. (2015) estimate that there are 5.5 million insect species globally. The distribution of Formicidae is well documented compared to most other insect taxa, so to estimate the species pool potentially available for transport in each source country, we divided 5.5 million by the proportion of native ant species present in that country using data from Global Ant Biodiversity Informatics database (Guénard, 2017). This follows the method used by Stork (2018) to estimate the number of insect species per biogeographic region. The number of native vascular plants per country based on the World Checklist of Vascular Plants (Govaerts et al., 2021) was highly correlated with our estimates of insect species richness (Pearson's $r = .84$), so we used the latter to quantify the size of the native species pools available for transport.

2.7 | Biosecurity regulations

National biosecurity programmes direct considerable efforts towards preventing insect invasions through extensive pre-border measures (Sequeira & Griffin, 2014). As a proxy for biosecurity efforts, we used the number of international treaties, regulations and legislation (referred to as regulations from here on) relevant to invasive species that a country is a member of. The number of regulations was based on the ECOLEX database, as per Turbelin et al. (2017). ECOLEX consolidates information on global environmental law, including international treaties, national legislation and technical guidance documents (FAO, IUCN, UNEP, 2016).

3 | STATISTICAL MODELLING

3.1 | Flows of transported species

A 'flow' here represents the species richness associated with a specific source country and destination pair, the commodity class insects arrived with, and the decade when insects were intercepted. Because interception data only record positive detections (they do not record absences), these data are inherently zero-truncated. Therefore, insect flows during transport were modelled using a generalized linear mixed model (glmm) with a zero-truncated negative binomial distribution from the 'glmmTMB' package (Brooks et al., 2017). We also considered a zero-truncated Poisson model to represent the counts of species but based on model AIC the zero-truncated negative binomial model provided a better fit. The model included the variables in Table 1, as well as an interaction term between the import value and commodity class, as the effect of trade intensity may differ between commodities. We included the decade of interception as a random effect to account for variation over time. There are differences in inspection methods, targets and efforts, as well as in trade patterns depending on the partners involved, so we also included the source country, the destination, and the source-destination pair as random effects.

3.2 | Flows of established species

A 'flow' here represents the number of species from a specific biogeographic region of origin that have established in a specific destination, per decade. We do not have information on the exact introduction pathway for most established species, but as plant products are the main commodities associated with insect movements through trade (Fenn-Moltu et al., 2022; Liebhold et al., 2012; Meurisse et al., 2019) we used the US dollar value of plant products imported to represent trade intensity. We assessed other trade metrics including total commodity import values, imports of agricultural commodities and imports of plant and wood products, as well as these values for the preceding decade, but plant product imports in the same decade was the best fit based on model AIC. We again used a glmm with a zero-truncated negative binomial distribution to predict the species richness per flow (Table 2). We included the decade in which a species established, and the area in which it established as random effects to account for variation in detectability and establishments over time and between destinations. We used the `Anova()` function in the 'car' package (Fox & Weisberg, 2018) to compute analysis-of-variance tables using type II Wald chi square tests for both models. All analyses were conducted in R (R Core Team, 2017).

4 | RESULTS

Overall, 8199 insect species were intercepted from 227 countries across all biogeographic regions (Figure 2). Insects were intercepted arriving with 14 different commodity classes. During transport, the

TABLE 1 The variables included in the model of species flows during transport, along with their description and the type of variable they represent.

