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ORIGINAL PAPER

Global drivers of historical true fruit fly (Diptera: Tephritidae) invasions

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Abstract

Given the high costs associated with fruit fly (Tephritidae) invasions, there is a need to better understand and predict the risks of future invasions. We assembled a global database of historical Tephritidae invasions with the objective to identify biological and socioeconomic drivers that explain invasions. We investigate the tendencies of certain species to invade and the characteristics of regions that make them more prone to invasions. Our database documented the occurrence (presence/absence) and status (native/non-native) of individual Tephritidae species in each country in the world. Values of several socioeconomic and environmental variables were also assembled and considered as explanatory variables. A generalized linear mixed-effects model framework was used to evaluate the utility of these variables for predicting the country-level occurrence of each species outside of its native range. A total of 44 species were identified as having been accidentally introduced. Most species of invading Tephritidae have established in five or fewer countries. The number of invasions has rapidly increased since the 1950s. Climatic similarity between native and invaded countries and gross domestic product of the invaded country significantly increased the incidence of invasion, whereas distance to the native range had a negative effect on the probability that a given country would be invaded. Our analysis revealed that both economic and biological factors explain patterns of historical Tephritid invasions. Despite the rising efforts to prevent new invasions, additional species may continue to invade, and many currently established species will likely continue to expand their ranges into new areas.

Keywords Tephritidae · Non-native species · Invasion drivers · Patterns of invasions · Global insect invasion dynamics · Generalized linear mixed-effects models · Risks of future invasions

Introduction

The emergence of advanced human civilizations in various world regions has historically been closely linked with the domestication of plants for agricultural purposes and their propagation (Rindos 1987; Sauer 1993). Many agricultural crops exhibit remarkable productivity when grown outside of their native range where they may escape the impacts of herbivores and plant pathogens. In many cases, however, such escape has been short lived as plant pests are accidentally moved outside of their native ranges and these invading species may adversely impact agricultural productivity, ultimately resulting in serious socioeconomic consequences (Paini et al. 2016; Santini et al. 2018).

Among such damaging non-native agricultural pests are the notorious true fruit flies (Diptera: Tephritidae), which comprise ca. 5000 species worldwide (White and Elson-Harris 1992; Norrbom et al. 1999; Norrbom unpubl. data). Most tephritids share a common life history of larval feeding on living plant tissue, feeding upon seeds, flowers, fruits or within galls or mines on leaves and stems, however, only about a third feed on fruits. Tephritids exhibit considerable variation in other life history traits, such as pre-adult survival and duration of immature stages, as well as variation in population demographics that may affect their success as

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invaders (Carey et al. 1988; Malacrida et al. 2007; Papadopoulos 2014; Vargas et al. 2000). The Tephritidae includes some of the world's most damaging fruit and vegetable pest species with particularly serious pests in the genera *Anastrepha* (native to the Neotropical Region), *Bactrocera* and *Zeugodacus* (mainly native to Indomalayan and Australasian Regions), *Ceratitis* (native to the Afrotropical Region) and *Rhagoletis* (native to the Nearctic, Neotropical and Palearctic Regions) (Courtney et al. 2009; White and Elson-Harris 1992; Norrbom et al. 1999).

While several Tephritidae species have had massive economic impacts as a result of direct losses to agricultural yield and increased pest management costs, additional impacts have also resulted from diminished access to export markets due to quarantine bans imposed by importing countries (Siebert and Cooper 1995; Mumford 2002; Papadopoulos 2014). Because of the severe socioeconomic consequences of Tephritidae invasions, many countries expend considerable resources to prevent establishment of new and potentially damaging species. Historically, the principal pathways responsible for Tephritidae invasions have been international movement of fruit and vegetables, either in trade or in passenger baggage (Kiritani and Yamamura 2003; Liebhold et al. 2006; Karsten et al. 2015). Biosecurity approaches to preventing the arrival of fruit flies include importation prohibitions, inspection and mandatory phytosanitary treatments (Li et al. 2013; Phillips 2013). In addition to these measures, biosecurity efforts include continual surveillance and if an incursion is detected, eradication (Quilici and Donner 2012; Suckling et al. 2016).

Given the extreme costs associated with Tephritidae invasions and the limited resources that most countries have available for carrying-out biosecurity programs, there is a need to better understand and predict the risks of future invasions (Qin et al. 2015). Here, we assemble a comprehensive database of all known historical Tephritidae invasions and analyze these data to identify biological and socioeconomic drivers that explain these invasions. We investigate whether there are tendencies of certain species to more successfully invade new regions and if there are characteristics of regions that make them more prone to Tephritidae invasions. These analyses provide insight into the factors that may promote new invasions and provide critical information for predicting invasions in the future.

Methods

Tephritidae invasion records

We compiled data on the global distribution of both the native and non-native ranges of all Tephritidae species that are known to be unintentionally established outside of their native ranges. Multiple Tephritidae species have been intentionally introduced as biological control agents of weeds (Bess and Haramoto 1972; White and Clement 1987; White and Elson-Harris 1992; Turner 1996), but these species were not included in our analyses (see Table S1.1 for the list of these species). The geographical distribution of each species was recorded as non-native, native or not established in each country in the world. These data were compiled from various published sources including the scientific literature (e.g., Foote et al. 1993; Wu et al. 2009) and online databases (e.g., CoFFHI 2020; EPPO 2014, 2020; GBIF Secretariat 2021) (see Table S2.2 for details). Only records of species that have clearly established a self-sustaining population in the non-native range were included. In some cases, incursions were historically reported using species names that are now considered synonyms, so we recorded these using the recognized senior synonym. Similarly, we used distinct names to differentiate among cryptic species. For species where the native range is uncertain, their presence in countries was considered to be part of the native range unless there was evidence otherwise; thus, the number of non-native species and the extent of their invaded areas may be underestimated. In defining non-native ranges, the Russian Federation was divided into its European and Asian portions. Outlying states, territories and other autonomous regions (e.g., Hawaiian Islands, Guam, Puerto Rico, Christmas Island, New Caledonia, Guam) with sufficient data available were treated as separate units in the analysis.

