

ARTICLE

The role of climatic similarity and bridgehead effects in two centuries of trade-driven global ant invasions

Paul Mwebaze¹ | Andrew M. Liebhold^{2,3} | Cleo Bertelsmeier⁴ |
Derek Kellenberg⁵ | Olivia K. Bates⁴ | Michael R. Springborn¹

¹Department of Environmental Science and Policy, University of California, Davis, Davis, California, USA

²Northern Research Station, USDA Forest Service, Morgantown, West Virginia, USA

³Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Praha 6 - Suchbát, Czech Republic

⁴Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland

⁵Department of Economics, University of Montana, Missoula, Montana, USA

Correspondence

Paul Mwebaze, Department of Environmental Science and Policy, University of California, Davis, One Shields Ave, Davis, CA 95616, USA.
Email: pmwebaze@ucdavis.edu and mpaul48@hotmail.com

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Abstract

International trade continues to drive biological invasions. We investigate the drivers of global nonnative ant establishments over the last two centuries using a Cox proportional hazards model. We use country-level discovery records for 36 of the most widespread nonnative ant species worldwide from 1827 to 2012. We find that climatic similarity combined with cumulative imports during the 20 years before a species discovery in any given year is an important predictor of establishment. Accounting for invasions from both the native and previously invaded “bridgehead” regions substantially improves the model's fit, highlighting the role of spatial spillovers. These results are valuable for targeting biosecurity efforts.

KEYWORDS

bridgeheads, climatic similarity, invasion, trade

JEL CLASSIFICATION

Q57: Ecological Economics: Ecosystem Services, Biodiversity Conservation, Q56: Environment and Development. Environment and Trade, Sustainability

1 | INTRODUCTION

Nonnative insect species outnumber all other alien animal species, with nearly 500 nonnative insect species established in Japan, over 1500 in Europe and nearly 4000 in North America (Yamanaka et al., 2015). Insects also include some of the most notorious damaging invaders, with ant species noted among the most widespread and costly nonnative insects (Angulo et al., 2022; Holway et al.,

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2002; Rabitsch, 2011). Five ant species are ranked among the 100 of the world's worst invaders by the International Union for Conservation of Nature (IUCN), including the Argentine ant, *Linepithema humile*, and the Red Imported Fire Ant, *Solenopsis invicta* (Global Invasive Species Database, 2020). Within introduced regions, nonnative ants can cause declines in native biodiversity, alter ecosystem processes and trigger declines in ecosystem services such as agricultural production and human health. Nonnative ants can lead to substantial economic costs (Angulo et al., 2022). In the United States alone, the total costs associated with *S. invicta* have been estimated at \$6.7 billion per year (Lard et al., 2006). In Australia, the total losses incurred from *S. invicta* in rural industries is estimated to be \$5.1 billion over 30 years (ISSG, 2014).

Most invasions of insects are unintended consequences of globalization manifested in trade and travel. Many types of insects are inadvertently transported in cargo or accidentally introduced directly with people and their belongings via tourism, migration and during wars (Brockerhoff et al., 2006; Liebhold et al., 2006, 2012). While individual countries and international conventions have made considerable progress implementing quarantine measures to limit the movement of insects (MacLeod et al., 2010), increases in trade and travel continue to drive insect movement worldwide (Liebhold et al., 2016). Garnas et al. (2016) and Roques et al. (2016) provide evidence to show that invasive insect species are spreading much faster now than in the past likely due to rapid changes in the pathways. To develop more effective strategies for minimizing future invasions and their impacts, it is necessary to understand both the biogeographic and socioeconomic drivers of invasions as well as their interactions. Even though there has been good progress in identifying specific invasion pathways that are responsible for transporting insects in trade (Gippet et al., 2019; Meurisse et al., 2019), the connection between imports and insect invasions remains murky.