Variable	Description	Type
Species richness	Number of insect species intercepted per flow (unique combination of source country/destination * commodity class * decade)	Response
Import value	Log value imported per flow in US dollars	Explanatory
Commodity class	Identity of 14 broad commodity classes that insects were intercepted with (e.g. plant products, machinery or stone/glass)	Explanatory
Biogeographic region	Biogeographic region the insects arrived from	Explanatory
Source species pool	Estimated number of native insect species in the source country	Explanatory
Regulations per source country	Number of regulations relating to invasive species the source country is a member of, ranging from 0 to 30	Explanatory
Regulations per destination country	Number of regulations relating to invasive species the destination country is a member of, ranging from 12 to 21	Explanatory
Gross National Income (GNI)	Log GNI per capita for the source country in constant 2015 US dollars	Explanatory
Geographic distance	Distance in km between the source and destination country centroids	Explanatory
Climatic dissimilarity	Climatic dissimilarity between the source and destination country, ranging from 0 (no dissimilarity) to 1 (complete dissimilarity)	Explanatory
Within or between regions	Whether species are transported within the same biogeographic region (intra) or not (inter)	Explanatory
Source	Which country intercepted species arrived from	Random
Destination	Area where species were intercepted; either Australia, New Zealand, Great Britain, mainland USA, Hawaii, Japan or South Africa	Random
Source and destination area	Specific combination of source and destination areas the insects are transported between	Random
Decade	Decade of port interception	Random

TABLE 2 The variables included in the model of established species flows, along with their description and the type of variable they represent.

Variable	Description	Type
Species richness	Number of established insect species per flow (unique combination of native region * destination * decade)	Response
Import value	Log value of plant products imported per flow in US dollars	Explanatory
Biogeographic region	Biogeographic region the established insects are native to	Explanatory
Regulations per destination	Number of regulations relating to invasive species the destination country is a member of, ranging from 12 to 24	Explanatory
Within or between regions	Whether species have established within their native biogeographic region (intra) or not (inter)	Explanatory
Destination area	Area where insects have established; either Australia, Great Britain, Hawaii, Japan, New Zealand, North America (continental USA and Canada) or South Korea	Random
Decade	Decade of establishment first record	Random

species richness per flow ranged from 1 to 967 species, with a median of three. The full output of the model predicting flow size during transport is in [Table S4](#). A total of 3994 species had established in the eight destinations we considered, encompassing insects native to the Afrotropical, Eastern and Western Palearctic, Sino-Japanese, Neotropical, Nearctic, Oceanian and Australasian regions ([Figure 2](#)). The decade when establishment was first recorded was available for 2076 of these species. The species richness per flow of established insects ranged from 1 to 107 species, with a median of three. The

full output of the model predicting flow size of established species is in [Table S5](#).

4.1 | Are insects from some biogeographic regions more likely to be successful invaders?

Interception records from the seven destinations analysed in this study documented the transport of a total of 2490 insect species

