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RESEARCH ARTICLE

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International imports and climatic filtering drive compositional variation in non-native insect establishments

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Abstract

Aim: Invasions of non-native insects can have substantial impacts on agriculture, forestry, human health and biodiversity with considerable economic and environmental consequences. To understand the causes of these invasions, it is important to quantify the relative influence of principal drivers such as international imports and climatic effects.

Location: North America, Chile, Europe, Australia, New Zealand and Japan.

Time Period: 1881–2020.

Methods: To evaluate the relative contributions of various factors in explaining global variation in numbers of non-native insect establishments in different world regions, we conducted two multivariate regression analyses to quantify temporal changes in family-level composition and native ranges of established non-native species in several world regions.

Results: There were temporal changes in the family-level composition of non-native species assemblages. Prior to 1900, invasions were dominated by scale insects, subsequently shifting to a more diverse set of species, except in North America, which had relatively small compositional change over time compared to other regions. Spatial

and temporal variation in the composition of established species was associated with differences in the origin of imports and climatic factors, each explaining 26.3% and 27.4% of the total variation, respectively. The analysis of native ranges of non-native species indicated that there was no consistent temporal variation across all regions. Established species in New Zealand were predominantly native to Australasia and species in North America and Chile were mainly from Europe. Non-native species in Europe mainly originated from the Nearctic region while those in Japan and Australia generally originated from multiple regions. Climatic factors in the destination regions had a primary effect (66.3%) on variation in the native range of established species, although imports also had substantial effects (45.4%).

Main Conclusions: Geographical variation in climate and imports act together as drivers of establishment success for non-native insects in all six regions.

KEYWORDS
biological invasions, Köppen–Geiger climate classification, multivariate regression, variation partitioning, world trade

1 | INTRODUCTION

Many non-native insect species have substantial negative impacts on agriculture, human health and biodiversity accompanied by major economic consequences around the world (Diagne et al., 2021; Simberloff, 2009). For example, fall armyworm (*Spodoptera frugiperda* [JE Smith]) (Lepidoptera: Noctuidae), native to the Neotropics and invasive across vast regions ranging from tropical to temperate climates, has devastating impacts on cereal crops and threatens food security (Chhetri & Acharya, 2019; Devi, 2018). The invasion of North America by the emerald ash borer (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae) has decimated native ashes (*Fraxinus* spp.), resulting in considerable economic hardship and loss of amenity values to urban areas with threats to biodiversity (Herms & McCullough, 2014).

In order to better manage the problem of non-native insect invasions, it is important to identify the principal causal factors driving species establishments. Modern increases in global trade and travel are, no doubt, the primary causes of increasing establishments of non-native insects through their impact on propagule pressure. In fact, precedent work found statistical associations between historical imports and numbers of establishment events of non-native insect species (Bonnamour et al., 2021; Levine & D'Antonio, 2003). It is also known that the rate of border interceptions (a proxy of propagule pressure) was positively related with establishment success of individual beetle species (Brockerhoff et al., 2014).

In addition to trade, which facilitates accidental transport of potential invaders, characteristics of individual insect species affect their invasion success. There are many examples that show association between the characteristics of insects and transportation pathways (Liebhold et al., 2016). For example, aphids (Aphidae) are small and sedentary hemipterans and they typically feed on phloem fluid of living plants. They are often found on imported live plants or fresh vegetables (Mille et al., 2020; Sugimoto & Kitagawa, 1995). Scale insects (e.g., Diaspididae and Coccidae) are sedentary plant pests typically found on nursery plants. Many countries started implementing strict biosecurity in the early 1900's, targeting imports of nursery plants pests including scale insects (Liebhold & Griffin, 2016; MacLeod et al., 2010). Non-native parasitic hymenopterans (e.g., Pteromalidae, Encyrtidae, Braconidae) may hitchhike on these plant pests. Early records indicate that ground beetles (e.g., Staphylinidae and Carabidae) and other soil-dwelling groups may have been transported in ships with soil and rock ballast from Europe prior to 1900 (Liebhold et al., 2021; Lindroth, 1957). Stored product pests (e.g., Dermestidae, Tenebrionidae and Nitidulidae) were known to be introduced with imported food or grain especially after World War II (Kiritani, 1963). Thus, insect characteristics interact with imports, influencing the likelihood of transport and establishment.

While trade is a primary driver of arrival rates and propagule pressure, the establishment of a non-native insect species is strongly affected by the environment in its destination region (Renault et al., 2017). Hayes and Barry (2008) stated that climatic similarity between source and destination regions is a universal factor affecting establishment success of non-native species. Chapman et al. (2017) calculated connectivity indices as a summation of imports weighted by climatic similarity between source and destination. They found that these indices were good predictors of the establishments of non-native plant pests in Europe. Considering these precedent works, import volumes, species characteristics and climatic similarity may each influence different invasion stages and ultimately impact the success of invading insect species.