For each record of a non-native tephritid species (excluding biocontrol agents) in a country, we recorded the year of first recorded discovery if such data were available. Furthermore, the Global Eradication and Response Database (GERDA; Kean et al. 2021) was used to summarize documented eradication attempts against non-native tephritids worldwide (Table S3.3).

To examine the inter- and intra-regional invasion dynamics and to determine the most common source-recipient combinations at the regional level, numbers of native and established non-native species were summarized for each of eight biogeographic regions: Nearctic, Neotropic, European Palearctic, Asian Palearctic, Indo-Malaya, Afrotropic, Australasia and Oceania. These regions were slightly modified from Wallace's classification to match national political boundaries in accordance with the country-level approach used here to record species distributions; for purposes of this analysis, all of any country that extends into two biogeographic regions was included in the region in which the majority of its territory occurs (Figure S4.1). Countries such as Mexico, China and Indonesia that are often split between biogeographic regions were not divided in our analysis because historical invasion data are not available for subdivisions of these countries. The Hawaiian Islands were included in the Oceania region rather than the Nearctic,

which includes the continental USA. The European portion of the Russian Federation was included in the European Palearctic region, and the Asian part of Russia was allocated to the Asian Palearctic region. Species that are only non-native within portions of the same countries that form part of their native ranges were excluded from these and further analyses.

The climatic distribution (combined native and non-native) of each non-native tephritid species was characterized using the proportion of georeferenced occurrence records for each species from the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/) recorded in each climatic subgroup of the Köppen–Geiger climate classification system (Kottek et al. 2006).

Explanatory variables

To explore possible mechanisms explaining the establishment of each non-native Tephritidae species in each country, we explored associations with a set of candidate socioeconomic and environmental variables (Table 1). Some of these variables were related to propagule pressure (numbers of individuals of a species entering a non-native region), while others were related to habitat invasibility.

Socioeconomic variables considered here that serve as proxies for propagule pressure included human population, gross domestic product (GDP), tourism and cumulative value of imports 1827–2014 to each country. Because of changes in national identities, independence of former colonies and other reasons, the imports of presently non-existent countries and previously colonial territories were grouped or divided to match current national boundaries. Annual imports were expressed in USA dollars per year, adjusted to 2018 values utilizing the Consumer Price Index (Federal Reserve Bank of Minneapolis 2021). The cumulative value of all imports from countries in the native region of each Tephritidae species to each remaining country was calculated to express total trade flow from the native region to every other country. Movement in airline and maritime passenger baggage has been reported as a common pathway for international movement of Tephritidae, but historical data on passenger volumes spanning the period of our study (1827–2014) were lacking, so it was not included as an explanatory variable.

Variables related to country invasibility that were considered included annual fruit production and climatic suitability. From the total of 44 non-native tephritid species identified, sufficient information for further analysis of climatic suitability was found for only 36 species. Climatic suitability was calculated for each country both as the total area of suitable climate for each species and as the fraction of the country with suitable climate. This suitability was characterized based on the climatic niche for each species. The climatic niche was estimated by identifying the climatic subgroups of the Köppen–Geiger system (Kottek et al. 2006) that overlapped the range (both native and invaded) of the species. The geographic range of each species was characterized by downloading georeferenced occurrence records for each species from the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/) database. Only records matching the country boundaries of the native and invaded ranges for each species were used. Then, we calculated the number of occurrence records falling in each of the 30 climatic subgroups. Climatic suitability of each country outside of the species native range was calculated using the Jaccard similarity coefficient as:

Table 1 List of explanatory variables for each country used for analysis of invasion probability for each tephritid species in each country

Variable	Description	Source
Human population	Total human population in each country in 2015	World Bank Open Data (https://data.worldbank.org/)
Gross domestic product (GDP)	Gross domestic product in each country 2015	World Bank Open Data (https://data.worldbank.org/)
Number of visiting tourists	Number of tourist arrivals in country in 2015	World Bank Open Data (https://data.worldbank.org/)
Cumulative imports	Total value of imports to each country (adjusted USD) from all countries in the native range	Bilateral Trade Historical Series: New Dataset 1827–2014 (TRADHIST, Fouquin and Hugot, 2017)
Fruit production	Total area of agricultural land producing fruit in each country in 2015 (km^2)	Food and Agriculture Organization of United Nations (http://www.fao.org/home/en/)
Country area	Total area of the country (km^2)	GIS analysis
Distance to native range	Shortest (border-border) distance between each country and the native range of species (km)	GIS analysis
Climatic similarity	Fraction of the country with suitable climate for specific Tephritidae invasion	Koppen classes; GBIF records (GBIF Secretariat 2021)
Suitable climate area	Area of the country with suitable climate for Tephritidae species invasion (km^2)	Koppen classes; GBIF records (GBIF Secretariat 2021)

$$CS_{i,j} = \frac{\sum_{KG=1}^{30} p_{KG,i} p_{KG,j}}{(\sum_{KG=1}^{30} p_{KG,i}^2 + p_{KG,j}^2)/2}$$

where $CS_{i,j}$ is the climatic similarity of country i with the estimated climatic niche of Tephritidae species j, $p_{KG,i}$ is the fraction of country i comprised of Koppen–Geiger climate subgroup KG, and $p_{KG,j}$ is the fraction of species j GBIF records located in subgroup KG. The suitable climatic area for each country-species combination was calculated as country area multiplied by $CS_{i,j}$. The same procedure was used to estimate the "suitable" native and invaded range of each species.