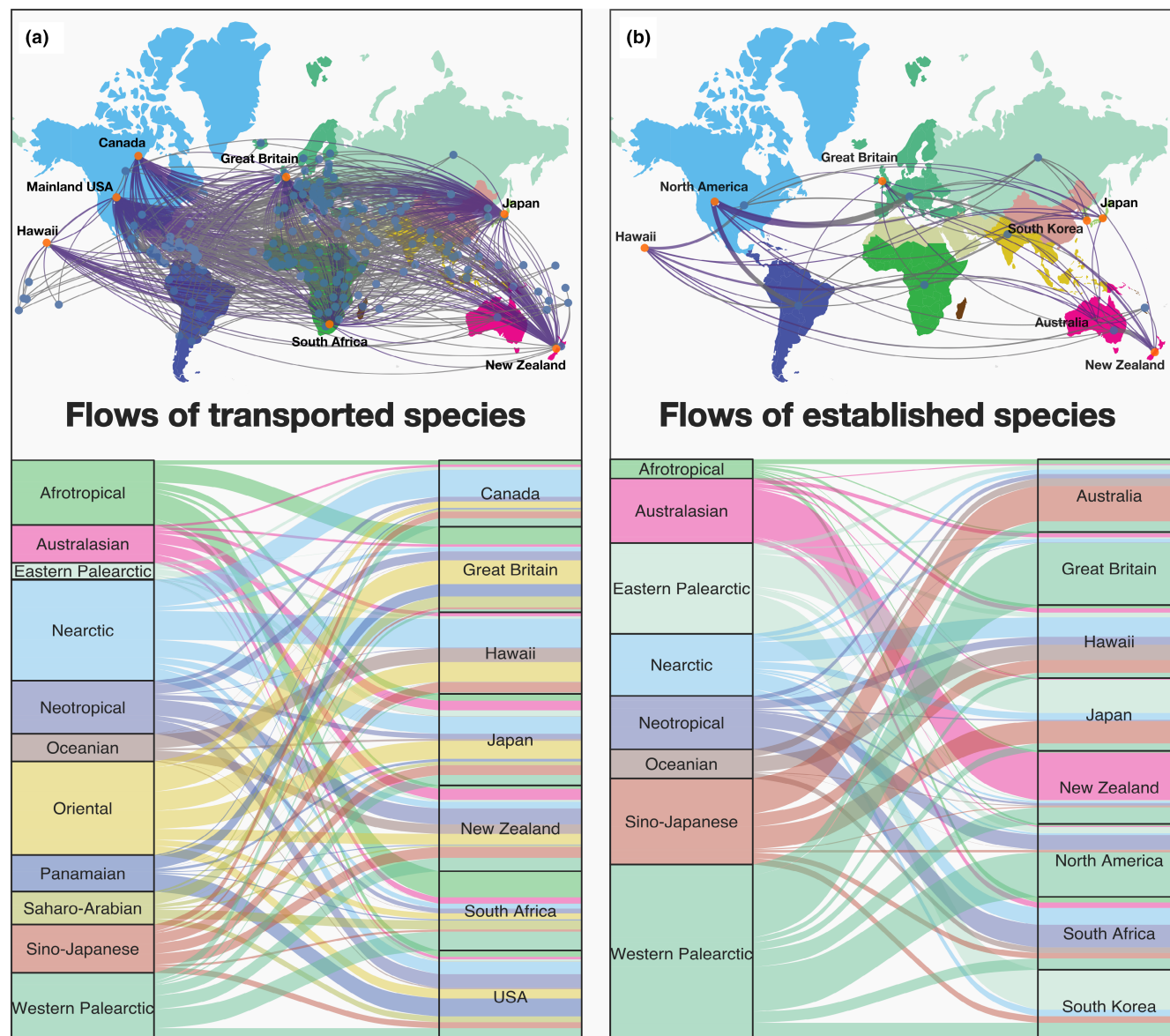


FIGURE 2 Flows of (a) transported and (b) established insect species. The maps show the geographical location of the flows analysed, and the links are proportional to the size of the flows. The alluvial plots show the percentage of species arriving in each destination from each biogeographic region of origin. In the alluvial chart (a) small flows from the Madagascan and Antarctic regions are not labelled.

from the Panamanian region, 2376 from the Nearctic, 2283 from the Western Palearctic, 2104 from the Neotropical, 1691 from the Oriental, 1090 from the Afrotropical, 1069 from the Sino-Japanese, 894 from the Saharo-Arabian, 668 from the Australasian, 464 from the Eastern Palearctic, 330 from the Oceanian, 31 from the Madagascan region and 1 species from the Antarctic region. On average, the greatest species richness per flow originated from the Nearctic (mean of 31.1 species, SD = 114), Panamanian (mean 21.8, SD 75.9) and Neotropical regions (mean 15.5, SD 60.8) at the transport stage. In the eight destinations where we had lists of non-native insects, 1482 Western Palearctic species had established, along with 561 Australasian, 512 Neotropical, 394 Nearctic, 365 Sino-Japanese, 298 Eastern Palearctic, 263 Oceanian species and 119 Afrotropical species. The mean species richness per flow was greatest from

the Western Palearctic (mean of 18.4 species, SD 20.3), Neotropical (mean 11.4, SD 20.4) and Australasian plus Oceanian region (mean 8.5, SD 12.3).