Here, we investigated the relative importance of import volume and climatic similarity between source and destination regions as drivers of the composition of non-native insect assemblages and how this may change through time. This was accomplished by applying multivariate regression analyses to the family-level composition of non-native assemblages and applying the same analyses to the variation in the global origin (native range) of insect species that have invaded various world regions. We assumed that individual

family-level phylogenies are associated with common species characteristics such as body size, feeding mode and specificity, behaviour, etc., and therefore that family-level composition reflects inherent variation in life-history traits (e.g., Hörren et al., 2022; Miller & Wenzel, 2003). We hypothesized that if the family-level composition of non-native insect establishments more strongly corresponds to the dynamic changes in international imports than it corresponds to climatic conditions in destinations, invasion pathways are stronger drivers than climatic conditions of where species establish. Conversely, if climate can explain the majority of variation in family composition of established species, we may conclude that characteristics of invaded regions are the primary factors affecting non-native insect faunas in destination regions.

For the native range analyses, if variation in the origin of non-native species is closely related to variation in climatic conditions of destinations, this would indicate that climatic similarity between the source and destination regions is the key for the success of establishment. On the other hand, we can infer that historical trade connections represent the main driver if imports explain variation better than climate.

In this paper, we quantified the effect of factors (i.e., the origin of imports and the climates in the destination regions) by applying multivariate regression analyses of family-level and native range, respectively. Additionally, a direct ordination was conducted in order to visually interpret the results from the multivariate regression analyses.

2 | MATERIALS AND METHODS

2.1 | Establishment records of non-native insects

We compiled the records of non-native insect species established in six world regions: North America (NA, United States and Canada excluding Mexico and Hawaii), Chile (CL), Europe (EP, including the European part of Russia), Australia (AU), New Zealand (NZ) and Japan (JP, excluding Okinawa and Ogasawara islands). These records were mainly from Turner et al. (2021) but were updated with recent records (e.g., López et al., 2023; Simpson et al., 2022; MPI, 2014–2023). These regions were selected based on data quality i.e., their records can be considered comprehensive lists of all known non-native species established in each region. The species names in our analyses have been cleaned of most typographic and taxonomic errors using the code in the R package *insectcleanr* (Brake & Turner, 2021), which is based on the Global Biodiversity Information Facility (GBIF) taxonomic backbone (GBIF Secretariat, 2022). The summary tables, used in this study, can be found in Tables S1 and S2.

For the family-level analysis, we included counts of established species within each family within each of the eight biogeographic realms for our multivariate regression analyses (Table 1 and Figures S1 and S2). We also allocated species into 20-year intervals according to their first introduction record. We excluded establishment records for species that were intentionally

TABLE 1 Numbers of records used in the study (counts of established species in each region excluding intentional introductions and temporary establishments).

	NA[a]	CL[a]	EP[a]	AU[a]	NZ[a]	JP[a]
Total established species[b]	3389	487	1386	1451	1577	500
Family-level analysis[c]						
Established in 1881–1900	176	20	47	53	18	7
In 1901–1920	309	19	47	91	45	20
In 1921–1940	277	22	66	139	155	17
In 1941–1960	210	47	69	100	130	24
In 1961–1980	251	59	125	86	150	23
In 1981–2000	251	67	164	98	81	47
In 2001–2020	129	58	142	70	66	34
Native range groupings[d]						
Established in 1881–1900	328	36	110	119	51	24
In 1901–1920	531	36	85	195	136	45
In 1921–1940	498	37	140	312	321	43
In 1941–1960	385	67	135	211	265	73
In 1961–1980	472	100	252	198	324	81
In 1981–2000	490	118	390	175	181	119
In 2001–2020	271	110	327	126	189	81

[a]NA: North America (the United States and Canada), CL: Chile, EP: Europe (including the European part of Russia), AU: Australia, NZ: New Zealand and JP: Japan (excluding Okinawa and Bonin islands).

[b]Total establishments include records of species in all families with and without year first found including those out of the study periods.

[c]We only used the top 30 richest family groups to eliminate effects from bias caused by minor taxonomic families.

[d]A species is used in multiple counts if the native distribution ranges spans multiple biogeographic realms.

introduced, species where established populations are limited to greenhouses and species that have been eradicated. It should be noted that we only used data from the 30 most species-rich families to eliminate impacts of high stochastic effects associated with small samples (Table S1).

For the native range analysis, we classified the native range of each species into eight world biogeographic realms (Nearctic, Neotropic, European Palearctic, Afrotropic, Asian Palearctic, Indomalaya, Australasia, and Oceania) of their native range. As in the family-level analysis, we further allocated species into 20-year intervals according to their first introduction record. Species recorded prior to 1881 or after 2020 or those lacking a first introduction record were excluded from the analyses. In the native range dataset, a single species is represented multiple times in the data if the native ranges spanned multiple biogeographic categories.