Country area and proximity to the native range of each individual species were calculated using ESRI Arcmap 10.5.1. Country borders were extracted from the GISCO database (https://ec.europa.eu) as GIS shapefiles of scale 1:10 mil. Distance to the native range was calculated for each country-species combination. The distance between the native region and each country outside of the native range was calculated as the shortest geographic distance (border to border).

Data analysis

A generalized linear mixed-effects model framework was used to analyze the incidence (0/1) of invasion for each species in each country. The analysis was based on a full matrix database such that each country was repeated in the data for each species and vice versa. To account for repeated observations on countries and unobservable effects of species, terms for country and species were fit as random intercepts. All models were fit with a binomial distribution and logit link function. Data were analyzed using the R statistical software v4.0.0 (R Core Team 2020) and mixed-effects models were fit using the lme4 package in R (Bates et al. 2014). Prior to analysis, several predictors were ln(x)-transformed to reduce skewness and, for predictors containing zero values, a small constant of 1 was added to all observations. Modeling was then conducted in two steps. First, we fit bivariate models between our response variable and each predictor and calculated Akaike information criterion (AIC) values for each model (Figure S5.2A). For the second stage, we aimed to develop a full, best-fitting model that evaluated all predictors simultaneously, but first checked for collinearity ($|r| > 0.5$) by calculating pairwise Pearson's correlation coefficients (Table S5.4). In instances of collinearity, predictors occurring in bivariate models with the lowest AIC were used.

While surveillance and eradication represent an important component of biosecurity measures targeting exclusion of non-native Tephritidae species, questions have been raised about the efficacy of some of these programs (Carey 1991; Papadopoulos et al. 2013). Specifically, some scientists believe that detections of insects in the same general area of the site of an earlier eradication most likely reflect the persistence of the initial population (i.e., as a result of eradication failure) rather than a new invasion following successful invasion (Zhao et al. 2019). However, this theory has been lively debated in the scientific literature (Gutierrez et al. 2014; McInnis et al. 2017). Here, we attempted to remain agnostic with regard to this theory and performed two versions of our analysis. In the first analysis, we fit the mixed-effects model using species-country records for which we only recorded a country as invaded based on the presence of a self-sustaining population. In the second analysis, we fit the same model but in addition classified countries as invaded if an eradication project for the species was carried out in the country even if there were no subsequent detections. Our logic here was that had the eradication not been carried out, then the species would have established. By analyzing these data both ways, we were able to avoid assumptions about the true success of eradication.

An additional analysis was conducted to determine which species, after adjusting for the effects of predictors remaining in our best-fitting model, exhibited the highest mean probability of invasion. This was achieved by estimating marginal means using the emmeans package in R (Lenth 2020). First, species were fit as a fixed (vs. random) effect with country still included as a random intercept to obtain species-level mean invasiveness, but this resulted in convergence issues in the mixed-effect framework. Thus, a simpler approach was used by (i) fitting a fixed-effects only model that included predictors from the best fitting model (i.e., human population density, proportional climatic similarity, distance from the native range; see "Results") along with a term for species and (ii) only evaluating species for which the number of countries invaded/total countries was > 10% (i.e., invaded more than 30 countries).

Results

Intra- and Inter-regional invasions

In total, we identified 44 non-native Tephritidae species (Table 2, Table S2.2).

The highest number of successful invasions are documented in the European Palearctic region (15 species), followed by the Asian Palearctic region (14 species each). Indo-Malaya has the lowest number (6) of invasions (Table 3). The most intra-regional invasions are documented in the Neotropical Region (8). The European Palearctic has the highest number of native Tephritidae species that invaded elsewhere (16), while Oceania has the lowest number of

Table 2 Tephritidae species known to have established in areas outside of their native ranges (excluding biocontrol agents purposefully introduced)

Species	Biogeographic region of native range	Biogeographic region of invaded range	No. of countries invaded
*Anastrepha curvicauda**	NT	NA	1
Anastrepha fraterculus "Brazil-1 morph"	NT	NT	4
*Anastrepha fraterculus "Peruvian morph"**	NT	NT	1
Anastrepha grandis	NT	NT	1
Anastrepha ludens	NT	NT	2
Anastrepha obliqua	NT	NT	13
Anastrepha suspensa	NT	NA	1
Bactrocera carambolae	IM	NT	4
Bactrocera dorsalis	AP, IM	AP, AT, AU, EP, IM, OC	54
Bactrocera frauenfeldi	AU, OC	AU	1
Bactrocera latifrons	IM	AP, AT, OC	4
Bactrocera ochrosiae	OC	OC	1
Bactrocera oleae	AT	AP, AT, EP, IM, NA, NT, OC	34
Bactrocera tryoni	AU	AU, OC	3
Bactrocera zonata	IM	AP, AT, EP	12
Campiglossa producta	AP, EP, IM	AP, IM	5
*Campiglossa sororcula**	AP, AU, AT, EP, IM, OC	AU, OC	2
*Carpomya incompleta**	AT, EP	AT	2
*Carpomya pardalina**	AP, EP, IM	AP, EP	8
*Carpomya vesuviana**	AP, EP, IM	AP, AT, EP, IM, OC	21
Ceratitis capitata	AT	AP, AT, AU, EP, NT, OC	61
Ceratitis quilicii	AT	AT	2
Chaetorellia succinea	AP, EP	NA	1
Dacus ciliatus	AT	AP, AT, EP, IM	19
Dacus frontalis	AT, EP	EP	5
*Dicheniotes ternarius**	AT	AU	1
Dirioxa pornia	AU	OC	1
Ensina sonchi	AP, EP, IM	AT, IM, OC	4
Euaresta bullans	NT	AP, AT, AU, EP, NA, NT	30
Euarestoides acutangulus	NA	NT	9
*Myopites tenellus**	EP	AP	1
Neoceratitis cyanescens	AT	AT	3
Rhagoletis batava	AP, EP	EP	4
Rhagoletis cerasi	AP, EP	NA	2
Rhagoletis cingulata	NA, NT	EP	12
Rhagoletis completa	NA, NT	NA, EP	14
Rhagoletis meigenii	EP	NA	2
*Rhagoletis pomonella**	NA, NT	NA, NT	3
Strauzia longipennis	NA	EP	1
Terellia fuscicornis	AP, EP	EP, NA	2
Terellia ruficauda	AP, EP	NA	2
Terellia tussilaginis	AP, EP	AP	1
Urophora jaceana	AP, EP	NA	1
Zeugodacus cucurbitae	AP, IM	AP, AT, AU, EP, OC	34

