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Prevalence and drivers of a tree-killing bark beetle, *Ips typographus* (Coleoptera, Scolytinae), in international invasion pathways into the United States

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Abstract

The unintentional transport of insects beyond their native ranges has greatly increased with globalization over the past century, leading to higher propagule pressure in non-native ranges of many species. Knowledge about the prevalence of a species in international invasion pathways is important for predicting invasions and taking appropriate biosecurity measures. We investigated the spatiotemporal patterns and drivers of interceptions – detections of at least one individual with imported goods that potentially serve as a proxy for arrival rates – for a tree-killing bark beetle, the European spruce bark beetle (*Ips typographus* L.; Coleoptera: Scolytinae), in the United States from 1914-2008. Across the study period, there were 505 interceptions of *I. typographus* with shipments originating from >25 countries at ports in 22 US states. Interceptions first occurred in 1938, peaked at 33 and 25 in 1984 and 1996, respectively, and declined after the mid-1990s. Interceptions of *I. typographus* did not have a statistically detectable relationship with outbreak levels in the native range, were inversely related to annual import volume (an artefact likely driven by changes in inspection policies), and more frequent during the winter. Thus, while interceptions of *I. typographus* are challenging to predict, we found evidence that (i) biosecurity practices against this beetle could be increased during winter but not in response to outbreaks in source regions and (ii) the overall abundance of this beetle in invasion pathways has recently decreased, probably because strengthened phytosanitary protocols have reduced contamination levels and/or decreased the perceived need for inspections.

Keywords: bark beetles, invasions, *Ips,* outbreaks, pathways, *Picea*, trade, wood packaging

Introduction

The rising volume of internationally traded goods with globalization has increased arrival rates of non-native insects (Bertelsmeier et al. 2017; Seebens et al. 2020). Non-native insects often arrive with imported host plants or through hitchhiking on non-host cargo goods and associated packaging materials (Meurisse et al. 2019; Gippet et al. 2019). Currently, a large fraction of general cargo is transported with solid wood packaging material that functions as a pathway for the movement of many types of bark and wood-boring insects (Aukema et al. 2010; Brockerhoff and Liebhold 2017; Meurisse et al. 2019). Increased arrival rates can equate to higher propagule pressure and enable arriving insects to overcome demographic barriers to establishment (Simberloff 2009; Brockerhoff et al. 2014). Thus, the processes preceding arrival, such as those governing entry of organisms into invasion pathways, play key roles in invasions (Sinclair et al. 2020).

The prevalence of wood-boring insects in invasion pathways is a complex function of socio-economic factors (Chapman et al. 2017; Saul et al. 2017; Faulkner et al. 2020), driven in part by (i) the selection of tree species and geographic region of source materials (Krishnankutty et al. 2020), (ii) efficacy of and compliance with phytosanitary treatments required under national and international phytosanitary regulations (e.g., International Standards for Phytosanitary Measures No. 15; ISPM 15) (Haack et al. 2014), and/or (iii) changes in import volumes associated with global invasion pathways (Seebens et al. 2018; Sikes et al. 2018). Indeed, ISPM 15 was implemented in 2006 in the US (Haack et al. 2014) and, by mandating the heat, chemical, and/or physical (e.g., debarking) treatment of wood packaging materials, was aimed at reducing infestations and/or the need for inspections. Furthermore, ecological factors that mediate intra- and inter-annual variation in abundances of insect populations located in exporting regions could also influence the composition and abundance of species in invasion pathways. For example, the increased abundance of a species at a single location or range expansion into novel locations could alter the likelihood that harvested trees or wood packaging are contaminated. Understanding the factors that govern species entry into pathways could provide crucial information on biosecurity risks, such as which species are likely to arrive.

In addition to total numbers of arrivals, the distribution of arrivals through space and time is of critical importance to establishment success (Drake and Lodge 2006; Simberloff 2009; Sinclair et al. 2020). Depending on the robustness of invading populations to demographic vs. environmental stochasticity, there likely exists an optimal dispersion of arrivals in space and time that maximizes the probability of establishment. For an insect with a high Allee threshold (i.e., needing to arrive with high densities of conspecifics), it might be beneficial for arrivals to be concentrated in a few locations and years to potentially maximize the arriving population size and chance of establishment. For a species with a low Allee threshold, arrival of populations over a wider area and over a greater number of years might increase the chance that some initial populations arrive in conditions that are suitable for establishment. Knowledge of how arrivals are distributed through space and time, and factors that govern variation therein, could help with forecasting invasion risks.

Bark beetles (Coleoptera: Curculionidae: Scolytinae) pose serious threats to biosecurity, owing to their frequent movement in raw wood and wood packaging, their potential damage to trees and timber, and the ability of some species to undergo large-scale outbreaks (Lantschner et al. 2020). Outbreaks of various scolytines cause extensive tree mortality in both their native and non-native ranges (Gregoire et al. 2015; Morris et al. 2018) and, potentially through salvage and export of beetle-killed timber, could increase arrival rates in non-native regions. The most economically damaging bark beetle in Europe, the European spruce bark beetle (*Ips typographus* L.), mainly colonizes Norway spruce (*Picea abies* (L.) H. Karst.), other species of *Picea*, and occasionally non-preferred *Pinus* spp. (Økland et al. 2011; Flø et al. 2018). Outbreaks of this insect frequently result in vast areas of killed trees. Landowners often attempt to recover value from these trees via salvage felling and some countries legally mandate sanitation felling to reduce the risk of infestations spreading. Consequently, the temporal dynamics of salvage and sanitation felling track the dynamic patterns seen in *I. typographus* outbreaks (Zahradník and Zahradníková 2019) and this could potentially cause pulses in infested wood packaging material used in exports. From 1950-2000, this beetle comprised approximately 11% of intercepted bark beetle species in the US (Brockerhoff et al. 2006), where several native *Picea* spp. are widespread and the climate is suitable for reproduction of *I. typographus* (Bentz et al. 2019). Indeed, this insect is one of the main target species for the Early Detection Rapid Response program operated by the USDA Forest Service (Rabaglia et al. 2019) and the USDA Exotic Wood Borer/Bark Beetle Survey (Jackson and Molet 2014). Moreover, trapping surveys have detected the presence of *I. typographus* three times in the US since the early 1990s, most recently in the early 2000s, but there is no evidence that reproducing populations have ever established in the US (Cavey and Passoa 1993; Waltz and Washington 1996; Humphreys and Allen 1999; CERIS 2013).

