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Drivers of global Scolytinae invasion patterns

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Abstract. Biological invasions are affected by characteristics of invading species, strength of pathway connectivity among world regions and habitat characteristics of invaded regions. These factors may interact in complex ways to drive geographical variation in numbers of invasions among world regions. Understanding the role of these drivers provides information that is crucial to the development of effective biosecurity policies. Here we assemble for the first time a global database of historical invasions of Scolytinae species and explore factors explaining geographical variation in numbers of species invading different regions. This insect group includes several pest species with massive economic and ecological impacts and these beetles are known to be accidentally moved with wood packaging in global trade. Candidate explanatory characteristics included in this analysis are cumulative trade among world regions, size of source species pools, forest area, and climatic similarity of the invaded region with source regions. Species capable of sib-mating comprised the highest proportion on nonnative Scolytines, and these species colonized a higher number of regions than outbreeders. The size of source species pools offered little power in explaining variation in numbers of invasions among world regions nor did climate or forest area. In contrast, cumulative trade had a strong and consistent positive relationship with numbers of Scolytinae species moving from one region to another, and this effect was highest for bark beetles, followed by ambrosia beetles, and was low for seed and twig feeders. We conclude that global variation in Scolytine invasions is primarily driven by variation in trade levels among world regions. Results stress the importance of global trade as the primary driver of historical Scolytinae invasions and we anticipate other hitchhiking species would exhibit similar patterns. One implication of these results is that invasions between certain world regions may be historically low because of past low levels of trade but future economic shifts could result in large numbers of new invasions as a result of increased trade among previously isolated portions of the world. With changing global flow of goods among world regions, it is crucial that biosecurity efforts keep pace to minimize future invasions and their impacts.

Key words: ambrosia beetles; bark beetles; biological invasions; forest insects; imports; pathways; Scolytinae.

INTRODUCTION

For most groups of organisms, the primary driver of the problem of biological invasions is globalization (Hulme 2009, Seebens et al. 2018). Specifically, the movement of humans and objects in trade has historically caused inadvertent transport of organisms outside of their native ranges, placing them in ecosystems where they have no previous evolutionary history. Because many of these invading organisms have substantial ecological impacts following their establishment in nonnative habitats, there is an urgent need to understand the specific drivers of invasions that cause variation both in numbers of alien species establishing in areas but also variation in numbers of species originating from different areas (Liebhold et al. 2016, Seebens et al. 2018). Ultimately, this knowledge can be of critical value in forming effective biosecurity policies aimed at minimizing numbers of future invasions (Hulme et al. 2008).

Analysis of geographical patterns of historical invasions is a useful method for inferring the relative importance of different factors influencing invasions. Geographic variation in numbers of established nonnative species may reflect both historical variation in propagule pressure as well as variation in habitat characteristics that make certain areas more prone to invasions, i.e., "invasibility" (Pyšek et al. 2010, Liebhold et al. 2013, van Kleunen et al. 2015, Liebhold et al. 2016, 2018, Dawson et al. 2017). Furthermore, recent work has also determined that geographical variation in source species pool sizes may play an important role in determining numbers of species invading other regions (Liebhold et al. 2017, Seebens et al. 2018).

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The Scolytinae (Coleoptera: Curculionidae) are a large and diverse group of insects, that exhibit many different habits and utilize various types of host tissues of trees and other plants. Several species in this group are capable of causing severe impacts on forests due to their ability to mass-attack and kill host trees (Raffa et al. 2008, Biedermann et al. 2019). The two major groups of Scolytinae are true bark beetles, which feed on the inner bark, and ambrosia beetles, which cultivate and feed on symbiotic ambrosia fungi that grow in the xylem. Additionally, there are several species that feed in seeds, cones, and roots of woody plants, and species that feed on stems and roots of non-woody plants (Kirkendall et al. 2015). Mating systems also vary among scolytines, ranging from simple monogamy, to heterosanguineous polygyny, and to consanguineous polygyny (inbreeding; Kirkendall et al. 2015). This variety of mating systems and host feeding habits, together with their cryptic nature that allows them to be accidentally transported in raw logs and wood packaging material (Brockerhoff et al. 2006, Meurisse et al. 2019) makes them very successful in invading new habitats (Wood and Bright 1992, Kirkendall and Faccoli 2010, Brockerhoff et al. 2013, Haack et al. 2013). Many Scolytinae species have already established in regions outside of their native ranges and several of these have become serious pests (Marini et al. 2011, Haack et al. 2013, Lantschner et al. 2017).

Several authors have explored patterns of Scolytinae invasion and possible drivers at sub-continental or continental scales. In the United States and Europe, it was found that volume of imports was a strong predictor of the number of exotic Scolytinae species. It has also been highlighted that drivers can differentially affect bark and ambrosia beetle invasions. For example, climatic factors (temperature and precipitation) were found to be important in determining the number and pattern of colonization of exotic ambrosia beetles in the United States but bark beetles were found to be able to colonize larger areas within the United States because of their lower dependency on strict climatic conditions (Marini et al. 2011, Rassati et al. 2016). Host breath and reproductive system are important biological attributes affecting establishment probabilities; in both the United States and Europe most established nonnative Scolytinae species are polyphagous and are capable of sib-mating (inbreeders) (Kirkendall and Faccoli 2010, Haack et al. 2013).

However, no studies have assessed invasion patterns of Scolytinae at a global scale, considering all biogeographic regions. In this study, we analyze global patterns of historical Scolytinae invasions. We used worldwide records of historical establishment of nonnative Scolytinae outside of their native ranges to test for the effects of factors explaining these patterns, considering their feeding habits and mating systems. Various explanatory characteristics that we considered included species pool sizes, propagule pressure (using trade volume as a proxy) and habitat characteristics related to invasibility (climate and forest area).