As the species discovery data were highly biased in favour of major families or large biogeographic realms and because compositional changes were our primary interest, numbers of establishments in each category were transformed as a square root of the numbers of species divided by the total number of species recorded in each 20-year bin, i.e., Hellinger transformation for multivariate regression analyses (Legendre & Gallagher, 2001).

2.2 | Trade data

Data on imports from each of the eight biogeographic ranges (Nearctic, Neotropic, Afrotropic, European Palearctic, Asian Palearctic, Indomalaya, Oceania and Australasia) to each of the six destination regions (NA, CL, EP, AU, NZ and JP) were obtained from the TradeHist database (Fouquin & Hugot, 2016). This database describes the value of reciprocal trade between every country or territory in the world from 1827 to 2014 using British pounds sterling. We standardized all trade values relative to 2020 based on the annual percent change of the UK consumer price index (Office of National Statistics, 2022). The summarized data used in the study can be found in Table S3.

For the multivariate regression analyses (see below) we focused on dynamic changes in composition of imports from eight biogeographic realms rather than the net number of imports. Therefore, the relative proportion of imports from each of the eight biogeographic realms to each of the six destination regions during each 20-year interval was used in the analyses. The final time period only contains import data from 2001 to 2014 because of the lack of recent data. We included import records in early periods (1827–1840, 1841–1860 and 1861–1880), which precede the period of species discovery records to evaluate the time lag between the actual establishment and the discovery of the non-native insects.

2.3 | Climatic similarity

To evaluate the climatic similarities among each of the destination regions (NA, CL, EP, AU, NZ and JP), similarity distances between each pair of regions were calculated using the 30 climatic categories described in the most recent Köppen–Geiger classification (Beck et al., 2018). The classification is based on threshold values and seasonality of monthly air temperature and precipitation also considering the vegetation at 0.0083° (approximately 1 km at the equator) resolution. The summarized data used in the study can be found in Table S4.

As we were specifically interested in compositional similarities among the six regions instead of the net area of each climatic category, the areas of 30 climatic categories were transformed into the square root of the relative proportion in each region, i.e., Hellinger transformation (Legendre & Gallagher, 2001).

2.4 | Multivariate regression analyses and variation partitioning

We employed multivariate regression analyses to quantify the effects of trade imports and the Köppen–Geiger climatic classification on the temporal changes in the family-level composition and in changes in the native regions (Wang et al., 2012; Warton et al., 2012). For species composition records, direct ordination analyses, such as redundancy analysis (RDA) or canonical correspondence analysis (CCA) with the forward factor selection, have been widely used (Legendre & Legendre, 1998; ter Braak & Prentice, 1988). Recently, however, it is recommended to use multivariate regression models with the factor selection procedure based on the Akaike Information Criterion (AIC) rather than ordination analyses. Direct ordinations often over- or under- estimate the effects of factors and the results obtained from the variation partitioning based on ordinations not being reliable for this purpose (Carlos-Júnior et al., 2020; Viana et al., 2022).

To evaluate the effect of international imports, we conducted multivariate regression analyses with a Gaussian link function. The predictors in the model are the proportional imports from eight biogeographic realms and the response community values are the compositional changes of establishments in the six destination regions during each 20-year interval. The proportional imports from eight biogeographic realms were sequentially incorporated into the regression model one-by-one based on the AIC value. From this forward selection procedure, we can obtain the import sets which provide the smallest AIC. The *manylm* function of the *mvabund* library in R was employed for the multivariate regression analyses (Wang et al., 2012). The *manylm* fits a separate linear model to each compositional unit, using a common set of predictors. No interaction terms were included, following common practice in species compositional analyses. It also has diagnostic tools such as *anova* or *summary* to quantify the significant effects by the permutation tests (Wang et al., 2012).

Typically, non-native insects need to establish and spread in the invaded region before they are discovered and there are usually time lags between establishments and discoveries of non-native species (Costello & Solow, 2003; MacLachlan et al., 2021). Thus, we

constructed multivariate regression analyses with AIC based factor selection using import values with no lag (i.e., current), lagged by 20 years, lagged by 40 years and lagged by 60 years. Then we chose the best model based on its AIC value. It should be noted that the models with imports lagged by 60 years were fit to truncated data because import data (TradeHist) only begins in 1827.

To evaluate the effect of climatic filtering, we also employed multivariate regression analyses in which the Köppen–Geiger climatic classification for all time intervals in each focal region were predictors. As previously mentioned, climatic classification values were transformed as the square root of relative proportions. Again, a forward selection procedure based on AIC values was used to obtain the best fitting climatic variables. As in the above analyses for imports, no interaction terms were included.