To address these issues, we analyze historical patterns of ant invasions globally and over many decades to elucidate the individual roles of—and interplay between—biogeographic and socioeconomic drivers. Biological drivers in the form of species attributes have been emphasized in the ecological literature as key drivers of invasion patterns for insects and other taxa (Allen et al., 2017; Capellini et al., 2015; Hill et al., 2016; Jeschke & Strayer, 2006; Lester, 2005; Sol et al., 2012). Specifically for ants, several studies have identified ecological traits often associated with invasive species (Fournier et al., 2019; Lester, 2005; Lloret et al., 2005; Wittenborn & Jeschke, 2011). While these studies make clear the important role of biology, they have typically done so in isolation from socioeconomic drivers. Two exceptions within the ecological literature highlight the important role of trade as a key driver, including Westphal et al. (2008) who found it was the most important explanatory variable in a global study of invasions across all taxa and Liebhold et al. (2016) who showed it was more strongly linked to global insect invasions than was the life history of the species involved.

The economics and environmental management literature has focused on imports as a key driver, highlighting that this risk varies among trading partners (Costello et al., 2007; Dalmazzone & Giaccaria, 2014; Hlasny & Livingston, 2008; Hulme, 2021). Using historical trade data, both Costello et al. (2007) and Essl et al. (2011) showed the importance of prior economic variables (trade and GDP) on current discoveries of biological invasions (in San Francisco, United States and European countries, respectively). Overall, these studies found that imports contribute significantly to biological invasions, however, they mostly focussed on trade and ignored biological drivers such as species characteristics and climatic similarity. However, as we show, these drivers do not operate independently but rather interact with one other.

An important feature of global invasions that was, until recently, absent from economic and ecological analyses of historical invasions is the so-called “bridgehead effect,” where previously invaded regions serve as the source of additional invasions elsewhere through secondary introductions (Bertelsmeier & Keller, 2018; Lombaert et al., 2010). Bridgeheads are a form of “spatial” spillover in trade-facilitated invasions, where invasion of a new region creates a spillover risk for their trading partners (Barbier & Shogren, 2004; Zipp et al., 2019). Yet, most analyses ignore the extent of these spatial spillover effects (e.g., Perrings et al., 2000). In the context of marine

invasions, Keller et al. (2011) was an early example of research highlighting the role of stepping-stone invasion processes. More recently, Bertelsmeier et al. (2018) showed that bridgehead effects play a major role in ant invasions in the United States and New Zealand. While these studies illustrate the pivotal role of bridgeheads in shaping insect invasions globally, the relative importance of bridgehead effects within the broader set of biogeographic and socioeconomic drivers still remain uncertain and thus important for study (Ricciardi et al., 2021).

A final key environmental driver—and one that modulates the role of imports and the network of potential bridgeheads—is the habitat suitability of the receiving environment. A proxy for this suitability is the climatic similarity (CS) between a species' native range and a new environment, which has been found to be a major determinant of the probability of species establishment (Duncan, 2016; Pauchard et al., 2004; Roura-Pascual et al., 2011; Thuiller et al., 2005). Three economic studies have either implicitly or explicitly accounted for this factor. Costello et al. (2007) allow for the “infectiousness” of imports to vary by exporting partner, but only at the aggregated scale of seven global regions. The regional distinctions thus coarsely account for a host of factors (CS and others like shipping technology and policy) specific to each region, which are not disentangled. While Springborn et al. (2011) is the first paper from the economics literature that explicitly introduces a metric for climate similarity in a study examining the risk of introductions of invasive species with trade, they ignore import volumes. Dalmazzone and Giaccaria (2014) incorporate CS between trading partners within a model that links the establishment of invasive species to import volumes disaggregated by the country and region of origin. They showed that accounting for the geographic structure of trade flows and CS between origin and destination countries significantly improves our understanding of the drivers of biological invasions. A limitation of this study is that they model aggregate numbers of invasive species, and do not account for individual species traits.