*insufficient records available in GBIF database to quantify climatic range; excluded from climatic analyses

Biogeographic regions are abbreviated: *AT* Afrotropic, *AU* Australasia, *AP* Asian Palearctic, *EP* European Palearctic, *IM* Indo-Malaya, *NA* Nearctic, *NT* Neotropic, *OC* Oceanian

Table 3 Intra- and inter-regional invasions of Tephritidae between biogeographic regions

Biogeographic region	No. of invading species native to the region*	Total No. of non-native species	No. of intra-regional invasions**	No. of inter-regional invasions***	No. of native species that invaded other regions							
					AT	AP	AU	EP	IM	NA	NT	OC
AT	9	13	5	11	–	3	2	3	2	1	2	3
AP	14	13	5	14	4	–	3	6	3	5	0	4
AU	4	8	1	4	0		–	0	0	0	0	3
EP	16	15	5	16	3	4	1	–	3	5	0	3
IM	10	6	4	10	4	5	1	2	–	0	1	4
NA	5	11	1	11	0	0	0	3	0	–	2	0
NT	11	11	8	6	1	1	1	3	0	4	–	0
OC	3	11	2	10	0	0	2	0	0	0	0	–
Total	44*	44*	–	–	–	–	–	–	–	–	–	–

*Only species that invaded other regions included

**Some species invaded multiple regions, hence sum of species across all regions does not match total species

***The native ranges of some species span multiple regions, and the origin of invading populations is unknown. Thus, some species may be listed as both intra- and inter-regional

Biogeographic regions are abbreviated: *AT* Afrotropic, *AU* Australasia, *AP* Asian Palearctic, *EP* European Palearctic, *IM* Indo-Malaya, *NA* Nearctic, *NT* Neotropic, *OC* Oceania

species invading elsewhere (3, Table 3). Most inter-regional invasions occur between neighboring regions such as between the Asian and European Palearctic (6) and between Indo-Malaya and the Asian Palearctic (5).

Country-level invasions history

Most species of invading Tephritidae have established in only five or fewer countries, with 13 species only invading a single country (Fig. 1A). Only six species have invaded more than 20 countries: *Carpomya vesuviana* (21), *Euaresta bullans* (30), *Bactrocera oleae* (34), *Zeugodacus cucurbitae* (34), *Bactrocera dorsalis* (54) and *Ceratitis capitata* (61). The first records of fruit fly invasion date back to the 1830s with *Ceratitis capitata* establishing in Madeira (Portugal) and the Azores (Spain). For the next 100 years, only about 20 more invasions were recorded until the 1930s when the number of new species-country records doubled to around 40 (Fig. 1B).

Since then, the cumulative number of Tephritidae invasions steadily increased to a total of 189 reported dated invasions in 2018 (Fig. 1B). Unfortunately, dates for the first records of species in many countries (more than 200) could not be located. The complete list of records is provided in Table S2.2.

Eradication attempts against non-native tephritids date to the early 1900s, and in total nearly 300 successful eradication programs are documented (Kean et al., 2021; Fig. 2). Numbers of eradication programs have been steadily increasing since the 1970s with more than 60 eradications documented each decade since the 1990s (Fig. 2). Most such programs were carried out against *Ceratitis capitata* and *Bactrocera dorsalis*, followed by *Bactrocera tryoni* in the last decades (Fig. 2).

Native and Invaded and native ranges

The current distributions of invading Tephritidae species span four out of the five main Köppen–Geiger climatic group areas. The largest number of occurrence records fall in group C (temperate) (62% of GBIF records), followed by group A (tropical) (16%), then group D (continental) (12%) and finally Group *B* (dry) (10%). There were no non-native Tephritidae records from the polar climatic group area. The climatic subgroup with the most native range records was the temperate oceanic subgroup followed by the tropical wet and humid subtropical subgroups (Fig. 3). Most of the records from non-native ranges are documented from the warm- and hot-summer Mediterranean climatic subgroups.

Total numbers of native and non-native species present in each country are shown in Fig. 4. The countries with the largest number of established non-native Tephritidae species (8) were the USA and Mauritius, though Reunion and the Hawaiian Islands were very close with 7 species. Australia, France, and several countries in the Middle East also have high numbers (6 species) of documented invasions (Fig. 4A). Overall, at least one tephritid invasion is documented in every world biogeographic region aside from Antarctica (Fig. 4A). The greatest number of non-native tephritids originate from the European Palearctic region (9 from Spain and France) and Indo-Malaya (8 from India) (Fig. 4B).