Materials and Methods

Study area

This study was conducted at a global scale with all land areas (excluding Antarctica) divided into six biogeographic regions: Nearctic, Neotropic, Palearctic, Indo-Malay, Afrotropic, and Austro-Pacific (Fig. 1). These divisions are slightly modified from Wallace's classification, to match national political boundaries. Australasia and Oceania were merged into a single Austro-Pacific region because there were relatively few Scolytinae species in Oceania.

Non-native Scolytinae data collection

We compiled records of Scolytinae species established outside of their native region from a variety of sources including both published scientific articles and public online databases of first discoveries prior to 2020 (see Appendix S1: Table S1 for a full list of sources). It should be noted that we considered only nonnative species originating from distant regions or other continents, i.e., we excluded species invading or expanding their ranges within portions of the same biogeographic region in which they are native. We searched primarily in regional monographs and catalogs (Wood 1982, 2007, Wood and Bright 1992), as well as in online databases (Atkinson 2019, CABI 2019) and published nonnative species compilation lists (Kirkendall and Faccoli 2010, Haack et al. 2013, Kirkendall 2018). We also conducted a search for published papers reporting the establishment of nonnative Scolytinae species at a global scale in Google Scholar, using the following key words "Scolytinae + nonnative" and "Scolytinae + invasive." We included in our analyses only records of species that have established self-sustaining populations in a nonnative region (i.e., species that have been found for consecutive years and at different locations in the invaded region). For each nonnative species, we compiled information (from the same sources) on both native and invaded ranges, classified into the six regions using the literature and databases. It should be noted that there are several species with widespread global distributions and for which there is no certainty on the identity of their native ranges. In these cases, we used the native region considered most likely based on the criteria of specialists (mainly Wood and Bright 1992, Wood 2007, Haack et al. 2013, as well as other updated specific publications. See Appendix S1: Table S1 for more detail). Widely distributed species for which the native range is very uncertain were excluded from analyses involving regions of origin and destination, but were included in the analysis

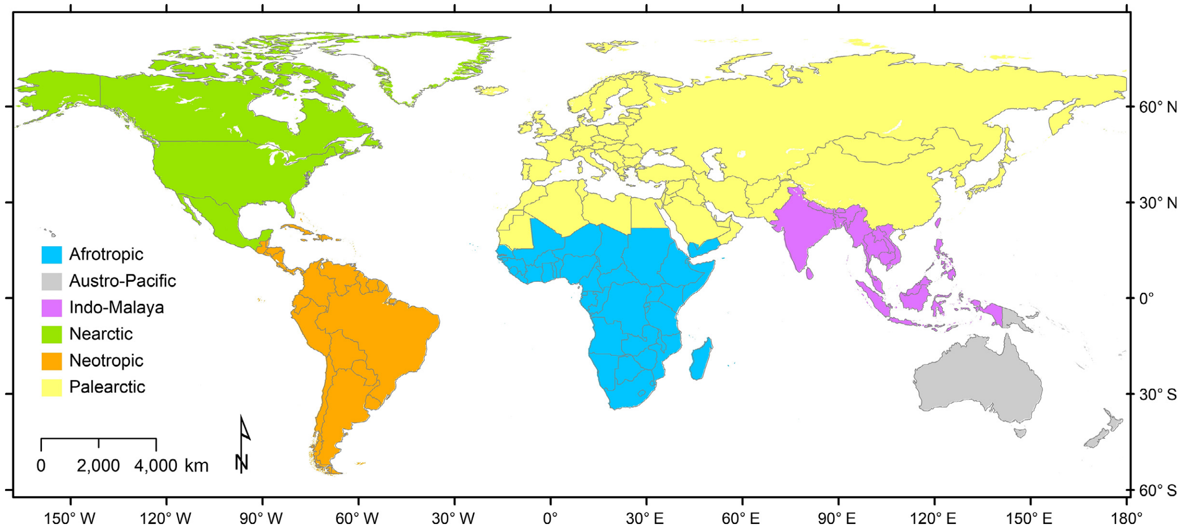

FIG. 1. Geographical ranges of the world's biogeographical regions.

of total colonized regions (see same section for more detail on this).

We also classified each species based on their feeding habit and mating system, since these biological attributes are expected to influence the introduction and establishment success of species. We considered four feeding groups: (1) bark beetles (BB), species that feed primarily on inner bark or phloem (i.e., phloeophagy) of trunks and branches; (2) ambrosia beetles (AB), species that feed primarily on fungi growing in galleries excavated in xylem tissue (i.e., xylomycetophagy); (3) seed and twig feeders (ST), species that feed in seeds or outer layers of fruit, (i.e., spermatophagy), or the pith (i.e., myelophagy) or phloem of twigs; (4) root feeders (R), species feeding in roots of herbaceous plants (i.e., herbiphagy) (Haack et al. 2013, Kirkendall et al. 2015, Vega et al. 2015). Furthermore, we considered two mating systems: (1) inbreeders, species for which sib-mating has been documented, and (2) outbreeders, species for which mating only occurs between unrelated individuals (Kirkendall et al. 2015).

Explanatory variables

We identified a set of variables that could potentially explain the observed patterns of global Scolytinae invasions.

Number of native Scolytinae species in the recipient region.—We obtained information on the number of native Scolytinae species for each of the three feeding guilds in each biogeographical region from Hulcr et al. (2015). Numbers of native species presumably reflect, in part, the diversity of ecological niches present in each region.