During the transport stage (assessed using interceptions), the species richness per flow varied significantly depending on the biogeographic region of origin ($\chi^2 = 29.32$, $p < .001$) (Figure 3), and decreased significantly with geographic distance ($\chi^2 = 10.43$, $p = .001$). The number of established species also varied significantly depending on their native biogeographic region ($\chi^2 = 410.10$, $p < .001$).

Larger pools of native species in the source country led to a marginally significant increase in species richness per flow during transport ($\chi^2 = 3.48$, $p = .06$). We lack the precise information on species' native ranges needed to test the effect of species pools on flows of established insects, but neither species richness per flow nor the

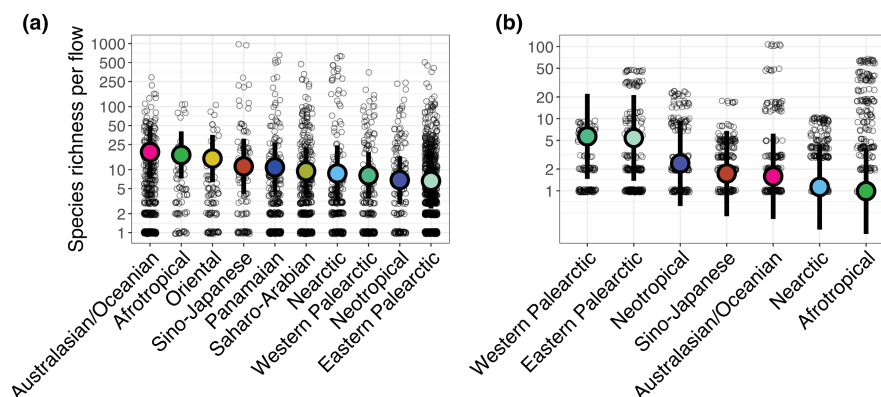


FIGURE 3 The species richness per flow depends on the biogeographic region of origin for (a) intercepted species and (b) established insect species. The grey circles represent individual flows (unique combinations of source/destination * commodity class * decade intercepted), and the coloured circles show model predictions using the `ggpredict()` function from the 'ggeffects' package (Lüdtke, 2018). The error bars are 95% confidence intervals. The x-axis has been log transformed for readability.

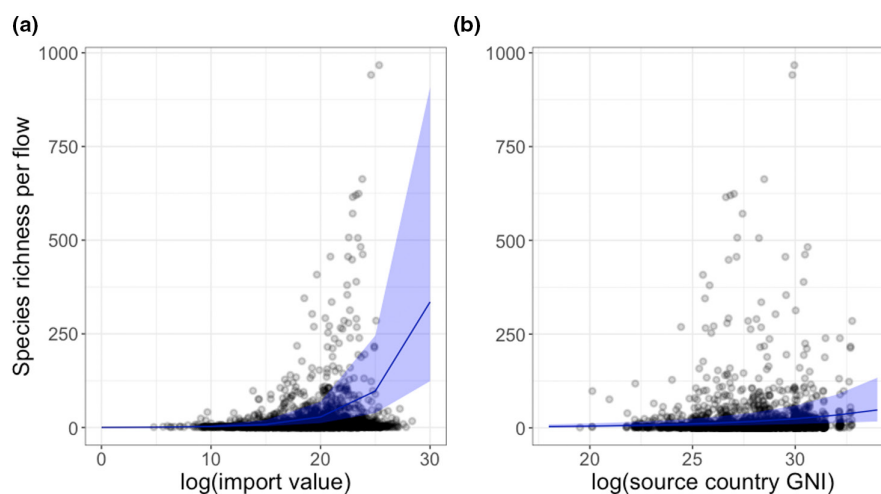


FIGURE 4 Species richness per flow during transport (estimated by interceptions) as a function of (a) the log transformed import value in US dollars (b) the log transformed Gross National Income (GNI) in the source country in US dollars. The grey circles represent individual flows (unique combinations of source and destination area * commodity class * decade intercepted), and the blue line shows model predictions using the `ggpredict()` function from the 'ggeffects' package (Lüdtke, 2018). The shaded blue areas represent 95% confidence intervals.

total number of established species were correlated with species richness in the native region (Table S3). For example, the greatest number of established species originated from the two Palearctic regions, which together only comprise the fifth-largest pool of native insect species.