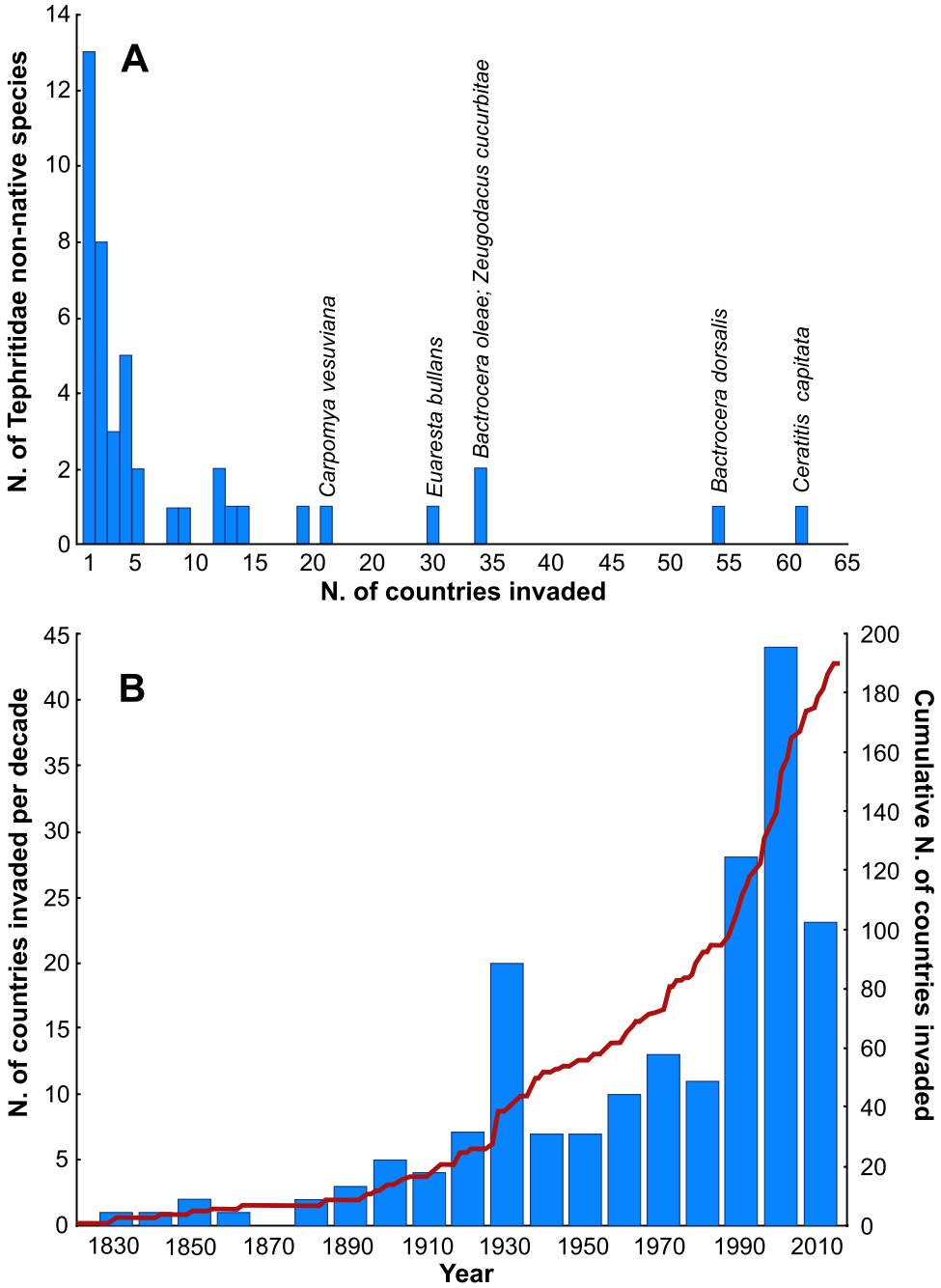

Fig. 1 Distributions of invasions among species and through time. **A**. Frequencies of number of countries invaded per species; **B**. Number of species-country invasion discoveries per decade (blue columns, left *y*-axis) and cumulative number of species-country invasion combinations since 1820 (red line, right *y*-axis)

Generalized linear mixed-effects invasion model

We first present results from analyzing insect-country records where classification of establishment was limited to the clear presence of self-sustaining populations. Collinear predictors (Table S5.4), defined as having a correlation >|0.5|, could be split into two groups: those related to human activity (human population density, GDP, fruit production, tourism and land area) or climate (climatic similarity, suitable climate area). For consideration in the full candidate model, we selected the variable from each group that occurred in the bivariate model with the lowest AIC: GDP and proportional climatic similarity (Figure S5.2A). Thus, a full candidate model considered GDP, cumulative imports, proportional climatic similarity, and distance from the native range as fixed effects. Cumulative imports did not appear to influence the incidence of invasion ($Z = 1.58$, $p > 0.05$) and was consequently removed as a predictor variable; the model was refit, and all remaining predictors were associated with changes in invasion incidence ($|Z| > 4.92$, $p < 0.0001$; Table 4). In the final model, climatic similarity

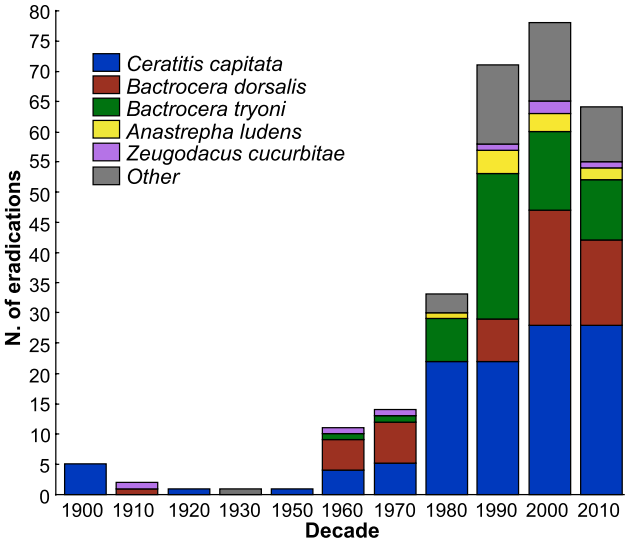

Fig. 2 Number of successful eradication programs of Tephritidae since 1900

between native and invaded countries and GDP increased the incidence of invasion, whereas distance to the native range significantly decreased the probability that a given country would be invaded (Table 4). Results from fitting the model to data where we included insect-country combinations based on the presence of an eradication program in addition to the presence of a self-sustaining population, yielded nearly identical results to those described above.