Cumulative imports.—We compiled information on the total value of imports between regions. We considered the total value of imports as proxy for propagule pressure, because scolytines are associated with wood and wooden products, such as pallets, crates, dunnage, and logs, which are present in a large part of cargo (McCullough et al. 2006, Haack et al. 2014). Annual value of import data was obtained from the Correlates of War project (Barbieri et al. 2009, Barbieri and Keshk 2016). These data consisted of annual bilateral trade (import/export) values between every country pair from 1870 to 2014 expressed in U.S. dollars. Because of changes in national identities, independence of former colonies and other reasons, there existed gaps in the bilateral trade data. Consequently, we filled the gaps in data derived from the Correlates of War database and extended it back to 1850 using a second trade data set obtained from Federico-Tena World Trade Historical Database (Federico and Tena-Junguito 2019). This global trade database includes exports and imports, in both current and constant prices (US$) from 1800 to 1938 and includes not only countries but also colonies (that are now independent countries). Imports were expressed in billions of U.S. dollars per year, adjusted to 2018 values utilizing the Consumer Price Index (Federal Reserve Bank of Minneapolis 2018). We grouped all countries by region and summed cumulative annual imports to all countries in each region to express total trade flow between each pair of regions. It should be noted that total values of imports include all types of commodities, most of which are associated with wood packaging, but not all (i.e., oil, petroleum gases). Unfortunately, more precise data, with imports broken down by commodity, are not available for the temporal and geographic span of this analysis.

Forest area.—We estimated land area covered with forests in each region, based on the Terrestrial Ecoregions of the World map (Olson et al. 2001) (downloaded as a GIS layer; *available online*).[6]

Climatic similarity.—We estimated a climatic similarity index between each pair of regions. Within the forest area GIS layer for each region, we estimated the area occupied by each major climatic group using the Köppen-Geiger system (Kottek et al. 2006). This classification system divides climates into five main groups: tropical, dry, temperate, continental, and polar. The measure of similarity (ranging from 0 to 1) for each pair of regions was calculated as

$$\mathrm{CS}_{i,j} = \frac{\sum_{\mathrm{KG}=1}^{5} p_{\mathrm{KG},i}\, p_{\mathrm{KG},j}}{\left(\sum_{\mathrm{KG}=1}^{5} p_{\mathrm{KG},i}^{2} + \sum_{\mathrm{KG}=1}^{5} p_{\mathrm{KG},j}^{2}\right)/2},$$

where $\mathrm{CS}_{i,j}$ is the climatic similarity between region i and j; and $p_{\mathrm{KG},i}$ is the fraction of forest in region i with Koppen-Geiger climate class KG.

Number of host plant families.—We compiled information on the number of host plant families for each Scolytinae species as a proxy of their diet breath. We classified the species in two categories, those that feed on species from one or two plant families, and those who feed on species of three or more plant families. This information was obtained from Wood and Bright (1992) and complemented with specific publications for the species for which information was not available (see Appendix S1 for a full list of sources).

Data analysis

We calculated average numbers of regions invaded by each species broken down by feeding habit and mating system. To evaluate whether the number of regions colonized by each species was related to their level of host specificity, feeding habit or mating system we performed a χ^2 test. We calculated total numbers of species invading two categories of numbers of colonized regions (including the native range): two to three and four to six. We classified species by their number of hosts in two categories: oligophagous (species that use hosts from one or two plant families) and polyphagous (species that use hosts from three or more plant families). In the case of feeding habit, we used three categories: AB, BB, and ST (we excluded root feeders from the analysis because of the low number of observations: two). For mating system, we considered two categories: inbreeders and outbreeders.

Simple cross-correlations were calculated between each explanatory variable and the number of nonnative Scolytinae invading from each pair of source and receiving regions. The variables were square root transformed to meet model assumptions of normality and homoscedasticity of errors. We also fitted linear multiple regression models to identify variables that explained observed global patterns of historical Scolytinae invasions. Specifically, we sought to explain variation in the number of species native to region i that invaded region j, expressed as $I_{i,j}$. Better model fits were obtained when we expressed number of invasions as the percentage of the total number of native species present in the source region $I_{i,j}/N_{i,j} \times 100$. We fitted regression models using all species, and independent models separating species by feeding habit (i.e., AB, BB, and ST; we did not fit a separate model for root-feeding species because of their low numbers) and by mating system (i.e., inbreeding and outbreeding). We evaluated potential explanatory variables, the number of native Scolytinae species in the native (source) region (in a given feeding guild), the number of native Scolytinae species in the invaded region (in a given feeding guild), historical cumulative imports, forest area, and climatic similarity between pairs of regions. We used all combinations of all six regions (30) as replicate observations. To avoid multicollinearity, we evaluated correlation coefficients between all possible pairs of predictor variables, setting a limit of $r < 0.7$ for retaining correlated variable pairs. As none of our predictors had $r > 0.7$, we retained all the variables. We started with a full model containing all variables and used a backward stepwise approach to identify a best fitting model for predicting the global pattern of Scolytinae invasions. Variables with the largest P value were dropped singularly in each step. Linearity between the independent and dependent variables was visually evaluated from a matrix of scatter plots and plots of residuals against the predicted values, and normality of the residuals was evaluated using the Kolmogorov-Smirnov test. The best models were identified based on Akaike Information Criterion corrected for small sample sizes ($\mathrm{AIC_c}$) and relative $\mathrm{AIC_c}$ ($\Delta\mathrm{AIC_c}$).