Interceptions at ports provide insight into the prevalence of species in international invasion pathways (Turner et al. 2021). Quantifying the presence of species in pathways and numbers of interceptions per year can serve as proxies for propagule pressure (Brockerhoff et al. 2014; Liebhold et al. 2017; Turner et al. 2020), elucidate intra- and inter-annual risks of introduction (Liebhold et al. 2006; McCullough et al. 2006; Nahrung and Carnegie 2021), and thereby assess invasion risk. Here, we quantify spatiotemporal patterns of annual interceptions of *I. typographus*, investigating the roles of outbreaks in the native range, import volume, country of origin, and seasonality in the prevalence of this species in international invasion pathways into the United States.

Materials and Methods

Interception/inspection data

Bark beetle interceptions from inspections across all inspected pathways (e.g., wood, wood packaging materials) at ports in the US from 1914-1984 were obtained from reports published by the US Department of Agriculture (USDA) and equivalent records from 1985-2008 were obtained directly from USDA – Animal and Plant Health Inspection Service (USDA-APHIS). Data from 2009-2018 were also obtained from USDA-APHIS but not formally analyzed because our outbreak data ended in 2008 (see below) and only 10 interceptions occurred post-2008 (2009 [1 interception], 2012 [2], 2013 [2], 2014 [3], and 2015 [2]). From 1985 onwards, there was improved documentation (e.g., source country, arrival location, month) for interceptions of *I. typographus*. Interceptions from 1914-1984 were published in book form as a summary in which total annual interceptions were reported with a list of source countries (i.e., interceptions were not reported by individual country). Owing to the improved data quality, some of our analyses, described in detail below, only evaluated the post-1985 data.

The data and associated inspection protocols are described in detail by Haack (2001, 2006) and Brockerhoff et al. (2014), but a generalized, brief description of the data are as follows. Inspectors from the US Departments of Agriculture and Homeland Security inspect cargo at ports, often prioritizing high-risk pathways (e.g., by cargo type and/or country), with typically <2% of cargo inspected annually (Haack 2001, 2006; Brockerhoff et al. 2006). Inspections are typically conducted at maritime ports, but some are also made at inland cargo transit facilities. Only discoveries of organisms that are categorized as "actionable" or "reportable" are typically recorded, but a species could change designation (e.g., from non-reportable to reportable, and vice versa) through policy updates (Haack 2006).

These data, therefore, do not constitute a random sample and represent only a small fraction of insects arriving at ports. Inspection priorities and import policies vary through time (e.g., biosecurity agencies may elect to fumigate a shipment vs. identifying intercepted insects), especially as new international phytosanitary regulations are implemented (Lawson et al. 2018). Annual interceptions are reported as the number of times a species was detected, but numbers of individual insects associated with each interception are rarely documented. Despite the limitations on these data, interception frequency can be statistically associated with probability of establishment for some (Brockerhoff et al. 2014; Turner et al. 2020) but not all species (Saccaggi et al. 2016), and interception data can provide insight into the composition of arrivals and intraspecific differences in abundance within a given pathway (Turner et al. 2021). Unless specified otherwise, all analyses were of *I. typographus* interceptions.

Spatiotemporal trends in interceptions (worldwide, 1914-2008)

All analyses were completed using R (R Core Team 2021) and the following packages were used for graphing and analyses: raster (Hijmans 2020), rgdal (Bivand et al. 2019), and tidyverse (Wickham et al. 2019). We first analyzed temporal trends in the annual raw numbers of interceptions. These counts were then standardized in order to remove trends driven by changes in inspection efforts and better isolate changes in the absolute prevalence of *I. typographus* in pathways. The data were standardized by dividing total interceptions of *I. typographus* per year by the total number of scolytine interceptions on the wood packaging materials pathway in the corresponding year. Interceptions of *I. typographus* were included in the total interceptions so that values ranged from zero to one. The materials on or in which *I. typographus* interceptions occurred were also qualitatively summarized.

The years reported in the interception data were US fiscal years (October to September), but before 1976 the fiscal year was July to June and we did not adjust the temporal resolution to account for this change or the fact that fiscal years span across parts of two calendar years. Moreover, there were three instances for which interceptions from two fiscal years were published jointly in a single report. For those few records spanning two-years, we divided the interceptions evenly between the two years.

Drivers of interceptions (central Europe, 1985-2008)

We evaluated whether annual outbreak levels of *I. typographus* in its native range and/or annual import volume drove changes in standardized interceptions from 1985-2008, a time period for which country of origin could be accurately determined for each interception. The approximate annual volume (m^3 per year) of timber loss attributed to *I. typographus* were previously reported in Marini et al. (2017). The interception and outbreak data were subset to central Europe, which meant that data from Austria, Belgium, France, Germany, Italy, and Switzerland were considered and data for Norway and Sweden (the only other countries analyzed in Marini et al. (2017)) were removed. Outbreaks in central Europe were generally synchronous compared with the time series from Norway and Sweden (Appendix 1), and thus focusing on Central Europe enabled us to analyze a congruent measure of region-wide abundance of *I. typographus*. Similarly, outbreak data from southern Europe were largely lacking so we did not consider interceptions from that region either. This step also served to remove interceptions of *I. typographus* from Asia, which we assumed were of the subspecies *I. typographus japonicus* (Christiansen and Bakke 1988). Outbreak data were standardized by region ([x-mean]/sd), averaged by country, and then averaged across all countries, producing one estimate of volume losses per year. We then obtained import volume for the corresponding central European countries from the US Census. To adjust for inflation, import values in each year *i* were expressed in 2008 US$ using the consumer price indices: CPI in 2008 / CPI in year *i* × imports (US$) in year *i*.