4.2 | Does the intensity of trade flows between regions determine how many insect species are intercepted and how many successfully establish?

Greater import values were associated with significantly more species intercepted during transport ($\chi^2 = 137.48$, $p < .001$), as was a higher GNI in the source country ($\chi^2 = 19.04$, $p < .001$; Figure 4). As expected, based on previous studies (e.g. Fenn-Moltu et al., 2022; Kenis et al., 2007; Liebhold et al., 2012; Ollier & Bertelsmeier, 2022;

Suhr et al., 2019), the species richness intercepted also depended on the commodity class ($\chi^2 = 2391.74$, $p < .001$). Greater plant product import values were associated with more established species per flow ($\chi^2 = 246.26$, $p < .001$).

4.3 | Do the variables driving successful transport and successful establishment differ?

Due to the lack of fine-scale spatial information on species' native ranges in our data, we could not directly compare many variables between transport and establishment (i.e. climatic distance, geographic distance, GNI of the source country, native species pool size or regulatory efforts in the source country). The species richness transported did not decrease significantly with either the number of regulations in the destination ($\chi^2 = 1.74$, $p = .187$), or the source

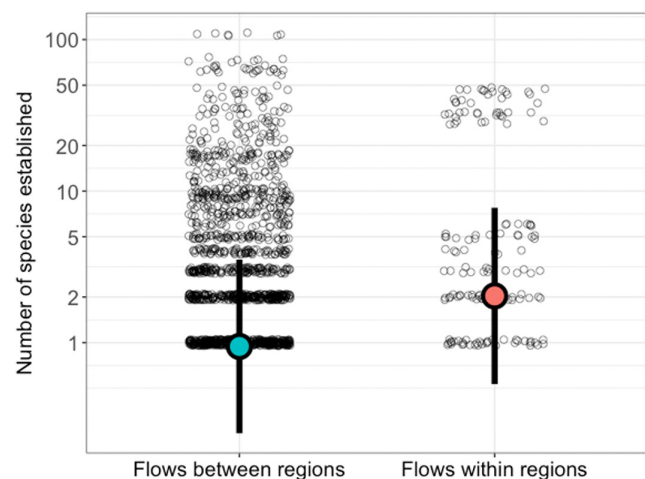


FIGURE 5 Species richness per flow of established insect species, when introduced between biogeographic regions (blue) or within their native biogeographic region (red). The grey circles represent individual flows (unique combinations of native biogeographic region * destination * decade established), and the coloured circles show model predictions using the `ggpredict()` function from the 'ggeffects' package (Lüdtke, 2018). Error bars are 95% confidence intervals. The x-axis has been log transformed for readability.

country ($\chi^2=0.07$, $p=.789$). We could only test the effect of regulations in the destination country for established species flows, but there was no significant effect at this stage either ($\chi^2=.21$, $p=.643$).

Whether species were transported within the same biogeographic region or not had a significant effect on the number of species establishing ($\chi^2=51.32$, $p<.001$) (Figure 5), but not on the number of species being transported ($\chi^2=.12$, $p=.734$). Climatic distance did not have a significant impact on transported species richness either ($\chi^2=0.05$, $p=.822$).

5 | DISCUSSION

We analysed border interception records and lists of established non-native insects to assess the factors driving invasion asymmetry during transport and establishment. Both trade intensity and species' biogeographic origins influenced the size of species flows throughout the invasion process, while the relevance of environmental matching differed pre- and post-introduction.