RESULTS

General results

We identified 123 Scolytinae species that have established outside of their native region: 42 bark beetles, 51 ambrosia beetles, 29 seed- and twig-feeding species, and 1 root-feeding species. Seventy-three (59%) of these nonnative scolytines are inbreeders, while 50 (41%) are outbreeding species (Appendix S1). The Nearctic is the region with the highest number of nonnative Scolytinae species (69), while Indo-Malaya has the lowest number (12, Figs. 2B, 3). Ambrosia beetles were the largest proportion of species established in the Afrotropical, Austro-Pacific, Nearctic, and Palearctic regions, while nonnative seed and twig species dominated the Neotropical and Indo-Malaya regions (Fig. 2B). In contrast, the

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[6] https://www.arcgis.com/home/item.html?id=be0f9e21de7a4a61856dad78d1c79eae

Palearctic region has the highest proportion of native Scolytinae species that invaded elsewhere (7.85%), while the Neotropic region, the most diverse in terms of number of native species, has the lowest proportion of species invading elsewhere (1.02%, Figs. 2A, C).

Considering all possible pairs of regions described by origins (native regions) and destinations (invaded regions) of invading species, we found that by far, the highest fraction of species from a region that invaded, $I_{i,j}/N_{i,j}$, was for species native to the Palearctic that invaded the Nearctic (5.4%), followed by species from Palearctic to Neotropic (3.1%), and from Indo-Malaya invading the Nearctic (2.7%, Fig. 3A). On the other hand, the highest cumulative trade between regions consisted of exports from the Nearctic imported to the Palearctic, and from the Palearctic to the Nearctic region, together comprising 41% of total global international trade (Fig. 3B). Regarding climatic similarity between regions, the Neotropic, Afrotropic, and Indo-Malaya were more similar with each other than with the other regions, while the Nearctic and Palearctic were similar to each other, and differed from the rest of the regions. The Austro-Pacific region, on the other hand, showed an intermediate climatic similarity with all regions (Fig. 3C).

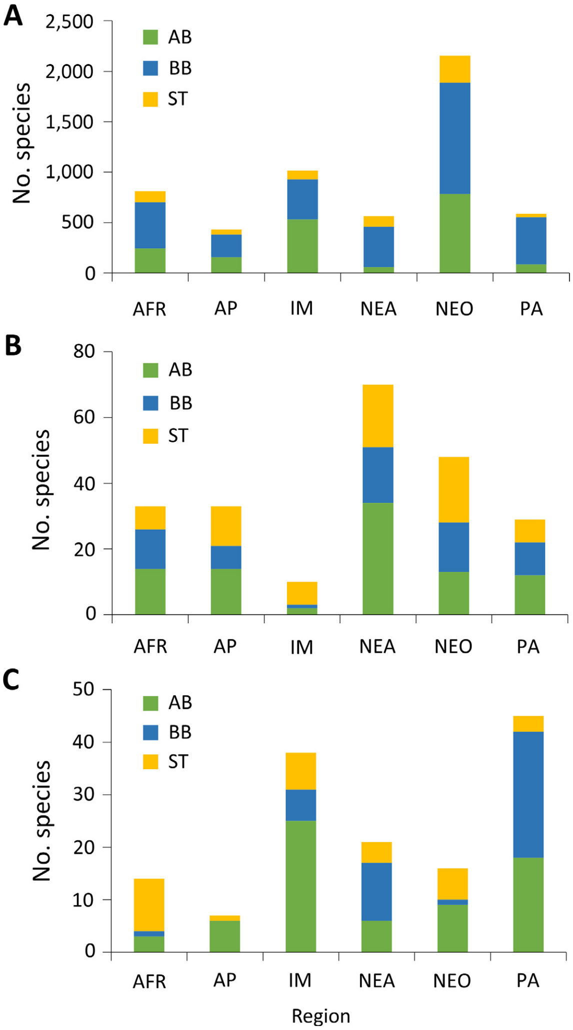

FIG. 2. Number of Scolytinae species of each feeding guild (A) native to each region, (B) nonnative and established in each region, and (C) native to each region that established elsewhere. AB, ambrosia beetles; AFR, Afrotropic; AP, Austro-Pacific; BB, bark beetles; IM, Indo-Malaya; NEA, Nearctic; NEO, Neotropic; PA, Palearctic; ST, seed and twig feeders.

We also identified seven additional species that have widespread distributions, but for which the native/nonnative range is unknown (i.e., *Dryocoetes krivolutzkajae*, *Hypothenemus eruditus*, *Hypothenemus fuscicollis*, *Eccoptopterus spinosus*, *Euwallacea xanthopus*, *Xyleborus bidentatus*, *Xylosandrus mancus*). Overall, 48.5% (63 species) of the analyzed Scolytinae species are established in two regions (including the region of their native range) and 7.7% (10 species) are established in all six regions. These species with global distributions are *Coccotrypes carpophagus*, *Coccotrypes dactyliperda*, *Euwallacea similis*, *Hypothenemus areccae*, *Hypothenemus eruditus*, *Hypothenemus seriatus*, *Xyleborinus saxesenii*, *Xyleborus affinis*, *Xylosandrus compactus*, and *Xylosandrus morigerus*. All of these species are ambrosia beetles or seed and twig feeders, and are host generalists (each had six or more host families) and were inbreeders (Fig. 4). The frequencies of species established in two to three regions vs. four to six regions was significantly different among feeding habits and mating systems ($\chi^2 = 11.79$, $P < 0.003$ and $\chi^2 = 11.22$, $P < 0.001$, respectively). Most bark beetles species only established in two or three regions, including the region of their native range (88% in two or three regions, 12% in four to six regions), for ambrosia beetles 71% of the species established in two or three regions and the remaining 29% in four to six regions, while for seed- and twig-feeding beetles, the percentage of species established in two or three regions was almost the same than those established in four to six regions (52% and 48%, respectively; Fig. 4). On the other hand, most outbreeding species established in only two or three regions (90% in two or three regions, 10% in four to six regions), while inbreeders had a much larger proportion of species established in a larger number of regions (61% in two or three regions, 39% in four to six regions; Fig. 4).