The estimated model for the mean probability of invasion (Table 5) indicated that *Ceratitis capitata* had the highest invasion probability (38%), followed by *Bactrocera dorsalis* (25%), *Bactrocera oleae* (18%), *Zeugodacus cucurbitae* (13%) and *Euaresta bullans* (11%).

Discussion

The family Tephritidae is one of the groups of insects with the greatest impact on agriculture and thus of high biosecurity concern (White and Elson-Harris 1992; Qin et al. 2015). The genera containing the most species that have established outside of their native range are *Anastrepha, Bactrocera* and *Rhagoletis* (Table 2). Along with *Ceratitis*, these three genera include some of the most destructive pests to global production of fresh fruit and vegetables (White and Elson-Harris 1992; Malacrida et al. 2007). Historical records show that the majority of non-native tephritids have established in only one or two countries and there are only five species (*B. dorsalis, B. oleae, C. capitata, Euaresta bullans* and *Zeugodacus cucurbitae*) that have invaded over 20 countries (Fig. 1A). Tephritids are found in almost all fruit growing areas of the world (White and Elson-Harris 1992). While the native ranges of the most damaging non-native pests within this group are mostly concentrated in tropical and subtropical climatic zones (Papadopoulos 2014), many of these species have invaded more varied climatic regions (Fig. 3, 4); for example, the two pest species *Ceratitis capitata* and *Bactrocera oleae* are native to the Afrotropics, but the non-native ranges of these species are more widely distributed, including temperate and continental regions (Duyck et al. 2004; Ekesi et al. 2009). Several studies also predict further expansion of fruit fly invasions to temperate and continental habitats, which will be increasingly suitable for tropical species as a result of climate change (e.g., Stephens et al. 2007; Ponti et al. 2009; Gutierrez et al. 2010). Furthermore, it is not unusual for species to expand or shift their climatic niche in invaded territories (Guisan et al. 2014; Hill et al. 2017) and this may explain why the

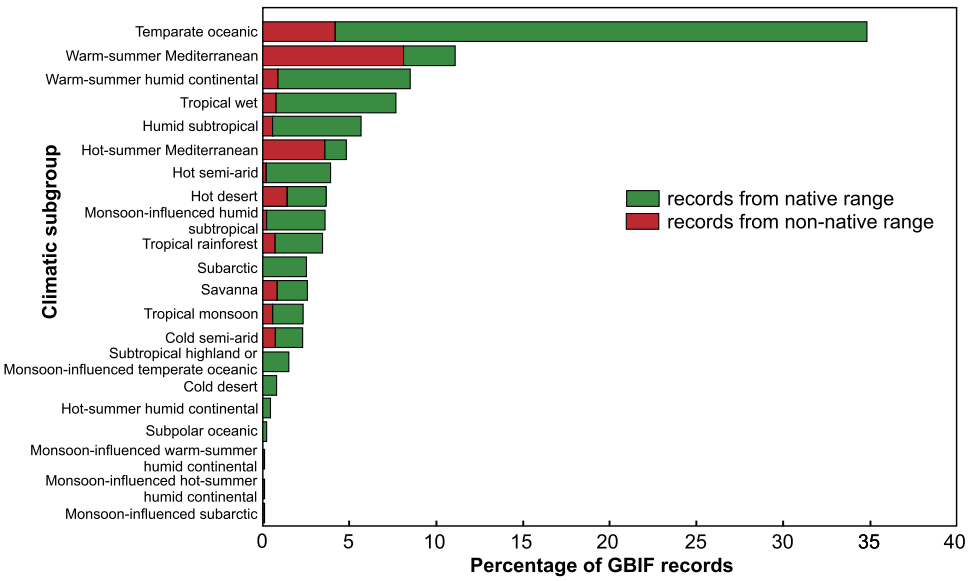

Fig. 3 Distribution of Tephritidae GBIF records among Köppen–Geiger climate classification subgroups