To quantify the relative contributions of the pure and mixed variation explained by imports and climate, we executed variation partitioning with the multivariate regression models of imports, climates and the combined model (Legendre & Legendre, 1998; Viana et al., 2022). The variations (i.e., explanatory powers) of these multivariate regression models were evaluated by their Hooper's R^2, which is the simple average of all univariate R^2. The combined multivariate regression model contains predictors of the import variables selected in the multivariate regression analyses of imports and also the climate variables selected in the climate analyses. The mixed variation both of imports and climates can be calculated as the difference between the simple summation of Hooper's R^2 from the import and climate models and that of the combined model. Then the pure variation of each factor can be calculated as the remainder of the variation in each model subtracted by the mixed one (Legendre & Legendre, 1998). To visualize the effects of imports and climate on the compositional changes in established species, an additional RDA was employed. The RDA was constructed using the predictors in the mixed model, which were selected by the multivariate regression analyses of imports and climate based on AIC values, against the species composition of the family-level and the native-range. The *vegan* library in *R* was employed for the RDA analyses (Oksanen et al., 2022).

3 | RESULTS

3.1 | Family-level evaluation

In the multivariate regression analysis, predictors of imports (with no time lag) from Asia, Australasia, Indomalaya, Nearctic and Oceania were selected based on the AIC values and all the predictors were statistically significant using a 5% α-level except for imports from Oceania imports (Figure 1c). The Cfc (Temperate_no_dry_season_cold_summer), Csc (Temperate_dry_summer_cold_summer), Cwc (Temperate_dry_winter_cold_summer), Dfb (Cold_no_dry_season_warm_summer) and ET (Polar_tundra) climate variables were selected based on AIC values in the climate regression model and Cfc, Cwc and ET were statistically significant at a 5% α-level. Variation partitioning among the multivariate regression models indicated that 26.3% and 27.4% of the total variation in the family-level composition were explained by imports and climates, respectively (Figure 1d). The mixed variation explained jointly by both imports and climate was 7.9% of the total variation.

To facilitate visual interpretation, post-hoc RDA for the family-level species composition was conducted using all of the predictors in the mixed model. From the region plot of the RDA, there were significant general trends in family composition from top-right to bottom-left of the RDA plot (Figure 1a). At the top-right region of the RDA plot, composition was dominated by scale insects (Diaspididae and Coccidae) prior to 1920 then shifted to a more diverse set of species at the bottom-left (Figure S4). However, North America did not exhibit a drastic compositional change during the entire 140-year period and was located in the middle-left region of the RDA plot. New Zealand (NZ) was also located in the same area after 1921. The far top-left portion of the RDA plot corresponds to families of predacious ground beetles (Staphylinidae and Carabidae) and slightly in the same direction were parasitic Hymenoptera (Pteromalidae, Encyrtidae and Braconidae) (see also Figure S1). Chile (CL) and JP typically had many establishments of Aphididae which are located in the far left of the bottom-left of the RDA plot (Figure 1a,b and Figure S1). Europe (EP), AU and JP progressed towards the centre area just below the horizontal line, which corresponds to families of stored product pests (Dermestidae, Tenebrionidae and Nitidulidae).

From the biplot of the RDA, we can see a slight concordance between the imports (Figure 1c) and the locations of destination regions in the RDA plot (Figure 1a) though the locations were generally moving from top-right to bottom-left and this makes interpretation difficult. New Zealand (NZ) has historically many imports from Australasia and Oceania, CL consistently imports largely from the Nearctic realm and JP and EP once had many imports from Indomalaya but shifted towards more from Asia (Figures 1a,c and also see Figure S3 and Table S3). Though the explanatory power was not large, a substantial 26.3% of the variation can be explained by these import trends in the six world regions. On the other hand, it was difficult to see a clear connection between imports and family-level composition (Figure 1b), though there may be some influence of imports, e.g., 45% of Diaspididae, which are scale insects and are commonly associated with nursery plants, were native to Indomalaya. Also, 32% Carabidae, which mainly inhibit in the soil, were from Australasia.

We can also see the concordance between the location of destination regions in the RDA plot (Figure 1a) and the climatic features in the six destination regions (Figure 1c) though it was difficult to discern the direct relationship between climates in destination regions and family-level composition (Figure 1b). Relatively large fractions of the area in CL are Csc (Temperate_dry_summer_cold_summer) or Cwc (Temperate_dry_winter_cold_summer) and these climates in the RDA biplots are trending towards CL (Figure 1a,c). ET (Polar_tundra) is present in NA and NZ. Dfb (Cold_no_dry_season_warm_summer) occurs widely in NZ, EP and JP. These correspond to the locations of the six world regions in the RDA plot. 27.4% of the total variation in the family-level composition was explained by climate (Figure 1d).