We found that species from some biogeographic regions were more likely to be transported and established successfully, but the key donor regions varied between the two stages. During transport, the largest species flows generally arrived from the Nearctic, Panamanian and Neotropical regions. Yet flows of established species were on average greatest for flows originating from the Western Palearctic, Neotropical and Australasian and Oceanian regions. Similarly, Isitt et al. (2023) found that Europe (i.e. the Western Palearctic) was the dominant source of established non-native insects between North America, Europe and Australasia. It is possible that the

difference in dominant donor regions between stages is due to the specific data we analysed, but it may also be that species which are particularly successful at entering introduction pathways, and at successfully establishing once introduced, arrive from different regions. We currently lack sufficient information to explore this further, but it would be an interesting focus for future studies on insect introductions. Due to the limited number of areas with data available for both invasion stages, the ranking of donor regions we observed may not be the same for insect exchanges globally. Furthermore, important introduction pathways such as mail and airline baggage may not be sufficiently captured by our model variables, and would require further study using representative data. The observed asymmetry in flows during transport may also be biased by the varying breadth and focus of inspections between destination countries, alongside differences in import volume, production practices, trade partners and biosecurity measures (Saccaggi et al., 2016; Turner, Bockerhoff, et al., 2021). Inspections often focus on introduction pathways that are considered particularly high-risk, and targeted inspections could thus generate more species detections with goods from certain regions (Eschen et al., 2015). We have also only considered records identified to species level, which may not be representative of less easily identifiable taxa. Randomized, statistically sound inspection systems, such as the USDA Agricultural Quarantine Inspection Monitoring system (USDA, 2011), would provide greater power to assess pathway risks and understand patterns in insect introductions.

We found that species richness increased significantly with import value during both stages, and that more species were transported from countries with a higher GNI. This likely reflects the dominant effect of trade on propagule- and colonization pressure (Levine & D'Antonio, 2003). The socio-economic and development status of a country likely influences their environmental standards and capacity to implement biosecurity measures (Brenton-Rule et al., 2016). While the effect of broad socio-economic variables like GDP or GNI on establishment success is debated (Brenton-Rule et al., 2016; Sharma et al., 2010; Westphal et al., 2008), more precise measures, such as the value of relevant commodity imports, appear to be better predictors of invasion risk for unintentionally introduced taxa (Ollier & Bertelsmeier, 2022). Isitt et al. (2023) conclude that plant introductions driven by European colonization is the most compelling explanation for the invasion asymmetry they observed, while native species pool sizes and total import values have little effect. The contrasting influence of trade value in our study may be due to using import values for plant products, a key insect introduction pathway (Fenn-Moltu et al., 2022; Kiritani & Yamamura, 2003; Liebhold et al., 2012; Meurisse et al., 2019), rather than total import values to predict establishments and using trade value per commodity type at the transport stage. As well as increasing opportunities for introduction, greater trade intensity could improve the chances of species establishing through repeated introductions (Lockwood et al., 2005). Isitt et al. (2023) further found no evidence for the hypothesis that a larger pool of native species leads to proportionally more species being exported. However, the history of European colonization in North America, and Australia and New Zealand may have obscured the impact of native species pool size.

We did not detect a significant effect of relevant treaties, regulations and legislation on non-native species richness at either stage, suggesting that regulatory efforts have a limited impact on insect introductions. This is in contrast with previous work, where a wider set of development and governance indicators indicated a greater risk of non-native species arriving from 'poorly regulated' countries (Brenton-Rule et al., 2016). The regulatory efforts we considered were not specific to insect invasions however, and it is possible that analysing more targeted regulations would be a better predictor of insect species movements. Turbelin et al. (2017) state that while much of regulation is focused on introductions, control and management of current invasive species, fewer measures are in place to prevent species being exported. They suggest that while countries are often concerned with non-native species within their borders, less attention is given to preventing species from leaving unless there are known public health impacts. Additionally, there is geographical bias in the information available on regulatory efforts, representing either a lack of data or a genuine lack of policy (Turbelin et al., 2017). If the latter applies, developing biosecurity efforts in these areas could help limit new introductions and reduce the spread and impact of existing non-native species (Early et al., 2016; Sikes et al., 2018).