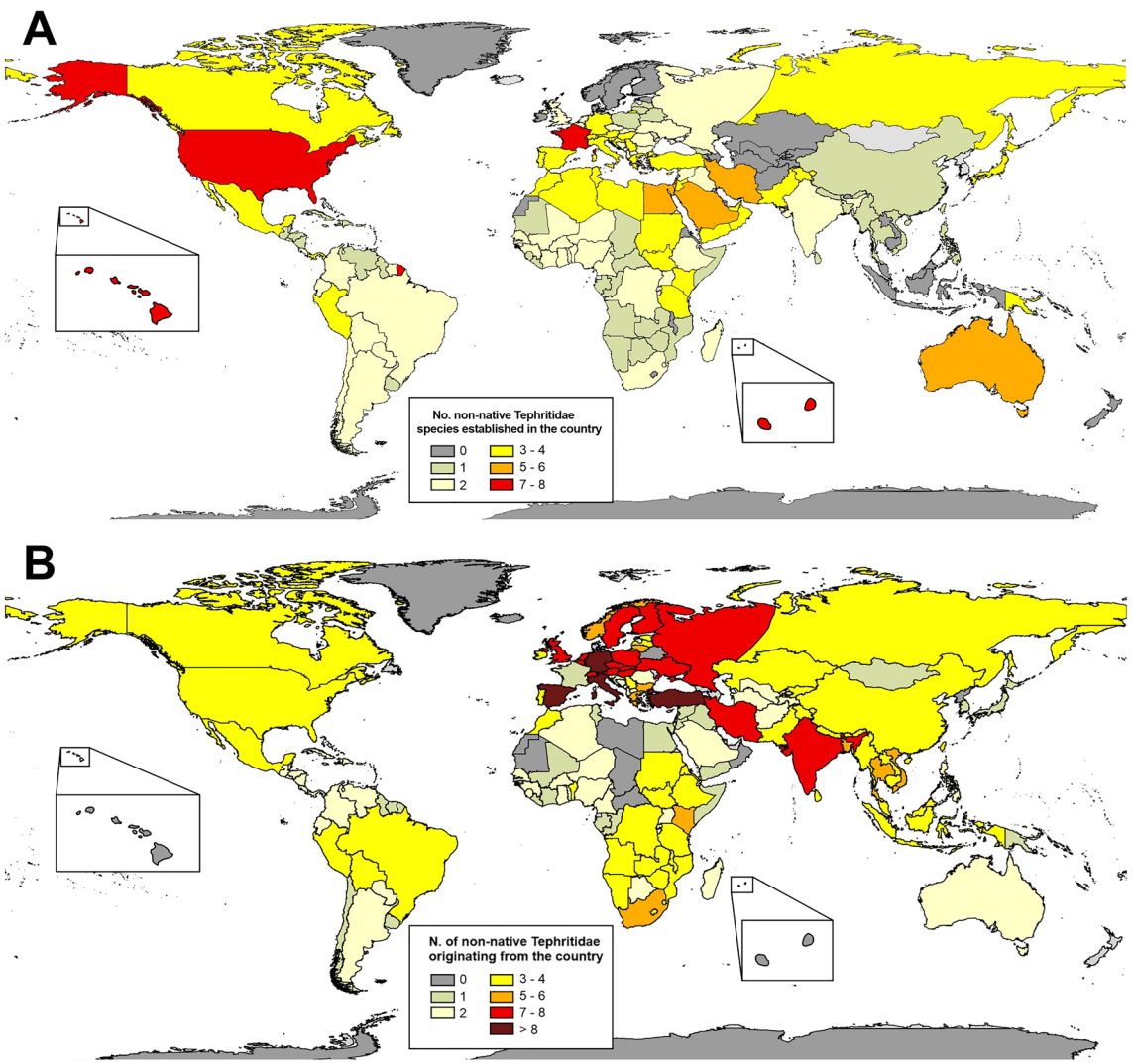

Fig. 4 Known number of non-native tephritid species established per country (**A**) and number of these non-native species originating from each country (**B**)

Table 4 Final generalized linear mixed-effects model of tephritid species invasion incidence per country. Model results including the eradication of successful invasions are presented in brackets. Model fit with a logit link function and binomial error structure with terms for species and country fit as random intercepts

Predictor	Coefficient	SE	*Z*	*P*
Intercept	− 9.87 (− 10.72)	1.25 (1.29)	− 7.93 (− 8.31)	< 0.0001
GDP	0.21 (0.24)	0.04 (0.04)	4.92 (5.50)	< 0.0001
Climatic similarity	3.47 (3.43)	0.28 (0.28)	12.26 (12.22)	< 0.0001
Distance to native range	− 0.15 (− 0.16)	0.03 (0.03)	− 5.18 (− 5.65)	< 0.0001

number of occurrences in each Koppen–Geiger classification differs between native and non-native ranges (Fig. 3).

Numbers of non-native Tephritidae vary considerably among the world regions. The Indo-Malaya region has the lowest number of established non-native species (Table 3) even though there are many species native to the region (it is the second largest source of invading species) including half of the non-native *Bactrocera* spp. The Nearctic region is the second most invaded region, mainly by *Anastrepha* spp. originating from the Neotropic region and *Rhagoletis* spp.

Table 5 Probability of invasion for the six most widely invaded Tephritidae species according to a fixed-effects only model after adjusting for predictors (i.e., estimated marginal means)

Species	Unadjusted means		Marginal means	
	P(Inv)	SE	*P*(Inv)	SE
Euaresta bullans	0.11	0.03	0.07	0.02
Bactrocera oleae	0.18	0.03	0.13	0.02
Zeugodacus cucurbitae	0.13	0.03	0.09	0.02
Bactrocera dorsalis	0.25	0.03	0.19	0.03
Ceratitis capitata	0.38	0.04	0.30	0.05

from the European Palearctic. Very strong historical trade connectivity and the high climatic similarity between the Nearctic and European Palearctic regions partly explain the high number of invasions among these regions with *Rhagoletis* spp. successfully invading from one region to another and vice versa (Tables 2, 3).

Despite its relatively low total land area, Oceania (especially the Hawaiian Islands) has been invaded by a large number of Tephritidae species, and these species have originated from all world regions. Favorable climatic conditions in the Oceanic islands, together with an abundance of cultivated non-native tropical fruit species, have facilitated numerous Tephritid invasions (Jang 2007).

Historically, the first documented Tephritidae invasions date back to the early ninetieth century with *C. capitata* establishing in Madeira (Portugal) and the Azores (Spain) (Fimiani 1989). These invasions most likely resulted from movement of contaminated fruit among countries. Several more, mostly European and Mediterranean countries, were then invaded by this species prior to its discovery in Australia in 1896 (Permkam and Hancock 1995). The number of fruit fly invasions accelerated as a result of increasing global movement of humans and international trade in agricultural commodities (Fig. 1B). Several major invasions were discovered during the early twentieth century, including the introduction of *C. capitata* and *Zeugodacus cucurbitae* to Hawaii between 1902 and 1907, *C. capitata* to Brazil in 1901 and *Anastrepha curvicauda* to Florida, USA in 1905. The number of documented invasions spiked between the two world wars (1930–1940) (Fig. 1B). Dramatic increases in global trade as a result of the free trade movement following the Second World War, as well as the burgeoning intercontinental air passenger transport network, presumably facilitated further increases in new invasions (Early et al. 2016; Paini et al. 2016). In addition, there are increasingly well-documented recent invasions and interceptions of various tephritid species globally despite major efforts to control their movement (Hill and Terblanche 2014; Papadopoulos 2014).