Graphical inspection of the data indicated that (i) quadratic and ln(*x*)-transformed terms were the most appropriate for evaluating the effects of outbreaks and imports, respectively, on interceptions, (ii) there were no positive, delayed effects of tree mortality on interceptions (i.e., interceptions did not appear to lag behind outbreaks; Appendix 2). We developed multiple competing models by regressing standardized interceptions of *I. typographus* on first and second order terms for annual timber losses ($volume+volume^2$), annual value of goods ($) imported to the US from central Europe (*imports*, ln(*x*)-transformed), and a full model with all terms ($volume+volume^2+imports$) using multiple linear regression. Temporal autocorrelation among residuals in best fitting models were checked using a Durbin-Watson test conducted using the lmtest package in R (Zeileis and Hothorn 2002) and no issues were detected (all $DW < 1.60$ and $p>0.05$). Graphical inspection of residuals was used to confirm assumptions of homoscedasticity and normality were met.

Selection between competing models was performed using a similar approach to Marini and Zalucki (2017) by using the MuMIn package (Barton 2022). The fit of each candidate model was evaluated using Akaike's information criterion corrected for small sample size (AICc). The *dredge()* command was used to rank models using ΔAICc compared with the model with the lowest AICc value (i.e., the best fitting model) and ΔAICc > 2 was used to determine if a model was a significantly better fit. Akaike weights (w_i) estimating the likelihood of each model relative to all models (Burnham and Anderson 2002; Wagenmakers and Farrell 2004) were calculated using:

$$\mathrm{w}_i = \frac{\exp(-0.5 \times \Delta\mathrm{AICc}_i)}{\sum_i^k \exp(-0.5 \times \Delta\mathrm{AICc}_i)}$$

where w_i can be interpreted as the probability that model *i* is the best model (Wagenmakers and Farrell 2004). Model averaged coefficients and 95% confidence intervals for models with ΔAICc < 2 were estimated using the *model.avg()* and *confint()* functions, respectively. A parallel modeling process was also conducted using the exact same steps as above but focusing on data from 1985-2005 to evaluate potential effects of the implementation of ISPM 15 in 2006 (Haack et al. 2014). This secondary analysis was conducted to determine if low interceptions from 2006-

2008 served as "leverage" points and potentially drove any relationships between standardized interceptions and our predictors.

Time series of interceptions and outbreaks were not analyzed individually by country (e.g., modeling interceptions from Italy as a function of outbreaks in Italy), given that (i) time series for annual number of interceptions and damage per country were limited and (ii) we had imperfect information on the origins of wood packaging material (e.g., wood packaging materials can be re-used, even leading to interceptions from countries where *I. typographus* is not established).

Geographical and seasonal pattern of interceptions (1985-2008)

We then investigated geographical patterns in *I. typographus* interceptions by analyzing source countries and arrival locations from 1985-2008. We first mapped the number of interceptions per country in Europe. Note that some interceptions were recorded from Yugoslavia but not any of the succeeding countries (i.e., Bosnia and Herzegovina, Croatia, Kosovo, Montenegro, North Macedonia, Serbia, and Slovenia), and thus Yugoslavia was represented on our map of continental Europe. All interceptions from the USSR occurred prior to 1985 whereas interceptions from Russia began in 1993 (see Results); thus, USSR interceptions were also not distributed across historical members for analyses. Given the high number of source countries, we extracted all countries that were associated with ≥5 total *I. typographus* interceptions across the time series and graphed both total interceptions per country and the time series of interceptions from those countries. To investigate geographical variation in interception locations, we mapped numbers of interceptions made in each US state, overlaying the locations of *I. typographus* discoveries in trapping surveys (Cavey and Passoa 1993; Waltz and Washington 1996; Humphreys and Allen 1999; CERIS 2013). The geographical distribution of host *Picea* spp. in the contiguous US was also mapped. Host tree data were obtained from interpolated rasters developed using USDA Forest Service - Forest Inventory and Analysis plot data (Wilson et al. 2013) and occurrence points obtained from the Global Biodiversity Information Facility (GBIF 2022). We also quantitively summarized the materials on or in which *I. typographus* interceptions occurred.

Lastly, data on time of year (month) of interceptions were analyzed to determine if insect seasonality influenced interceptions. These data were only available from 1985 onwards and interceptions were modeled as a function of second and first order terms for month (integers, 1-12). Graphical inspection of residuals was used to confirm assumptions of homoscedasticity and normality were met. In the results, estimates are provided as mean ± SE unless specified otherwise.

Results

Ips typographus was intercepted 505 times in the US from 1914-2008, averaging 5.3 (± 0.83; range: 0-33) interceptions per year. Across the entire time series, interceptions occurred in 48.4% of years. After the first interception occurred in 1938, however, this insect was intercepted in 64.8% of years from 1938-2008. This meant that there were 49 years in which no interceptions occurred, but from 1974-2008, there had been at least one interception of *I. typographus* per year. Indeed, interceptions were highly variable through time and exhibited peaks of 33 in 1984 and 25 in 1996 (Figure 1a). Interceptions were associated with a variety of materials (crating, pallets, dunnage, and wood) and goods that ranged from tiles and machinery to circuit breakers and books. In some instances when the host material was listed as wood, *Pinus* sp. or *Picea* sp., we could not determine whether the documentation was referring to wood packaging materials. There was one interception documented in baggage, one on a *Paphiopedilum* sp. (lady slipper orchid, Orchidaceae), and two listed as "at large" (potentially indicating that beetles had emerged in transit). Considering that most of the interceptions were from shipments of inanimate goods (e.g., tile, machinery, etc.), we conclude that *I. typographus* was transported in packaging accompanying these goods. Standardizing interceptions (Figure 1b) by total scolytine interceptions (Figure 1c) indicated that, in addition to becoming less prevalent in international pathways into the US, *I. typographus* comprised a smaller percentage of intercepted scolytine species by the mid-1990s (i.e., decreases in interceptions of *I. typographus* were apparently not only attributable to decreases in inspection efforts).