With a few exceptions (e.g., Costello et al., 2007; Hlasny & Livingston, 2008), the studies summarized above equated species discoveries with species introductions and restricted analyses to short periods. This is problematic because there are typically long lags on the order of decades between introduction and discovery. Many previous studies also suffer from the difficulty of using a flow variable such as imports measured for a specific year to explain the variation in a stock variable, such as the cumulative number of invasive species up to a certain date (Dalmazzone & Giaccaria, 2014; Perrings, 2007; Perrings et al., 2000). We address these issues by using a long-run multidecadal data set for both imports and nonnative ant discovery records and account for lags between species establishment and discovery by relating historical species discoveries to historical trade-flows and dates during periods that well precede the time of discovery.

Just as multidecadal invasion dynamics require a long run temporal scale, the global nature of trade and the complexities of bridgeheads motivate a global scale of analysis. Prior studies of invasion drivers have been conducted at various scales, from national (Areal et al., 2008; Levine & D'Antonio, 2003; Liebhold et al., 2013; Lin et al., 2007; Ward et al., 2020) to regional (Hulme, 2007; Pyšek et al., 2010; Vilà & Pujadas, 2001) and global (Bellard et al., 2016; Dalmazzone & Giaccaria, 2014; Liebhold et al., 2016, 2018; Lin et al., 2011; Westphal et al., 2008). Despite the broad spatial coverage of some of these analyses, several are confined to a few species and countries (except Bellard et al., 2016; Dalmazzone & Giaccaria, 2014; Fournier et al., 2019; Liebhold et al., 2018) and examine pathways and species traits in isolation (except Liebhold et al., 2016). To date, most of these drivers are considered separately, with little examination of the interactions between the level of imports and other variables that can also influence biological invasions (Hulme, 2021).

We address the limitations surveyed above by estimating a model of ant invasions that incorporates both species traits and trade as well as modulating factors of CS and bridgeheads in a multidecadal and global analysis. We use a Cox proportional hazards model (Cleves et al., 2016), to estimate the relative role of these drivers in contributing to the “hazard” or likelihood of a nonnative species establishing. We model the accumulation of nonnative ant species as a hazard function of historical trade-flows while accounting for biogeographic factors such as source native regions, CS, and species-specific attributes. The model incorporates imports from both native regions and

invaded (or bridgehead) countries over a period spanning 185 years. Our study addresses the following questions: (1) How much do imports increase the risk of the introduction of nonnative ant species globally? (2) How does invasion risk change over time and vary by different trading regions? (3) How significant are imports, species attributes and CS as drivers of ant species invasions? (4) Is the bridgehead effect important in explaining historical ant invasions?

Our study offers four contributions relative to the existing literature. First, it unifies two strands of models which are more narrowly focused on establishment risk from either: (A) species attributes and CS, or (B) trade. Our approach integrates these static and dynamic factors and allows assessment of the significance of each to forecast invasion risk. Second, it expands the scope and scale of analysis by utilizing global bilateral imports data spanning 185 years (1827–2012) and using individual species-level establishment records (rather than simple cumulative counts). Third, the model accounts for invasions from both the native range and from previously invaded regions (i.e., bridgehead regions). Fourth, we incorporate CS between source country and recipient country. No previous studies of species invasions have integrated data on species attributes, CS and dynamic propagule pressure (trade) at a global scale. We show that CS interacted with cumulative imports during the 20 years before a species discovery in any given year is an important predictor of establishment, consistent with a delay between initial species establishment and discovery. Ultimately, our results can be used to target biosecurity efforts to prevent new ant establishments, while the methods are easily generalizable to other taxa that hitchhike through international trade pathways.