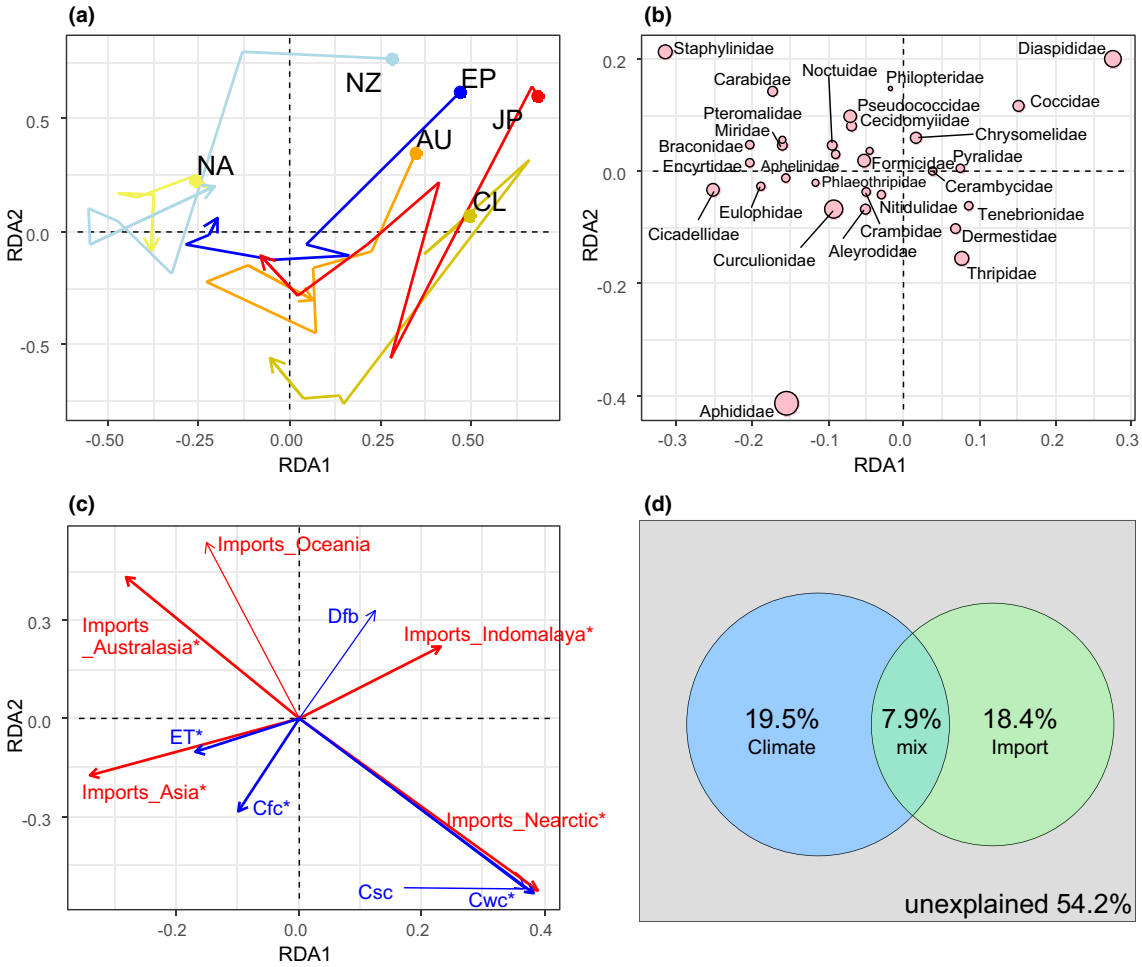

FIGURE 1 Results of the multivariate regression analysis and those of the subsequent combined RDA for the family-level composition. (a) Trajectories of the establishment records of non-native insects classified by family in each region in the combined RDA, where NA: North America, CL: Chile, EP: Europe, AU: Australia, NZ: New Zealand and JP: Japan. Trajectories start from a point (representing the first period, i.e., 1881–1900) and end with an arrowhead (2001–2020). (b) Family plot. Circle sizes represent square root values of total number of species established in each family. (c) Biplots of imports (red arrows with lag = 0 years, see the text for lag selection) and climate (blue arrows), where Cfc: Temperate_no_dry_season_cold_summer, Csc: Temperate_dry_summer_cold_summer, Cwc: Temperate_dry_winter_cold_summer, Dfb: Cold_no_dry_season_warm_summer and ET: Polar_tundra. Details of the Köppen–Geiger classification can be found in Table S4. The significance (*) of the predictors were tested by permutation ANOVA in the multivariate regression. (d) Variation partitioning of two factor groups of import and climate from the multivariate regression analyses. See details in the text.