While biogeography and trade intensity were important for insect flows throughout the invasion process, the influence of environmental matching (exchanges within or between regions, climatic distance) differed pre- and post-introduction. We found that more species were able to establish when introduced within their native biogeographic region, but, along with climatic distance, this did not influence species flows during transport. The impact of environmental similarity on establishment success has been shown in previous studies, for example, in fruit flies (Trombik et al., 2022), reptiles and amphibians (Bomford et al., 2009; Capinha et al., 2017), and mammals (Broennimann et al., 2021). Similarly, for insects, analogous climates have been used to identify potential sources of non-native species (Peacock & Worner, 2006; Worner & Gevrey, 2006), and insect invasions have further been linked to climate change (Renault et al., 2018; Ward & Masters, 2007). Environmental similarity after introduction could potentially affect spread rates as well as establishment success (Abellán et al., 2017). Furthermore, we found that the number of transported species decreased with geographic distance, similar to Suhr et al. (2019). This could potentially be due to lower survival rates over longer journeys, but we would need additional information on survival and detectability to verify this.

Our results support previous research highlighting globalization as a key driver of invasion patterns, and reinforces the importance of including processes occurring prior to establishment in analyses of invasion risk (Bonnamour et al., 2021; Chapman et al., 2017; Essl et al., 2020; Hulme, 2009). Using border interceptions to quantify flows of insects during transport allows us to assess the factors influencing this largely unobserved stage of the invasion process. Moving forward, thorough records of introductions, establishments and native species from a wider range of areas, including developing countries, would provide a more comprehensive picture of the invasion risk presented by trade between different biogeographic

regions. More precise information on the native ranges of established species could further improve our understanding of the link between climatic conditions and establishment success. Ultimately, biosecurity resources are limited both nationally and internationally, and any information that enables more efficiently targeted measures is of considerable value for limiting insect invasions.

ACKNOWLEDGEMENTS

We are grateful to the Australia Department of Agriculture Water and Environment, Canadian Food Inspection Agency, European Plant Protection Organization, Japan Ministry of Agriculture Forestry and Fisheries, New Zealand Ministry of Primary Industries and USDA APHIS PPQ for granting access to inspection data. This study does not necessarily reflect the views of APHIS. We thank Rebecca Turner and Barney Caton for constructive advice and discussions during various stages of this work. This research was funded by the Swiss National Science Foundation (grant 310030_192619), the Canton de Vaud and the Fondation 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. AML received support from grant EVA4.0, No. CZ.02.1.01/0.0/0.0/16_019/0000803 financed by The Czech Operational Programme 'Research, Development and Education'. Support was also provided by the National Socio-Environmental Synthesis Center (SESYNC) under funding received from the National Science Foundation DBI-1639145.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13772>.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available in Dryad at [10.5061/dryad.dv41ns243](https://doi.org/10.5061/dryad.dv41ns243).

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BIOSKETCH

Our research interests lie in understanding large-scale anthropogenic changes to ecosystems and patterns of biodiversity. Our current research focuses on the impacts of globalization on biological invasions, using the human-mediated dispersal of insects to study the mechanisms driving unintentional species introductions.

Author Contributions: GFM curated and analysed the data, with support from SO and CB. GFM and CB conceived the original idea. AML, HFN, DSP and TY curated and provided access to the interception records. OKB calculated climatic distance measures. All authors contributed to the design, discussed the results and contributed to the writing of the manuscript.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Fenn-Moltu, G., Ollier, S., Bates, O. K., Liebhold, A. M., Nahrung, H. F., Pureswaran, D. S., Yamanaka, T., & Bertelsmeier, C. (2023). Global flows of insect transport and establishment: The role of biogeography, trade and regulations. *Diversity and Distributions*, 29, 1478–1491. <https://doi.org/10.1111/ddi.13772>