2 | METHODS

2.1 | Econometric model

We used a Cox proportional hazards model (Cox, 1972), which includes time-dependent and time-independent predictors (Cleves et al., 2016), to estimate the relative drivers of invasion risk. We combined two groups of predictors. First, we considered the intensity of the import pathway, specifically the value of region-specific imports recently received (leading up to any given year), as potentially modulated by the CS between source and receiving region. Second, we considered a set of species attributes, that is, morphological and life-history traits potentially associated with invasiveness (Bertelsmeier et al., 2017). Given the panel structure of the data and to control for spatial variation between regions that is constant over time, we included fixed effects for (1) species native regions and (2) importer regions. While survival analyses have been used to estimate invasion risk as a hazard function for individual invasive insect species such as the emerald ash borer in the United States (Ward et al., 2020), these studies do not fully integrate invasion risk from pathway volumes with species attributes.

The invasion status for each species in each receiving country in the data set is a binary variable set to “uninvaded” annually until the discovery of invasion occurs, triggering a status of “invaded” thereafter. In our Cox proportional hazards model framework, the probability of discovering species k , in receiving country i , in year t is given by:

$$d_{tik} = h_0(t) \exp(f(\bar{M}_{tik}, \bar{CS}_{ik}|\alpha) + \beta Z_k + \varphi_l + \varphi_j), \quad (1)$$

where $h_0(t)$ is the baseline hazard, Z_k is a vector of species attributes, l is region in which receiving country i is located, j is the source region of the imports, and φ_l and φ_j are importing region and exporting region fixed effects, respectively. In this case, the effects of all regions are treated as fixed and we can account for them by including indicator variables identifying regions in the model. The function $f(\bar{M}_{tik}, \bar{CS}_{ik}|\alpha)$ specifies the way in which imports ($\bar{M}_{tik}$) and climate similarity ($\bar{CS}_{ik}$) enter

the model. In addition to fixed effects, the coefficients to be estimated include the vectors α and β . Next, we describe our approach to characterizing relevant imports and CS before specifying possible forms for their combination in the imports-CS function, f .

The import summary variables were constructed as a vector of aggregate lags, $M_{tijk}^{u,v} \equiv \sum_{s=u}^v m_{sijk}$, where m is annual imports from year u through v . Specifically, we considered imports from j to i over the most recent decade ($M_{tijk}^{t-9,t}$), the decade before that ($M_{tijk}^{t-19,t-10}$) and, alternatively, over the most recent 20 years ($M_{tijk}^{t-19,t}$). Thus, the import measure may either be a scalar, for example, $M_{tijk}^{t-9,t}$, or a vector, $M_{tijk} = [M_{tijk}^{t-9,t}, M_{tijk}^{t-19,t-10}]$. We included these aggregate (over time) lags since we expect that the likelihood of discovering a species in year t depends on the likelihood it was introduced via imports in a year leading up to t . These import summary variables are the time-varying measures of interest in the model, which are the main potential drivers of dynamic estimates of invasion risk (along with the expansion of newly invaded bridgehead regions).¹

We define J_{ik} as the set of countries in which species k is present by year t . Recall that M_{tijk} summarizes cumulative imports to country i from country j which has species k over a fixed number of years leading up to year t . We aggregated over the n_{ik} relevant countries in J_{ik} for species k and take the natural log: $\bar{M}_{tik} = \log(\sum_{j \in J_{ik}} M_{tijk})$. $\bar{CS}_{ij}$ is an index of climatic similarity between source and receiving countries. The average CS across the n_{ik} relevant countries is given by $\bar{CS}_{tik} = (1/n_{ik}) \sum_{j \in J_{ik}} \bar{CS}_{ij}$.² Our “full” specification is given by direct and interacted import and climate similarity terms in the imports-CS function:

$$f(\bar{M}_{tik}, \bar{CS}_{tik} | \alpha) = \alpha_0 \bar{M}_{tik} + \alpha_1 \bar{CS}_{tik} + \alpha_2 \bar{CS}_{tik} \bar{M}_{tik}. \quad (2)$$

We considered models with each term in this function on its own as well as all three together (as indicated in Equation 2) to identify a preferred specification. While these specifications allow us to test for whether CS is a significant contributing variable in general, they constrain the impact of CS to a linear form.