3.2 | Native range evaluation

From the multivariate regression analyses of imports, predictors based on imports from Afrotropic, Australasia, Europe, Indomalaya and Nearctic with a time-lag of 60 years were selected based on the AIC values and they were all statistically significant at a 5% α-level (Figure 2c). Climatic values of Cfb (Temperate_dry_summer_cold_summer), Csc (Temperate_dry_summer_cold_summer), Dfb (Cold_no_dry_season_warm_summer), Dsc (Cold_dry_summer_cold_summer) and Dwa (Cold_dry_summer_hot_summer) were selected in the climate analyses and they were all statistically significant at a 5% α-level except for Dsc. From the results of the variation partitioning, 45.4% and 66.3% of the total variation in the native range composition were explained by imports and climates, respectively (Figure 2d). The mixed variation both of imports and climates was 40.4% of the total variation.

From the post-hoc RDA, we can see that the native range composition for each of our destination regions was stable through time, contrary to the family-level analyses (Figure 2a and Figure S2). Established species in NZ were predominantly from Australasia and those in NA and CL were mostly native to Europe (Figure 2b). Origins of the species established in JP and AU were more closely associated with the Afrotropic, Neotropic, Asia and Indomalaya regions. Europe (EP) was consistently located towards the Nearctic indicating that non-native species from that region are continuously flowing into EP.

We can see a clear relationship between the location of the native range in the RDA plot (Figure 2b) and the biplot of import values (Figure 2c). Invasive species which originated in Australasia, Europe, Nearctic, Afrotropic and Indomalaya seem to have clear correspondence to the imports from those realms (Figure S3 and Table S3). 45.4% of the total variation can be explained by the imports.