International movement of plant parts, particularly fruit, is considered the dominant pathway by which Tephritidae have been accidentally introduced around the world (Gould 1995; Kiritani and Yamamura 2003; Kendra et al. 2007). Fruit is moved internationally in both commercial shipments but also by international air passengers. While early Tephritidae invasions may have resulted from commercial shipments of contaminated fruit, modern biosecurity policies impose bans on fruit imports from certain regions or require preclearance inspection in the country of origin or phytosanitary treatments (fumigation, cold treatments, etc.) that greatly reduce introduction risk (Hennessey et al. 2013; Peterson et al. 2013). Consequently, during the post-World War II era the pathway of increasing dominance for Tephritid invasions has been movement of immature life stages in fruit carried by airline passengers (Satoh et al. 1985; Liebhold et al. 2006; Ma et al. 2012; Papadopoulos 2014). Thus, it seems likely that the rapid acceleration of invasions from 1950 onward (Fig. 1B) can be attributed to the expansion of commercial air passenger travel over the last 6 decades (Matsumoto 2007).

Successful invasion and establishment outside the natural range is a complex process influenced by characteristics of the environment that affect habitat invasibility, but also external processes related to propagule pressure (Simberloff 2009). For most insects, critical factors that influence habitat invasibility include climatic suitability and the availability of suitable hosts (Ward and Masters 2007; Bacon et al. 2014). Our analysis revealed that climate suitability is a key predictor of historical Tephritid invasions (Table 4). Hill et al. (2016) used climate suitability as a prerequisite for predicting future Tephritid invasions; however, they pointed out that propagule pressure and host availability are also critical to invasion success (Ward and Masters 2007; Bacon et al. 2014). Further, it should be pointed out that irrigation in arid climates might create conditions favorable for certain species in regions that would otherwise be inhospitable. We included national fruit production as another candidate explanatory variable with the expectation that it reflects Tephritid host availability in the receiving country; however, it did not enter as a significant factor predicting probabilities of invasion. This lack of prediction may reflect the fact that commercial fruit plantations are not the only resource facilitating Tephritid establishments; natural stands of native plant species and plantings of native or introduced fruit trees in residential settings may also provide crucial habitat for nascent populations (Shimizu et al. 2007; Leblanc et al. 2014).

In order to capture the effect of propagule pressure as a driver of historical tephritid invasions, we included as explanatory variables, human population, gross domestic product, number of air passengers, total cumulative imports and distance to native range (Table 1). Of these,

only GDP and distance to native range significantly contributed to explaining invasion probabilities in our final model (Table 4). However, all of these variables were positively associated with invasion incidence when fit individually (Figure S5.2B). Invasions of many types of organisms are often related to human population size (Cadotte et al. 2017; Ward et al. 2019). Urbanization may be closely related to propagule pressure associated with general movement of humans and their goods but also with invasibility related to disturbance and habitat modification. The latter is likely important in the case of tephritid resource availability in residential gardens as described above. Countries with less-developed economies typically have weaker biosecurity programs (Early et al. 2016), and this could increase invasion probabilities. Such an effect would act opposite of the positive effect of GDP described above and possibly mask a stronger impact. On the other hand, countries with low GDP may take longer to discover and report new invasions, and this may have artificially inflated the effect of GDP on invasion probability.

The negative effect of distance to the native range on invasion probability (Table 4) probably reflects higher levels of trade and travel from nearby countries along with natural diffusive spread. The absence of fruit imports from our final model may initially seem perplexing. However, fruit imports was a highly significant predictor when fit alone, but not as strongly correlated with invasion incidence as GDP (Figure S5.2C). Fruit imports likely represent a small variable fraction of total imports and as discussed earlier may no longer represent the dominant pathway by which tephritids are introduced. Unfortunately, data on cumulative fruit imports dating back to the early 1800s were not available which would have allowed more critical testing of this pathway. Furthermore, we only considered imports from native ranges, whereas new invasions often originate from previously invaded regions, a phenomenon described as the "bridgehead effect" (Bertelsmeier and Keller 2018). Indeed, for widespread non-native tephritids, such as Ceratitis capitata, most new invasions may not originate from the native range (Karsten et al. 2015).

Despite these limitations, results of our analyses can inform the planning of tephritid surveillance programs. Specifically, they suggest that at large spatial scales, incursions are more likely in regions of high economic intensity; given the elevated invasion risk in these regions, it may be preferable to concentrate surveillance in such areas. Additionally, certain species such as *Ceratitis capitata* have higher probabilities of invading new regions after adjusting for other factors (Table 5). Overall risk can be assessed by combining these probabilities with anticipated impacts and can guide the selection of pre- and post-border biosecurity programs (e.g., Lance et al. 2014).

Despite the implementation of intense biosecurity efforts designed to prevent new tephritid invasions in many countries (including extensive surveillance and eradication programs, Fig. 2) (Suckling et al. 2016), it can be anticipated that more invasions will continue in the future. Probably most species have not yet invaded all areas that contain suitable hosts and are climatically suitable, especially under a changing climate (Vera et al. 2002; Stephens et al. 2007). Though Fig. 1B suggests a drastic decrease in numbers of new invasions since 2010, this may be an artifact of the typical delay in reporting (Smith et al. 2018). As is the case for most invading species, there is likely a considerable "invasion debt" of Tephritidae, i.e., species may have established that have not yet been discovered (Essl 2010, MacLachlan et al. 2021). Furthermore, it is probable that many of the species that so far have only invaded relatively small areas (Fig. 1A) may continue to expand into much larger areas in the future.

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