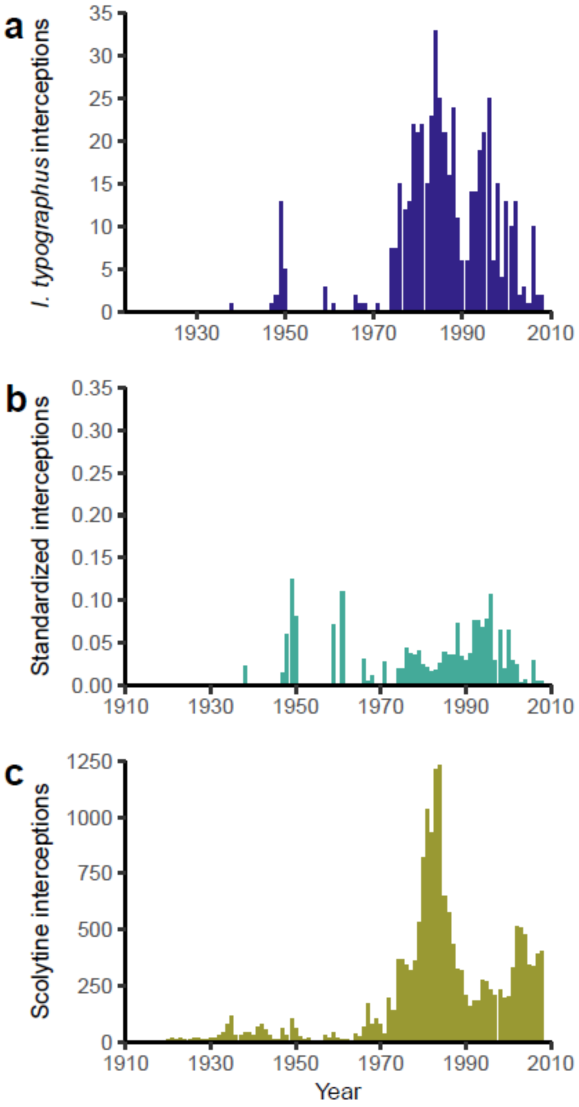

Figure 1 (a) Unstandardized and (b) standardized interceptions of European spruce bark beetle, *Ips typographus*, along with (c) interceptions of all scolytines at ports in the US through time (1914-2008). Standardized interceptions are the number of *I. typographus* interceptions divided

by the total number of scolytine interceptions on an annual basis. Only interceptions made on wood packaging material were analyzed.

Over 25 countries exported cargo that was found to be infested. Note that interceptions from Asia (China, India, Japan, South Korea) occurred in 11 years from 1966-1998, five of which occurred post-1984 (two in 1985, one in 1997, and two in 1998); such interceptions were likely the subspecies *I. typographus japonicus*. Prior to 1985, there were 9 years that had at least one interception with an unknown origin whereas from 1985 onwards there were five interceptions (1.88%) for which the origin was completely unknown and eight interceptions (3.0%) from an unknown location in Europe. Most *I. typographus* interceptions occurred on materials imported from the insects' native range, but some interceptions were found with cargo that arrived from countries (e.g., United Kingdom, Malta) in which the insect was not known to be established; such countries likely re-used infested wood packaging materials that was originally imported from the native or invaded range of *I. typographus*.

The multi-model inference analysis indicated that the best fitting model only included the effects of import volume on interceptions; all other models were associated with ΔAICc > 2 (Appendix 3). The best fitting model suggested that standardized interceptions were negatively correlated with import volume (slope: -0.03 ± 0.01, $t = -2.77$, $p < 0.0110$; model AICc: -110.08). When analyzing these data from 1985-2005 to exclude potential effects of ISPM 15, there was no longer a statistically clear effect of imports on interceptions (Appendix 3). Taken together, these analyses indicated that neither outbreaks in the native range (Figure 2a) nor import volume (Figure 2b) influenced the prevalence of *I. typographus* in invasion pathways from central Europe.

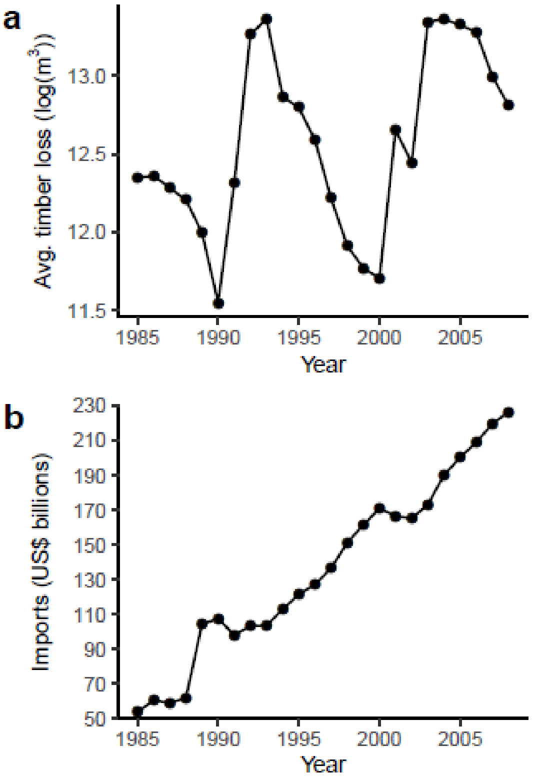

Figure 2 Time series (1985-2008) for (a) volume of timber loss attributable to *Ips typographus* and (b) annual imports (US$ billions adjusted for inflation) from central European countries (Austria, Belgium, France, Germany, Italy, and Switzerland).