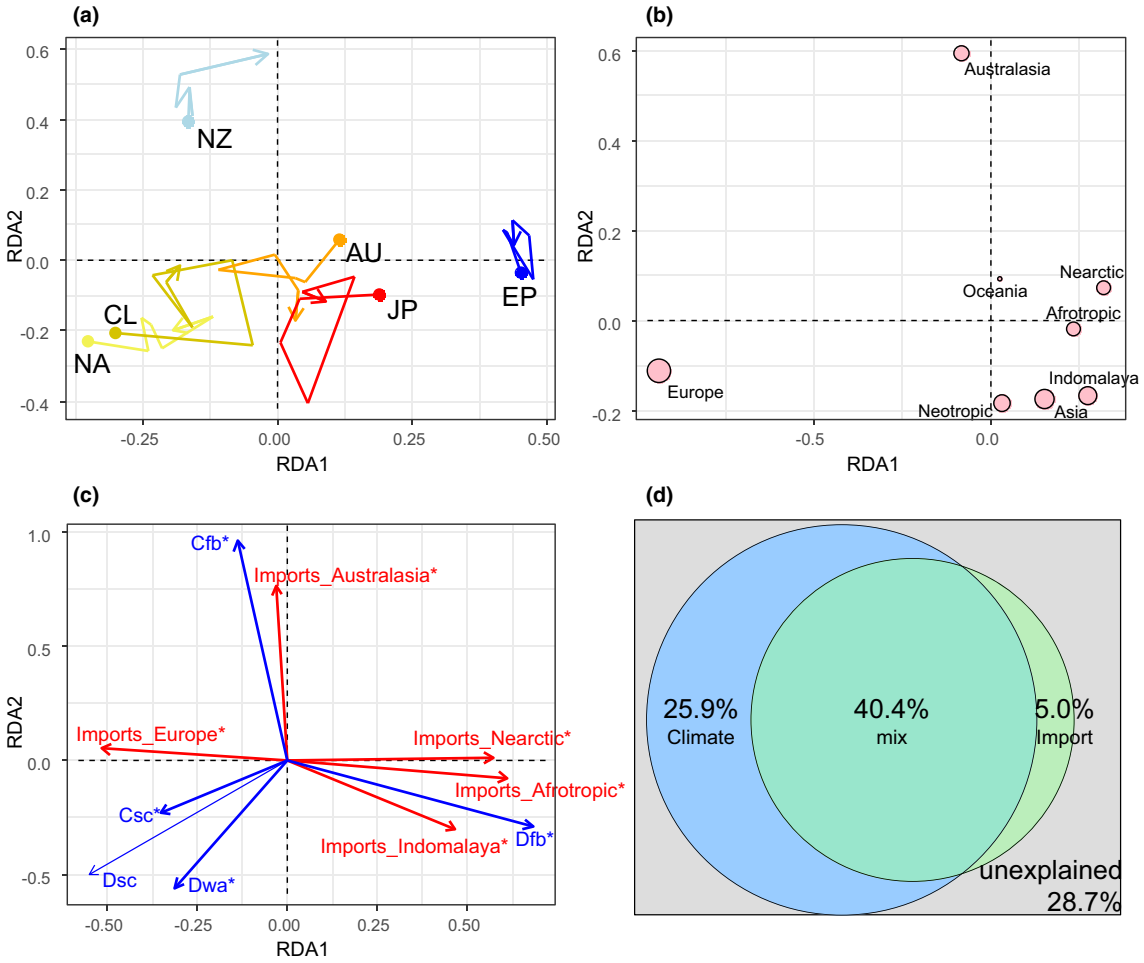

FIGURE 2 Results of multivariate regression analysis and of the subsequent combined RDA for the native range. (a) Trajectories of dynamical changes in the establishment records of non-native insects classified by their native ranges in the combined RDA, where NA: North America, CL: Chile, EP: Europe, AU: Australia, NZ: New Zealand and JP: Japan. Trajectories start from a point (1881–1900) and end with an arrowhead (2001–2020). (b) Native range plot. Circle sizes represent the square root numbers of total establishments of the native range in total. (c) Biplots of the import (red arrows with lag = 60 years, see text for lag selection) and climate (blue arrows), where Cfb: Temperate_dry_summer_cold_summer, Csc: Temperate_dry_summer_cold_summer, Dfb: Cold_no_dry_season_warm_summer, Dsc: Temperate_dry_summer_cold_summer and Dwa: Temperate_dry_summer_cold_summer. Details of the Köppen–Geiger classification can be found in Table S4. The significant predictors by permutation ANOVA in the multivariate regression analysis are marked with *. (d) Variation partitioning of two factor groups of import and climate by the multivariate regression analyses. See details in the text.

We can also see a clear concordance between the climatic features (Figure 2c) and the destination regions in the RDA plot (Figure 2a) but not to those of native range in the RDA plot (Figure 2b). Cfb (Temperate_dry_summer_cold_summer) and Csc (Temperate_dry_summer_cold_summer) typically exist in NZ and CL (Table S4) and their biplots in Figure 2c were heading towards their locations in the RDA plot of Figure 2a, respectively. The same relationship was evident for Dfb (Cold_no_dry_season_warm_summer) in Figure 2c and EP in Figure 2a and Dwa (Cold_dry_summer_hot_summer) and JP and NA. Therefore, the composition of non-native species, based on their native range, relates more strongly to their destination climates than to the climate of their origins. 66.3% of the total variation in the composition of the native region was explained by climate.

4 | DISCUSSION

Using multivariate regression analysis, we found that imports from various world regions (45.4%) and climatic conditions in destination regions (66.3%) explain a substantial fraction of the variation in the native range of established species. We thus conclude that both imports and climatic conditions are important drivers of successful establishment. Though the importance of imports and climate have been explored in the past, many studies analysed these effects independently (Hayes & Barry, 2008; MacLachlan et al., 2021; Ollier & Bertelsmeier, 2022; Renault et al., 2017). Chapman et al. (2017) evaluated both effects in an integrated manner using connectivity indices. They found that the connectivity index, which was the summation of imports weighted by climatic similarity between source

and destination, was the best predictor of the numbers of establishments in various European countries. Their result suggests that both factors should be considered for evaluating invasion risks. Though our general conclusion was not greatly different from previous studies, our quantification of their relative pure and mixed contributions estimated by the variation partitioning provides further insights.

We found that the effects of imports and climate largely overlapped with each other (40.4%) in the native range analysis though climate in the destination explained a larger percentage of the variation than did imports. We suspect that this overlap was caused by legacy effects and similarity in trade and climate. These legacy effects likely reflect historical influences of European colonialism, especially in NA and CL. In fact, establishments in NA and CL were mainly from Europe and they also correspond to imports from Europe (Figure 1 and Figure S2). Also, imports lagged by 60 years, had a substantial effect on non-native insect establishments in the native range analysis. Lenzner et al. (2022) found compositional similarities in established non-native plant species among regions that were once occupied by the same colonial empire and such similarities can persist over long periods. Casado et al. (2018) also concluded that unintentionally introduced herbaceous species in five Mediterranean-climate regions mainly came from the Iberian Peninsula and that this was the consequence of both historical trade and migration, as well as climatic similarity. Since established non-native plants can facilitate further invasions of non-native insects (Liebhold et al., 2018), a legacy effect could have contributed to the stable temporal dynamics of compositional differences in native ranges in our analysis (Liebhold et al., 2016; Turbelin et al., 2017).

Disentangling the effects of variation in imports from different regions and climates in destinations is generally difficult because many species may not have arrived directly from the native region. Relationships with trade from native regions is therefore obscured (Bertelsmeier & Ollier, 2021; Lombaert et al., 2010). Approximately 25% of the species in our database are recorded as native to multiple regions. We suspected that a number of these multiple records (e.g., for cosmopolitan species), originated from successive invasions, a primary invaded region having served as a source for further invasions (bridgehead effect). Such primary invaded regions were then erroneously considered as a "native" range. We tried the same analyses after removing species "native" to multiple regions and found no qualitative difference from the current results (Figure S4). Therefore, we assume that this effect had a negligible impact on our interpretation.