To assess whether the effect of varying CS depends on the level of CS, we also considered a heterogeneous CS effects model using a dummy variable for each block of CS values I in the set of blocks, L , where I denotes CS percentiles. In this case, the imports-CS function is given by:

$$f(\bar{M}_{tik}, \bar{CS}_{tik} | \alpha) = \sum_{I \in L} \alpha_I \cdot 1(\bar{CS}_{tik} \in \bar{CS}_I) \cdot \bar{M}_{tik}. \quad (3)$$

We evaluated two approaches to specifying J_{ik} . In the first, $J_{ik} = J_k$ does not vary over time and is limited to countries in which species k is *native*. In the second “bridgehead” specification, newly invaded regions may themselves become source regions for further invasion, thus we allowed for J_{ik} to grow over time, adding countries in which species k is newly discovered. We used robust standard errors clustered at the importing country-species level and Cox-Snell residuals to evaluate model fit (Cox & Snell, 1968).

We estimated multiple versions of the Cox model, which differ in three ways. First, we considered two approaches to the scope of imports to include: imports from countries within the native range of each species only versus combined imports from native range *plus* bridgehead (previously invaded) countries. Second, we allowed for CS to enter as a standalone variable and/or

¹We also estimated models including the three import summary variables separately and jointly in the same model. However, there were strong collinearity problems in the latter model, which was subsequently dropped. The current analysis estimated separate models for the three import summary variables.

²Instead of a simple average of CS values, another logical way to specify CS is by computing a trade-weighted CS index. We compared results from such a model to the specification in the main text and found that results were very similar. We do not report these additional results for brevity purpose.

interacting with imports, or not included at all.³ Third, we allowed for the length of recent import history driving discovery likelihood each year to be either the past 10 years or 20 years (including the current year). We included a set of dummy variables for each native region and each importing biogeographic region in the model. The omitted reference region (for both native and importing region) was selected to be Asia. These fixed effects capture nontime varying factors such as the underlying invasibility of the destination region, and properties associated with the invasiveness of species from different source regions. This would include the persistent effect of export or import commodity mix, shipping technology, and policy-related variables including implementation of sanitary and phytosanitary standards (SPS) that are specific to either native or destination regions (Lichtenberg & Olson, 2018).

2.2 | Data

For estimation, we merged the economic and ecological data listed in Table 1. Information on the year that each established nonnative ant species was first discovered in each country represents the core outcome data. These were compiled by Bertelsmeier et al. (2017) from different sources including public online databases, scientific publications, books and personal collections. The data set contains historical first records for the 36 most widespread alien ant species across the world (1793–2012) for which dates of first observation at the country level were available from the literature (Bertelsmeier et al., 2017). For each ant species included, the data set specifies native regions as well as each country outside of its native region where it has been discovered and the year it was first reported there. We also compiled two key life-history traits for each species that have previously been associated with invasiveness (Bertelsmeier et al., 2017): (i) Gyny, indicating whether the species typically has single or multiple queens (0,1; 0 = monogynous, 1 = polygynous), and (ii) Habitat generalism, indicating the number of different habitat types in which the species occurs (integers, 1:8).⁴ This data set was compiled by Bertelsmeier et al. (2013) using the Antprofiler database, which leveraged expert opinion from professional ecologists. We combined ecological data with global bilateral import value data obtained from the TRADHIST database (Fouquin & Hugot, 2017).⁵ The data set contains nominal trade flows for 197 countries from 1827 to 2014, converted to real values (2019 US\$).