Bivariate correlations

Cumulative trade was the explanatory variable most highly correlated with numbers of invasions occurring between pairs of regions, $I_{i,j}$; however, this correlation was only marginally significant (Appendix S1: Table S2). When invasion frequency was expressed as a fraction of species native to the source regions, $I_{i,j}/N_{i,j}$, trade was again the most highly correlated explanatory variable and this correlation was significant. None of the other explanatory variables were significantly correlated.

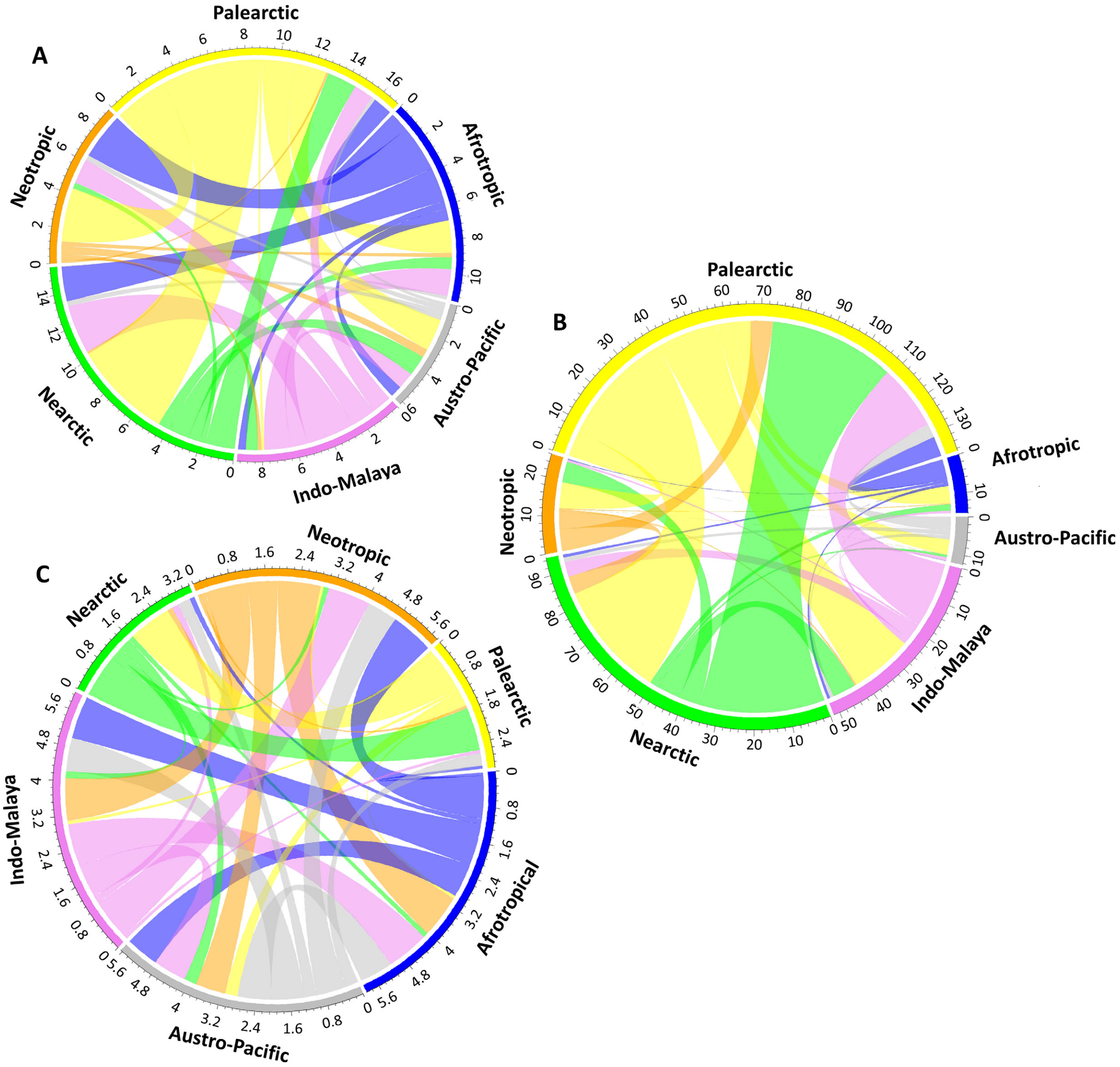

FIG. 3. Chord graphs showing (A) the percentage of native species from each region that invaded other regions, and (B) cumulative imports between regions for the period 1870–2014, expressed in constant trillions of USD; (C) climatic similarity between regions, based on the Köppen-Geiger climate classification system.

Regression model

Expressing invasion frequency as the number of nonnative Scolytine beetles occurring between pairs of regions, $I_{i,j}$, regression models for all Scolytinae, ambrosia beetles, bark beetles, seed and twig feeders, outbreeders, and inbreeders explained between 8% and 40% of the variation among combinations of regions (Appendix S1: Tables S3, S4) and, in most cases, the percentage of explained variability in the number of nonnative species invading between pairs of regions was less than when invasion frequency was expressed as a fraction of species native to the source regions, $I_{i,j}/N_{i,j}$. Consequently, we present below the results of the models using this second dependent variable. We found consistent patterns in terms of the relative importance of the variables included in the best models for each of the six groups (Tables 1, 2). The best fitting models explaining the percentage of all Scolytinae species, ambrosia beetles, bark beetles, as well as inbreeding and outbreeding species from each region that invaded other regions included only one variable, cumulative import value, which was positively related to the percentage of species invading. Each model explained different percentages of the variation; for all species together, the model explained 19% of the variation, for ambrosia beetles 19%, for bark beetles 37%, for outbreeding species 40%, while for inbreeding species the percentage of explained