A total of 283 interceptions occurred from 1985 onwards, 265 of which originated from 24 European countries (Figure 3). The remaining 18 interceptions were either of an unknown origin (13), China (3), or Japan (2).

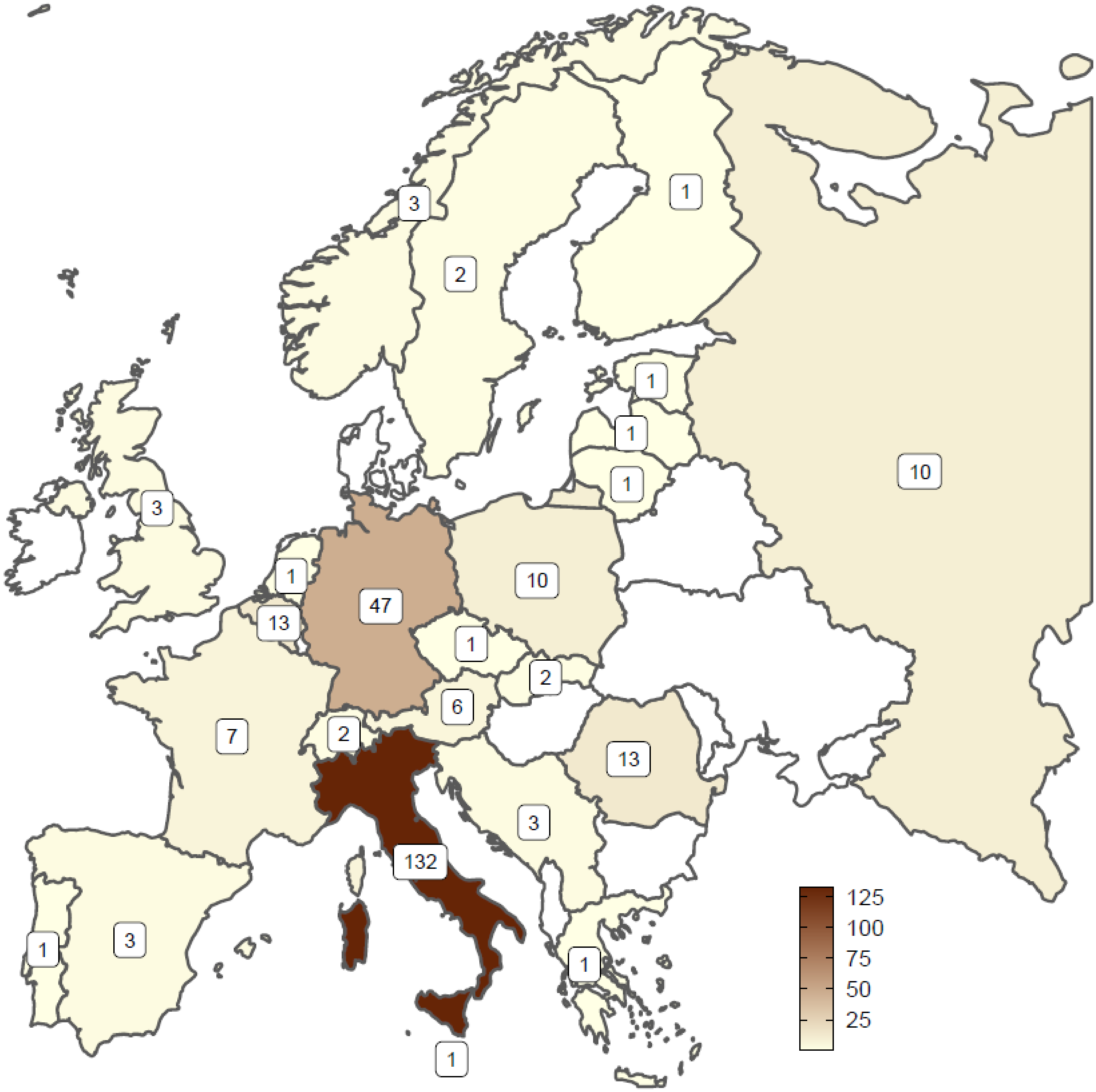

Figure 3 Total number of interceptions from countries on the European continent from 1985-2008.

Eight exporting countries were associated with ≥5 interceptions: Austria, Belgium, France, Germany, Italy, Poland, Romania, and Russia (Figure 4a). Patterns of arrival from source countries varied through time; for example, all interceptions from Russia occurred between 1993-1999 (there were no interceptions from 1985 onwards from the USSR) whereas interceptions from Romania only occurred after 2000 (Figure 4b).