Many studies have shown that CS between a species' native range and a new environment is a major determinant of the probability of species establishment (Pauchard et al., 2004; Roura-Pascual et al., 2011; Thuiller et al., 2005). We calculated CS for each country pair as follows. First, we quantified the land area of each of the 32 Köppen–Geiger Climatic subgroups in each country (Kottek et al., 2006). Then, we specified a distance measure between each Köppen–Geiger climate using 19 bioclimatic variables sourced from the WorldClim Global Climate Database at a resolution of 5 arc-minutes globally (Hijmans et al., 2005). Finally, we took the proportion of land area falling in each Köppen–Geiger subgroup land area for each country pair and weighted it by the distance measure between each subgroup category. After normalizing values to the unit interval and subtracting from 1 we arrived at a CS index spanning from 0 (no similarity) and 1 (identical) (see Supporting Information: Appendix). In Supporting Information: Figure A1, we show the distribution of CS index levels for the full set of country pairs. The CS index is relatively low for country pairs that are distant in terms of climatic conditions (e.g., Canada–Brazil, $CS_{ij} = 0.36$) and relatively high for climatically similar countries (e.g., Canada–United States, $CS_{ij} = 0.78$).

³As a robustness check we considered additional specifications for CS, which are discussed in the Supporting Information: Appendix.

⁴Habitats include: tropical rain forest, tropical dry forest, temperate forest, boreal forest (taiga), tundra, grasslands, scrubland, riparian zones, desert, coastland, urban areas and agricultural areas.

⁵Available at: <http://www.cepii.fr/CEPII/en/welcome.asp>

TABLE 1 List of variables and data sources.

Variable	Description	Years	Source
Discovery years	Year of discovery for each species and invaded country (years)	1793–2012	Bertelsmeier et al. (2017)
Value of imports	Bilateral trade (\$billions/year)	1827–2014	TRADHIST (Fouquin & Hugot, 2017)
Species attributes	Morphological and life history traits	static	Bertelsmeier et al. (2017)
Climatic similarity	Climatic similarity between origin and importing countries	static	Derived from Kottek Koppen–Geiger climate subgroups (Kottek et al., 2006)

3 | RESULTS AND DISCUSSION

3.1 | Descriptive statistics

Figure 1 shows the temporal distribution of the year a species was discovered in each country, pooled across importing countries. From 1793 to 2012, a total of 1485 discoveries were reported across all countries, giving an average of approximately seven discoveries per year. Recorded invasions increased in the second half of the 19th-century corresponding to the first wave of globalization (Baldwin & Martin, 1999) while the second increase in invasions corresponds to the post-World War II second globalization (Bertelsmeier et al., 2017). Thus, ant invasions have been increasing over time, although with fluctuations due to changes in trade. This is consistent with a more general finding from Bonnamour et al. (2021) that insect and plant invasion rates surged following the two globalization waves. The average number of countries invaded by each of the 36 species is approximately 53. Supporting Information: Appendix A2 shows an example of the geographical distribution of the year of discovery for one selected species, the red imported fire ant, *Solenopsis invicta*.

In Table 2 we present descriptive statistics of key variables used in the final regressions. The overall data set spans 197 countries, 36 ant species and about two centuries. In Supporting Information: Appendix A3, we show annual imports for seven regions over the last several decades, during which time imports to North America, Asia and Europe have sharply increased. To bridge the slight mismatch between the spans of datasets covering ant discovery (1793–2012) and imports (1827–2014) we truncate to 1827–2012. At the start of the data set, this means that the two species discovered before 1827 (both in 1793) are treated as being discovered in 1827. We also tested the effect of dropping the two earlier discoveries and found that it had no impact on the model estimates. Figure 1 illustrates that the vast majority of species discoveries occur from 1850 onward.

3.2 | Cox hazard regression model results

We now turn to the results of the hazard model estimation. The full estimation results are shown in Supporting Information: Tables A4–A7. Our preferred model (3B in Supporting Information: Table A1, based on Akaike and Bayesian information criteria) features a cumulative import over the last 20 years (vs. 10) and imports interacted with CS (vs. uninteracted). In Table 3, we present the full set of hazard ratio estimates for this preferred model (3B). For any country in any year, we estimate that an increase in CS-interacted cumulative imports from the previous 20 years leads to a significant increase in the likelihood of discovering a new species invasion in that year. With respect to the combined impact of CS and imports, these results align with those of Hlasny and Livingston (2008);