Another difficulty in disentangling the effect of imports from those of climate also arises from the tendency of large economies to be located in temperate climates and thus high trade volumes often come from regions with similar climatic ranges (Essl et al., 2015). In addition, there is an alternative hypothesis that the composition of established species resulted from climatic filtering upon arrival even though international imports could have brought various other species from around the world that could not successfully establish (Casado et al., 2015). However, established species originated in Indomalaya and Afrotropic seem to have correspondence to the imports from those regions (Figure 2b,c). A substantial amount of the mixed variation may be explained by the effect of imports.

In the family-level analyses, imports (26.3%) and climates (27.4%) also explained substantial variation though both explained less than in the native range analysis. Though we cannot conclude that biological traits that vary among families were not important for establishment success, we believe that they were not sensitive to total imports or climate. However, we found interesting dynamic changes in assemblage compositions. In all regions, there was a general transition from being dominated by scale insects prior to 1920 to a more diverse set of species in recent decades (Figure 1). Many countries (NA, AU and JP) implemented stricter biosecurity regulations around 1910, especially targeting imports of nursery plants (Liebhold & Griffin, 2016; MacLeod et al., 2010) and this may have effectively reduced the inflow of scale insects. The composition of non-native insects establishing early in NZ and NA had a large representation of ground beetles (Staphylinidae and Carabidae), which probably arose from the practice prior to 1900 of ships carrying soil and rock ballast from Europe which was unloaded upon arrival (Liebhold et al., 2021; Lindroth, 1957). North America (NA) seems to have many non-native parasitic hymenopterans (Pteromalidae, Encyrtidae and Braconidae); this may reflect the historical practice of introducing biological control agents for pest insects in this region without documentation and there may also have been unintentional introductions of cryptic species (Hajek et al., 2016). New Zealand (NZ) also seems to have many non-native parasitic hymenopterans but unintentional introductions especially from Australia, were conspicuous (Ward & Edney-Browne, 2015). Since the trajectory of invasions in NZ shifted from scale insects to parasitic hymenopterans (Figure 2a,c), non-native hymenopterans might have come together with unintentional introductions of host scale insects that had previously established. Japan (JP), AU and EP had many early establishments of stored product pests (Dermestidae, Tenebrionidae and Nitidulidae) during 1940–1960 (Figure 1a,b) which might have been accidentally introduced to these regions with imported food or grain after World War II. They could have easily established in newly constructed grain mills in the 1950s (Kiritani, 1963). The establishment of Aphididae was conspicuous especially in CL, AU and JP in recent years, possibly because greenhouses became popular around the 1960s in these regions (Kiritani, 2001). Aphids are also common on imported live plants or fresh vegetables so historical live plant introductions may also explain this trend (Mille et al., 2020; Sugimoto & Kitagawa, 1995).

Overall, temporal changes in family-level composition can be interpreted in terms of historical conditions during each time period, though climate had less contribution to the variance than in the native range analyses. Each family is comprised of many species and these species typically vary in their climatic limitations. Therefore, there may not be a clear correspondence between family composition and climate. In addition, the imports may not have strongly influenced family-level composition because imports from similar climatic regions contain various commodities, each harbouring various types of insects. These changes may also result from bridgehead effects as mentioned above. If historical (back to 1880) trade records were classified by commodity

types, it might have been possible that such import records could explain a greater percentage of compositional changes. However, such commodity-level import data prior to 1980 are not readily available for many countries. In addition, socio-economic factors other than trade may have contributed to the observed dynamics. Further accumulation of such data is needed for future analyses.

Based on these results, we conclude that both imports and climatic filtering act as drivers of establishment success for non-native insects in all six regions while the legacy of European colonialism remains especially in NA and CL. Historical and social factors may also have influenced the taxonomic composition of non-native insect establishments, though we could not quantify their relative contribution. It is possible that this information could be incorporated into border biosecurity practices, whereby biosecurity efforts could be focused on imports from regions with similar climatic condition as the importing country. This analysis also emphasizes the potential risk of introducing herbivorous insect pests whose host plants have been already introduced. We believe the multivariate regression analyses and the variation partitioning applied here can provide visual and quantitative evaluation of factors affecting variation in studies of other groups of non-native species in various world regions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data underlying the analyses presented here can be found at Tables S1–S4. Tables S1 and S2 summarize the family-level and the native range composition in six world regions in 20-year intervals according to their first introduction records. Tables S3 and S4 are summaries for the historical trade records based on British pound (GBP) and for the Köppen–Geiger classification in six world regions.

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BIOSKETCH

Takehiko Yamanaka is a quantitative ecologist and also an applied entomologist. He is applying statistical analyses to several field insect records and is constructing simulation models to explore theoretical insect population dynamics. This study was based on the working group discussion of "Pursuit: Global Socioeconomic Drivers of Insect Invasions" hosted by the National Socio-Environmental Synthesis Center (SESYNC).

Author contributions: TY curated and analysed the data, with support from RMT and AML. TY, RMT, REB, HFN, AR and AML curated and provided access to the records of non-native insect species established in six world regions. 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.

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