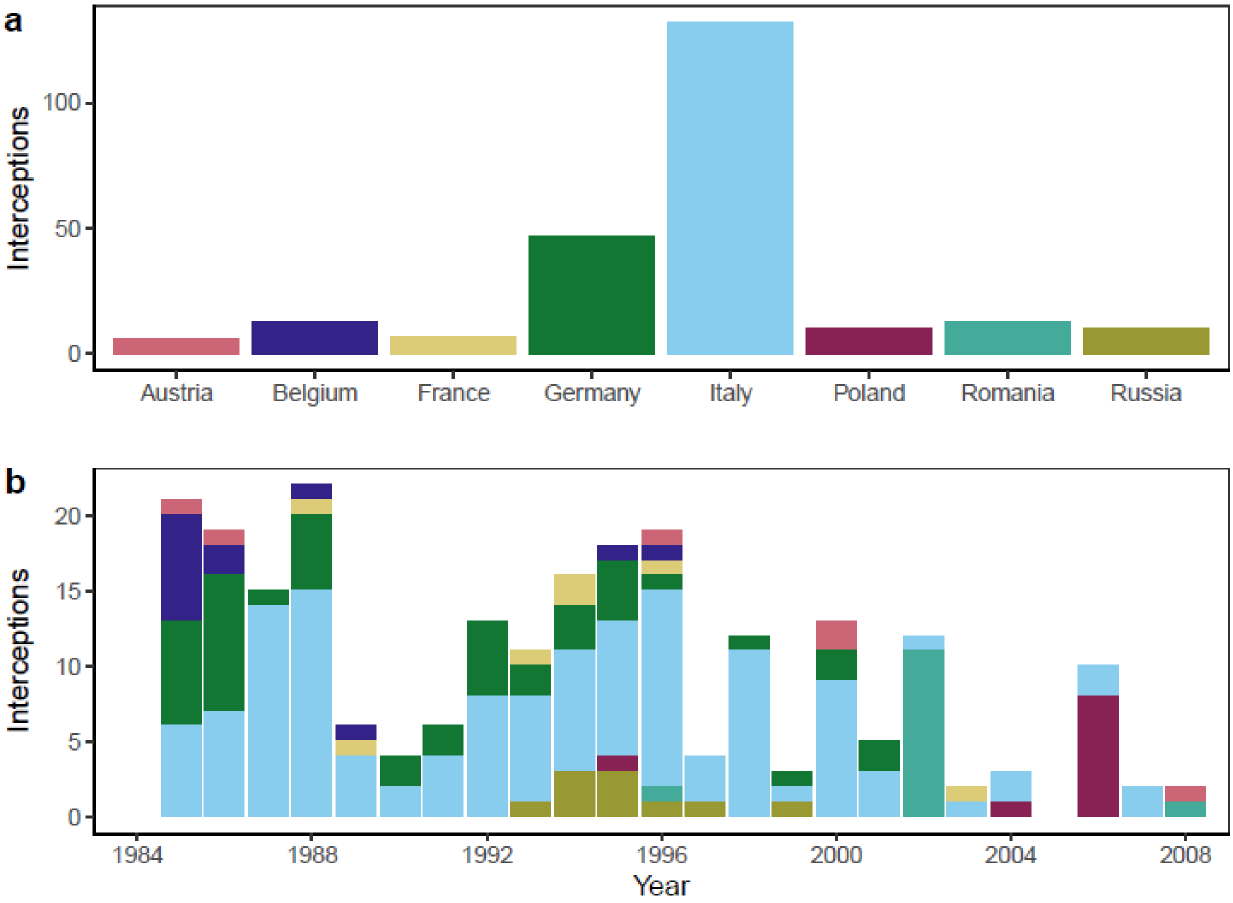

Figure 4 (a) Total interceptions from each country and (b) number of interceptions per year from each country for *I. typographus* in the US from 1985-2008. Color-country pairings are consistent between panels. Due to the high number of origin countries (Figure 4), only countries associated with ≥5 interceptions are displayed.

Interceptions were concentrated at ports in the southeastern US (Figure 5a), a region with few naturally occurring, preferred host trees (i.e., spruces, *Picea* spp.) (Figure 5b). However, some interceptions did occur in the Northeast, Midwest, and Pacific Northwest, regions which contain extensive forested areas with preferred host tree species (Figure 5).