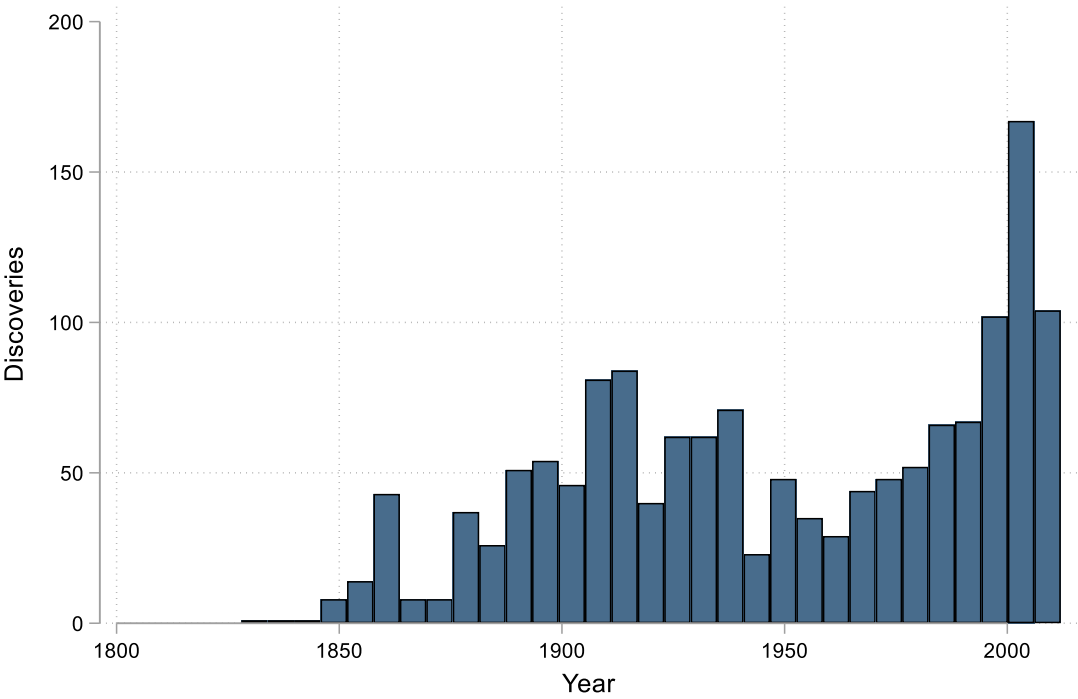


FIGURE 1 Worldwide nonnative ant species discoveries (new species-country combinations) during the period 1793–2012.

TABLE 2 Summary statistics for regression variables.

Variable	Obs.	Mean	SD	Min.	Max.
Dependent variable					
Year of discovery (by species and country)	1485	-	-	1793	2012
Trade partner variables (bilateral)					
Value of imports (US\$2019, billions)	1,129,259	0.13	2.03	0.00	365.9
Climatic similarity index	17,952	0.63	0.10	0.00	1.00
Species attributes					
Gyny (queen number)	36	1.33	0.48	1.00	2.00
Habitat generalism	36	4.42	2.06	1	8

Costello et al. (2007); Westphal et al. (2008); and Dalmazzone and Giaccaria (2014) showing imports to be the major determinant of invasions.

We also confirmed findings in the literature that species attributes are significant predictors of invasion risk for individual ant species (Table 3, first column). Our results show that species that have a wide habitat range (habitat generalism) present a higher relative risk of invasion. Thus, a unit increase in the habitat range is associated with an 11% increase in the hazard rate. This can be explained by the fact that habitat generalists can exploit many different habitats spanning many countries (Bertelsmeier et al., 2017). The effect of multiple queens per colony (polygyny) was also statistically significant. Polygynous ant species present a 20% higher hazard compared to

TABLE 3 Full Cox regression model hazard ratio results for the preferred model specification, model 3B, where imports are from native and bridgehead regions over the past 20 years and are CS-weighted.