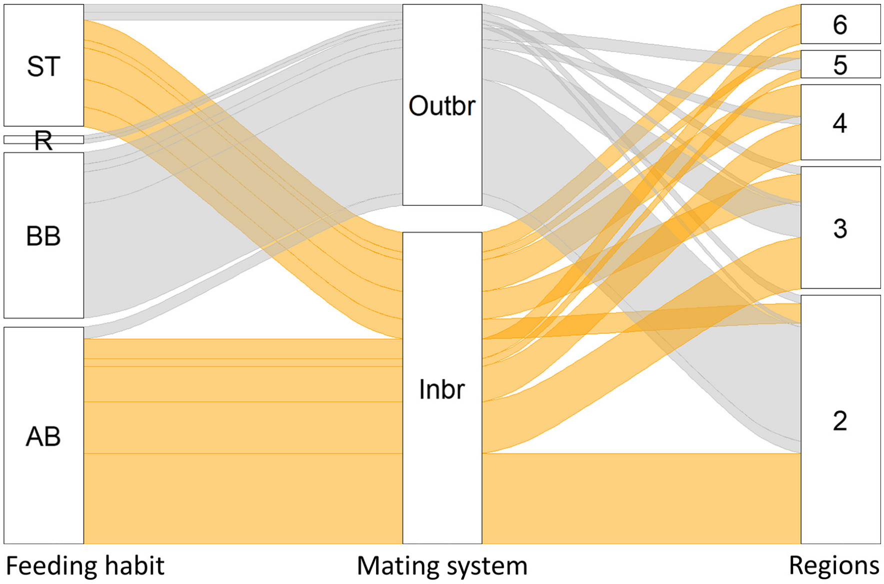

FIG. 4. Alluvial diagram showing the frequencies of Scolytinae species of each feeding guild and mating system established in two to six regions (including the region of their native range). AB, ambrosia beetles; BB, bark beetles; Inbr, inbreeding; Outbr, outbreeding; ST, seed and twig feeders.

variation was very low (5%). On the other hand, the best fitting model explaining the percentage of seed and twig feeders from each region that invaded other regions included two variables, trade and the number of native species in the region of destination, and both variables were positively related to the dependent variable. This model explained 45% of the variation (Tables 1, 2). When considering other plausible models (ΔAIC < 2) obtained for each group of species, we found that models for all Scolytinae species, bark beetles only, and outbreeding species only included a positive effect of the number of native species at destination (Table 1). For ambrosia beetles, plausible models also included a positive effect of climatic similarity (Table 1), while for seed and twig feeders and inbreeders, the plausible models also included negative effects of forest area (Table 1).

DISCUSSION

The Coleoptera is globally the most species-rich insect order and Curculionidae is the largest Coleoptera family, so it comes as no surprise that there are a large number of Scolytinae species that have established outside of their native range. The success of the Scolytinae as invaders can be attributed, in part, to the existence of an effective invasion pathway, namely movement in wood and wood packaging material, objects that are ubiquitous in global trade (Haack 2001, Brockerhoff et al. 2006).

There are estimated to be almost 6,000 Scolytinae species worldwide (Hulcr et al. 2015) but only a small fraction (2.17%) has been detected to be established outside of their native region. Most of these invading species (59%) are inbreeders, a much higher proportion than inbreeders comprises in the world Scolytinae fauna (about 27%, Kirkendall et al. 2015). The majority of nonnative scolytine species have only established in one nonnative region outside of their native range (Fig. 4). Moreover, 10 species have established in all six regions, and all of these species are polyphagous (utilize more than five plant families as hosts) ambrosia, twig- or seed-feeders and inbreeders. Based on chance, host generalists are more likely to encounter suitable hosts and successfully establish than a host specialist and this likely explains the apparent greater invasion success of generalist species. On the other hand, inbreeders are probably more successful in invading new regions because they might have lower Allee effect thresholds than outbreeders, since mating takes place among siblings before dispersal, avoiding difficulties of mate location, and inbreeders probably suffer much less from inbreeding depression than outbreeders (Jordal et al. 2001, Peer and Taborsky 2005). Both inbreeding and polyphagy have been described as traits that favor Scolytinae invasibility in Europe and the United States (Kirkendall and Faccoli 2010, Haack et al. 2013). It should be noted that host breadth and mating system are generally different among feeding guilds, most bark beetles (i.e., phloeophagous species) are specialists, breeding in one family of host plants, and are outbreeders; while most ambrosia beetles and seed and twig feeders are polyphagous and regular inbreeders (Fig. 4; Beaver 1979, Kirkendall et al. 2015).

Numbers of nonnative scolytines vary considerably among the six world regions (Fig. 2C). The Indo-Malaya region has the lowest number of established

TABLE 1. Summary of variables included in multiple regression models explaining the percentage of species from each region that established in others considering (1) all species, (2) ambrosia beetles, (3) bark beetles, (4) seed and twig feeders, (5) outbreeders, (6) inbreeders.