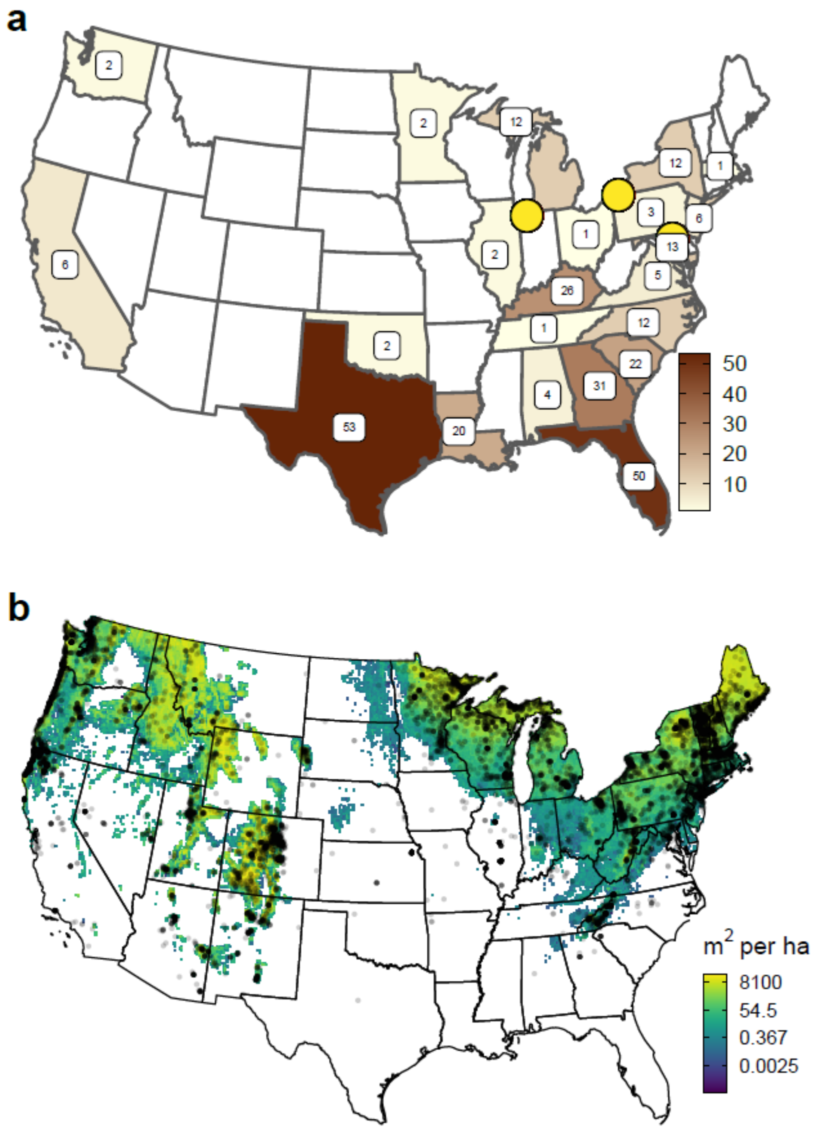

Figure 5 (a) Number of interceptions of *I. typographus* per US state (1985-2008) with locations of three historical detections in traps in Pennsylvania (early 1990s), Indiana (1995), and Maryland (2002). State-level interception records were not available before 1985. (b) Presence of preferred hosts (*Picea* spp.) in the conterminous US according to USDA FS Forest Inventory and Analysis data (yellow-green scale) and GBIF records (black dots). Note that (i) interception locations do not often reflect final destinations of infested cargo and (ii) spruce species are widely used in urban plantings in the US but a complete inventory of such plantings does not exist, and (iii) white areas on panel b do not contain spruce.

From 1985 onwards, tiles were the imported good most commonly associated with interceptions, with 83 (29.3%), followed by machinery (n = 27, 9.5%), marble (17, 6.0%), parts (14, 4.9%), steel (9, 3.2%), and granite (8, 3.2%). We caution that some interceptions were listed on dunnage (41, 14.5%) or crating (18, 6.4%) and that items such as marble or granite could also refer to tiles. Interceptions exhibited some seasonality, with peak interceptions occurring in October-April (21-49 interceptions per month) and markedly lower interceptions from May-September (1-11 per month) (model summary statistics: $F_{2,9}$=7.98, p =0.0031, R^2 = 0.56; Figure 6).

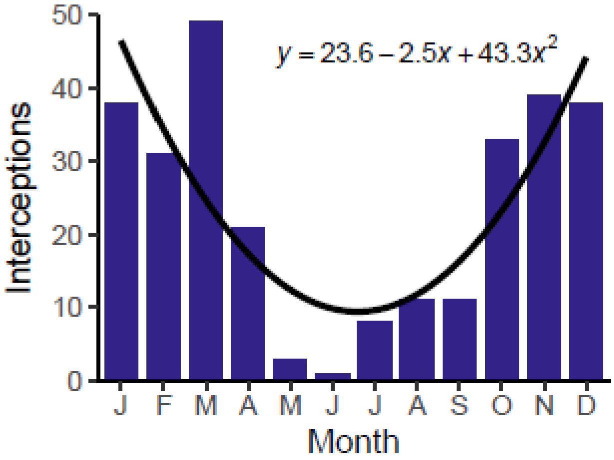

Figure 6 Monthly patterns of *Ips typographus* interceptions in the United States (1985-2008). Model summary statistics: $F_{2,9}$=3.99, p =0.0101, R^2 = 0.56.

Discussion

Ips typographus has been frequently detected in international invasion pathways into the US (Figure 1a) and, given its economic importance in Europe, poses serious threats to North American spruce forests if it were to establish (Bentz et al. 2019). Given the high frequency of historical arrivals, it is not surprising that this species has been detected in surveillance traps in the US three times. But despite the high propagule pressure, no known establishment has ever occurred in the US, although the beetle has demonstrated its potential for invasion by recently establishing in the United Kingdom (UK Forestry Commission 2021). Invasion failure by this species in the US may be explained by the existence of Allee effects (Nelson and Lewis 2008), as a sufficiently high number of conspecifics is required for *I. typographus* to overcome host resistance of live trees, although it readily attacks freshly dead spruce such as windthrown timber and large diameter slash (Eriksson et al. 2005; Hroššo et al. 2020). Such hosts are likely highly ephemeral in densely populated urban areas where most non-native insect arrivals likely occur (Branco et al. 2019; Ward et al. 2019). Although *I. typographus* has been present frequently in cargo arriving from Europe, beetles may not arrive in sufficient numbers to overcome host tree resistance and successfully reproduce. We caution that our analyses were entirely focused on pathways into the US, and do not necessarily reflect trends in international invasion pathways into other countries or regions.

The negative association of *I. typographus* interceptions with annual import volume along with recent (mid 1990s onwards) declines in *I. typographus* interceptions (Figure 1c) may indicate changes in phytosanitary practices, including a potential decrease in prioritization of inspecting wood packaging material. Increased awareness of the risks of wood packaging material and associated biosecurity practices began in the late 1990's as a result of incursions by the Asian longhorned beetle and other woodboring insects (Haack 2006). These efforts culminated with the implementation of ISPM 15 in the 2006 which required phytosanitary treatment of wood packaging material prior to export (Strutt et al. 2013; Haack et al. 2014).

Indeed, no association between interceptions and import volume was present when analyzing data from 1985-2005 (Appendix 3). The increase in scolytine interceptions in the 2000s, however, could be driven by a broadening of the pathways inspected rather than a true increase in arrivals; reliable temporal data on inspection efforts by pathway are not available, however.