Dependent variable and model	Variables	R^2	*k*	AICc	Δ AICc
Percentage of total					
4	Trade	0.191	2	−44.78	0.00
3	Trade + Nat spp D	0.210	3	−43.03	1.75
2	Trade + Nat spp D + Clim Sim	0.227	4	−40.99	3.79
1	Trade + Clim Sim + Nat spp D + Forest	0.228	5	−38.13	6.65
Percentage of AB					
4	Trade	0.192	2	−3.26	0.00
3	Trade + Clim Sim	0.224	3	−2.00	1.26
2	Trade + Nat AB spp D + Clim Sim	0.251	4	−0.41	2.85
1	Trade + Nat AB spp D + Clim Sim + Forest	0.252	5	2.49	5.75
Percentage of BB					
4	Trade	0.374	2	−48.98	0.00
3	Trade + Nat BB spp D	0.400	3	−47.79	1.19
2	Trade + Nat BB spp D + Forest	0.432	4	−46.77	2.21
1	Trade + Nat BB spp D + Forest + Clim Sim	0.435	5	−44.02	4.96
Percentage of ST					
3	Nat ST spp D + Trade	0.452	3	0.44	0.00
2	Nat ST spp D + Trade + Forest	0.516	4	0.68	0.24
4	Nat ST spp D	0.330	2	1.34	0.89
1	Nat ST spp D + Trade + Forest + Clim Sim	0.525	5	3.20	2.75
Percentage of Outbr					
4	Trade	0.400	2	−52.01	0.00
3	Trade + Nat spp D	0.431	3	−51.09	0.92
2	Trade + Nat spp D + Forest	0.441	4	−48.95	3.06
1	Trade + Nat spp D + Forest + Clim Sim	0.442	5	−46.11	5.90
Percentage of Inbr					
4	Trade	0.052	2	21.67	0.00
3	Trade + Forest	0.113	3	22.14	0.47
2	Trade + Forest + Clim Sim	0.120	4	24.57	2.90
1	Trade + Forest + Clim Sim + Nat spp D	0.121	5	27.45	5.78

Notes: Models are ranked according to their Akaike information criterion corrected for small sample sizes (AIC_c). Clim Simil, climatic similarity index; Forest, forest area; Nat AB spp D, number of native ambrosia beetle species in the region of destination; Nat BB spp D, number of native bark beetle species in the region of destination; Nat spp D, total number of native Scolytinae species in the region of destination; Nat ST spp D, number of native seed- and twig-feeding species in the region of destination; Trade, total cumulative imports; AB, ambrosia beetles; BB, bark beetles; Inbr, inbreeding; Outbr, outbreeding; ST, seed and twig feeders.

nonnative species. This may reflect the relatively low total forest area in that region as well as trading patterns; while the Indo-Malaya region historically imported a reasonably large amount from the Palearctic, it has not imported much from elsewhere (Fig. 4B). On the other hand, since the Indo-Malaya region has a large species pool of native Scolytinae (Fig. 2B), it is no surprise that it is the second largest source of invading species (Fig. 2A). In contrast, the Nearctic is the most invaded region (Fig. 2C) but it has only a moderate size native species pool (Fig. 2B) and has not been the source of a large number of species invading elsewhere (Fig. 2A). This may be explained in part by the very strong trade connectivity between the Nearctic and Palearctic (though it has relatively weak connectivity to the rest of the world) and secondly because of the high climatic similarity between these regions compared to others (Fig 3B). Even though the Nearctic and Palearctic are strongly connected via trade and show similar climates (Fig. 3B), there is a strong difference in invasion patterns. The Palearctic is the largest source of invading species but relatively few species have established there; the Nearctic exhibits the opposite pattern. Mattson et al. (2007) noted this same phenomenon when analyzing global patterns of invasions of all forest insects (including Scolytinae) and hypothesized that these differences might be explained by the comparatively low species richness of European trees as a result of the last glaciation. These authors stated that the reduced richness of woody species in the Palearctic regions makes it generally more difficult for randomly invading phytophagous species to establish successful populations because there are fewer potential hosts (Mattson et al. 2007). This appears to be a plausible explanation, and generally supported by recent studies positively linking insect invasion success with plant diversity (Liebhold et al. 2013, Guo et al. 2019).

TABLE 2. Parameters of the best fitting models (lowest AIC$_c$) explaining the percentage of species from each region that established in others (inv spp) considering all species, ambrosia beetles, bark beetles, seed and twig feeders, outbreeders, and inbreeders.

Dependent variable and predictor	Coefficient	$\lvert t \rvert$	*P*
Total inv spp			
Intercept	0.655	5.013	0.000
Trade	0.142	2.572	0.016
AB inv spp			
Intercept	0.690	2.646	0.013
Trade	0.284	2.577	0.016
BB inv spp			
Intercept	0.067	0.550	0.587
Trade	0.210	4.086	0.000
ST inv spp			
Intercept	-0.155	-0.242	0.810
Trade	0.212	1.792	0.084
Nat ST spp D	0.123	2.314	0.029
Outbr spp			
Intercept	0.047	0.402	0.691
Trade	0.211	4.323	0.000
Inbr spp			
Intercept	1.443	3.650	0.001
Trade	0.206	1.237	0.226

Note: Trade, square root of total cumulative import value.

The pattern of nonnative species of each feeding guild (i.e., bark beetles, ambrosia beetles, and twig and seed feeders) established in the different regions was similar (Fig. 4B), but the origin of these species varied. In the Palearctic and Nearctic regions, most of the native species that established elsewhere were bark beetles, while in the other regions ambrosia beetles and twig and seed feeders where more common (Fig. 4C). This probably reflects the fact that most Scolytinae species in tropical regions (dominant in Indo-Malaya, Neotropic, and Afrotropic regions) are ambrosia beetles, while most Scolytinae species in temperate forests (dominant in Palearctic and Nearctic regions) are true bark beetles (Hulcr et al. 2015, Kirkendall et al. 2015).

It should be noted that the degree of exploration for Scolytinae in different parts of the world is likely to be uneven. While the scolytines of the Nearctic, most of the Palearctic, as well as Australia, and New Zealand are well known, the native and nonnative species of most of the Neotropic, the Afrotropic, and the Indo-Malay regions have been less intensely studied (Hulcr et al. 2015) and, consequently, there could be a bias in the observed patterns. Another limitation of our analysis is that we only attempted to account for trade connecting invaded regions with the native ranges of species. But recent analyses indicate that for many species, invasions of new regions often originate from previously invaded regions, a phenomenon described as the "bridgehead effect" (Bertelsmeier and Keller 2018). Unfortunately, for most species, the precise global topology of historical global invasion histories is unknown and reconstructions of these topologies based upon genetic analyses are available for only a few species.

Comparison of various models explaining frequencies of invading Scolytinae species, separately considering the different feeding habits and mating systems, indicated that the value of cumulative imports was consistently the strongest explanatory variable (Tables 1 and 2). This likely reflects that wood packaging provides an excellent pathway for historical Scolytinae invasions and wood is ubiquitous in international trade (Haack 2001, Brockerhoff et al. 2006). While trade is not the primary pathway for all invading species, it is a primary pathway and explains geographical variation in numbers of nonnative species of a variety of taxa (Pyšek et al. 2010, Liebhold et al. 2013, 2016, 2018, van Kleunen et al. 2015, Chapman et al. 2017, Dawson et al. 2017, Meurisse et al. 2019). Our results are consistent with those found at a smaller scale in Europe and the United States, where the value of imports explained variation in numbers of nonnative bark and ambrosia beetles (Marini et al. 2011, Rassati et al. 2016). Interestingly, when analyzing the independent effect of trade on the percentage of species of each feeding and mating guild from a region that invaded other, the models that explained higher percentages of variation were those for outbreeders (40%) and bark beetles (37%), followed by ambrosia beetles (19%), while the explanatory power of the models for inbreeders and seed and twig feeders was very low (5.2% and 4.6%, respectively). This probably reflects the fact that propagule pressure is more relevant for the establishment of bark beetles, which represent the largest part of outbreeding species, since these species are probably exposed to higher Allee effect thresholds during invasions than inbreeders. Additionally, it is likely that some of the ambrosia beetles and most seed and twig feeders were introduced in association with other products like seeds, fruit, cuttings and live plants (Haack et al. 2013), which are not as well represented by the total value of imports. Therefore, we recognize that total trade volume is only an approximate estimate for scolytine propagule pressure, since not all species have the same probability of being transported in wood products and packaging material associated with general trade. Consequently, other more precise variables, such as scolytine interception frequency from border inspections would be a better proxy for propagule pressure, but such data are available from only a few countries and may not represent a random sample of arriving species (Brockerhoff et al. 2006, Haack et al. 2013).

Additional predictor variables were relevant in explaining invasion frequencies when we performed separate analyses for each feeding guilds. Climatic similarity between donor and receiver regions was slightly relevant only for ambrosia beetles (the second best fitting model included this variable, Tables 1 and 2), indicating that ambrosia beetles have a higher probability of invading regions with climates similar to their native ranges

(Table 2). Rassati et al. (2016) also found that nonnative ambrosia beetles tended to be more diverse in wetter and warmer regions within the United States, in contrast to nonnative bark beetles, which were able to colonize larger areas. These authors hypothesized that this might be because ambrosia beetles have a strict dependence on the growth of symbiotic fungi and consequently on rainfall, while bark beetles appear to have a lower dependency on climatic factors (Rassati et al. 2016). Our analyses also indicate that native species richness in the invaded region has a positive effect on the percentage of bark beetles as well as outbreeding species invading (Table 2). This suggests that competition with native species (i.e., biotic resistance) does not adversely affect invasion success at this large scales, but instead, numbers of native species reflects the diversity of ecological niches available for invading bark beetle species, or the availability of certain hosts (i.e., tree phylogenetic groups) that are most commonly preferred by a large number of Scolytinae species (e.g., *Pinus* species or family Moraceae; Wood and Bright 1992).

Although we considered the availability of forest area in each region, we did not attempt to account for the availability of suitable host species when modeling invasion frequencies, but this factor would have obvious effects on invasion success. In this sense, it should be noted that plant taxa are geographically structured at a global level with the greatest phylogenetic differences occurring between plants in the southern and northern hemisphere (Box 2002). Because herbivore host specialization tends to be structured around host phylogeny (Futuyma and Agrawal 2009), it probably is less likely for invasions to be successful following transport between the northern and southern hemispheres than within the same hemisphere, particularly for non-tropical species. This may be why there have been comparatively few historical Scolytinae invasions between regions in the northern and southern hemispheres (Fig. 3). It should be added that insect seasonality is another factor that can hinder invasions between hemispheres and could also explain this pattern in Scolytinae invasions. The opposing seasonality of a species transported between hemispheres could represent a strong barrier to their successful establishment, especially for species with obligate diapause requirements (Schebeck et al. 2017). Although it would have been very interesting to analyze how host similarity between regions explains the historic Scolytinae invasion pattern, there are insufficient data available to quantify its effect. Also, it should be noted that historical trade connectivity and host similarity between regions may be confounded since the most heavily trading regions, Palearctic and Nearctic, are also very similar in the phylogenetic composition of their tree flora. Consequently, our results should be interpreted cautiously, and further studies are needed to explore the combined effect of trade and host plant similarities in explaining invasion frequencies. This is especially relevant in the context of increased implementation of plantation forestry using nonnative tree species (Wingfield et al. 2015) and planting of alien tree species in urban settings. The introduction of exotic tree species around the world creates opportunities for associated herbivore insect species to expand their range and invade new regions where suitable hosts were previously unavailable (Branco et al. 2015, Hurley et al. 2016).

Data on Scolytinae invasions show that there have been relatively few invasions between certain world regions, and this can be mainly explained by low rates of trade connecting these regions. In the future, it is likely that global trading patterns may realign, and this can be anticipated to result in increased numbers of invasions between these portions of the world. In order to minimize future impacts of invasions by scolytines and other invading organisms, it is essential that the intensity of biosecurity programs, such as phytosanitary treatment of imported commodities, as well as border and post-border surveillance (Poland and Rassati 2019), in these previously isolated regions track increases in trade volumes (Early et al. 2016).

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