Interceptions of scolytines can serve as a proxy for propagule pressure, as some scolytine species that were intercepted more frequently than others have been found to have a greater probability of establishment (Brockerhoff et al. 2014). Correspondence between insect abundance in the native range and propagule pressure could theoretically be used to guide inspection efforts. Indeed, increases in seasonal abundance for some species related to insect phenological development can increase the probability they get introduced (Gray 2010). Our analyses indicated that interceptions were not detectably influenced by outbreaks in the native range but varied seasonally, being less frequent during the summer months (Figure 6). We do caution that outbreak data may not be complete and that could have influenced results. For example, Italy contributed the most interceptions – which we attribute to large volumes of tiles imported to the US from Italy even though the outbreak area in Italy comprised a relatively small fraction of the total *I. typographus* outbreak area in Europe. Wood-infesting insects are often intercepted with materials used to package tiles (Haack 2006). It is possible that some interceptions originating from Italy were in pallets made from infested spruce timber imported from other European countries.

The seasonal trend could be attributable to seasonality in inspection efforts but might also be due to higher densities of *I. typographus* expected to be within trees or wood packaging materials during the overwintering period compared with the flight period in warmer months. That is, some inspections during summer might have occurred after many beetles had already emerged. Residency time in beetle-killed trees – and thus wood packaging materials – can vary markedly. Development from egg to adult averages ~34 days at 20 °C and there can be up to three generations per year, with development dependent on temperature and photoperiod (Doležal and Sehnal 2007; Schebeck et al. 2017). Adults can re-emerge within a few weeks after initial attack (Anderbrant 1989), however, and depending on the time of year and diapause, beetles can reside in trees for several months during their overwintering period (Schebeck et al. 2017). Moreover, *I. typographus* can colonize windthrown trees for at least two years following a storm (Göthlin et al. 2000), which would serve to extend the time beetles reside in trees following harvest.

We caution that interception frequency is not always an indicator of invasion risk, as several beetle species have been intercepted at ports but failed to establish, potentially owing to high Allee thresholds, lack of hosts, or high variability in the availability of environmental conditions conducive to successful establishment (Duncan et al. 2014; Essl et al. 2015; Sinclair et al. 2020). Conversely, others have established yet never been intercepted, potentially owing to high invasibility, lack of identification of intercepted specimens, and/or that import volumes are so enormous that only a small fraction can be inspected (Brockerhoff et al. 2006; Faulkner et al. 2016; Turner et al. 2020). We also note that total scolytine interceptions is not a perfect proxy for inspection efforts, as total scolytine interceptions can decrease with consistent inspection efforts if phytosanitary measures become more effective.

Ips typographus has arrived in US ports with shipments from several different countries (and was subsequently destroyed upon detection), but the exporting countries that serve as sources for contaminated cargo have varied through time (Figure 4). Moreover, the arrival of *I. typographus* in the US with cargo from countries outside of its known range indicates a possible scenario in which such source countries (i) imported infested timber to be used for wood packaging materials, (ii) reused imported wood packaging materials that were previously infested to package an export bound for the US, and/or (iii) actually harbor undetected populations of the beetle. Note this process differs from a bridgehead effect, in which previously established non-native populations serve as the source for subsequent propagules and invasions (Lombaert et al. 2010; Bertelsmeier et al. 2018).

Most interceptions of *I. typographus* in the US, as well as three detections in surveillance traps, occurred on the margins or outside of the range of naturally occurring *Picea* spp. (Figure 5), potentially inhibiting establishment. Interceptions of *I. typographus* in the southeast reflect spatial patterns of other scolytines intercepted in the US (Haack 2006), which could be driven by high import volumes into southern ports (Liebhold et al. 2013). Urban forests near ports and other cargo destinations typically contain a wide variety of planted tree species and can facilitate invasions (Poland and McCullough 2006; Colunga-Garcia et al. 2010). Indeed, Norway spruce, *Picea abies*, which is the primary host of *I. typographus* in its native range, is widely planted as an ornamental in much of the northeastern US and eastern Canada. The three locations where *I. typographus* was detected in traps (Figure 5a) were in that region. It is not clear whether the adult *I. typographus* detected in these traps emerged from imported material, were progeny from a successful colonization of host material in the US by populations that eventually went extinct (i.e., failed establishment), or represented an established population that continues to persist at low, undetectable numbers. There is a high abundance of less-preferred hosts, however, in the southeastern US. Nonetheless, we caution that interceptions at a given location are often not a reliable metric for propagule pressure and invasion risk in the surrounding area, as shipments are typically transported well beyond ports (Colunga-Garcia et al. 2009).

Our analyses provide insight into the space-time dynamics of a damaging bark beetle in international invasion pathways into the US, information that may be of use in guiding biosecurity efforts. Specifically, we show that interception frequencies of *I. typographus* were not measurably influenced by outbreaks in the insect's native range but that interception frequencies varied seasonally. Taken together, we found evidence to suggest that biosecurity practices against this beetle in the US could be increased during winter but not in response to outbreaks in source regions. However, variance in interceptions driven by changes in policy could obscure actual changes in arrival rates. Our analyses also suggest that inspection priorities might have shifted over time and this limits the use of inspection data for detecting increases or decreases in propagule pressure that would be associated with invasion risk. These results thus provide support for the ongoing shift in inspection practices in the US involving the adoption of statistically-based inspection (Katsar et al. 2017) that would provide greater power in detecting spatial and temporal shifts in propagule pressure.

Statements and Declarations

Ethical Approval

Not applicable.

Consent to participate

Not applicable.

Consent to publish

Not applicable.

Competing interests

The authors have no relevant financial or non-financial interests to disclose.

Authors' contributions

SW, EB, and AL conceived study and planned analyses. SW conducted analyses and wrote initial draft of the manuscript. RT, EB, TY, and LM helped with data curation, analysis, and interpretation. All authors contributed to writing and editing subsequent drafts of the manuscript.

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Availability of data and materials

Data reported and analyzed were collected by the US Department of Agriculture, Animal and Plant Health Inspection Service (APHIS) and are subject to data agreements. For details of the data and how to request access contact Phytosanitary.Advanced.Analytics.Team@usda.gov.

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