Variable	Preferred model (3B)	Trade-focused model	Species-focused model
Log imports		1.04 (2.50)*	-
CS			1.39 (1.05)
CS*Log imports	1.04 (3.70)**		
<i>Species attributes</i>			
Monogynous	0.80 (-2.60)**	-	0.81 (-2.44)*
Habitat generalism	1.12 (5.11)**	-	1.12 (5.33)**
<i>Native region</i>			
Africa	0.80 (-2.27)*	0.71 (-3.74)**	0.84 (-1.85)
Central and South America	0.65 (-3.71)**	0.77 (-2.45)*	0.67 (-3.61)**
Indo-Pacific	0.78 (-2.51)*	0.75 (-3.02)**	0.80 (-2.31)*
Other	0.84 (-1.63)	0.84 (-1.65)	0.85 (-1.44)
<i>Importer region</i>			
Central and South America	1.03 (0.25)	1.03 (0.27)	
Europe	0.68 (-3.44)**	0.67 (-3.68)**	
Middle East & North Africa	1.13 (1.02)	1.12 (0.93)	
North America	1.38 (1.74)	1.17 (0.91)	
Oceania	1.15 (1.01)	1.18 (1.20)	
Sub Saharan Africa	0.91 (-0.75)	0.94 (-0.46)	
<i>Model statistics</i>			
χ^2	80.3	42.6	57.3
LL	-4958.5	-4978.8	-4974.5
AIC	9942.9	9979.6	9963.0
BIC	10,063.7	10,081.8	10,028.0
Obs.	79,997	79,997	79,997

Note: Alternative limited models (trade- and species-focused) are also presented in the final two columns. Figures in parentheses are *t* values; significance levels: omitted category for native and importer regions is Asia. Abbreviation: LL, log pseudolikelihood.
p* < 0.05; *p* < 0.001; ****p* < 0.01.

monogynous species. Our results for these attributes agree with those of Bertelsmeier et al. (2017) who showed that species traits are important for ant establishment. We advance the analysis of Bertelsmeier et al. by considering multiple variables in the regressions simultaneously in a probabilistic fashion. More generally, these results are consistent with existing findings that such species traits are significant predictors of invasion risk for many taxa (Allen et al., 2017; Sol et al., 2012).

As anticipated, the relative risk of invasion varies across native/source regions as well as across importing/receiving regions (Table 3). The omitted region in both groups is Asia, which thus carries an implicit hazard ratio of 1. Compared to Asia, we found that ant species from Africa, Central, and

South America, and Indo-Pacific regions have decreased risk. For example, ant species from Africa present a 20% lower hazard than species from Asia. Similarly, ant species from Central and South America and Indo-Pacific convey a 36% and 22% lower hazard, respectively, compared to species from Asia. This finding is consistent with several studies which suggest that invasion risks from certain regions are higher—although these studies are not for individual species and part of the elevated invasion risk identified in these studies may arise because there may simply be more species, that is, a larger species pool (Hui et al., 2016; Liebhold et al., 2017). Bellard et al. (2016) reported that most of the invasion of invertebrates and plants into Europe and Central America originated from species native to Asia, especially India, China, and Indonesian islands. Dalmazzone and Giaccaria (2014) reported that countries in Asia are the riskiest trading partners for invasive species. The higher invasion risk that we identified for individual species native to Asia may reflect the inherent greater invasiveness of these species, though it remains unclear what species characteristics may drive such a difference. This result suggests that exports from Asia—and from countries in which Asian species have established bridgehead populations—present a higher-risk source region for ants and should be considered for biosecurity focus.

Turning to importing regions, our results indicate that Europe faces a significantly lower hazard compared to Asia (Table 3). Countries in Europe face only 68% of the risk of invasion faced by Asia. North America and Oceania have hazard ratios greater than one but are not significant. No other regions were significant at a 5% level compared to Asia. This may reflect differences in the inherent invasibility of these regions but the reasons for these differences also are not disentangled here. One possible hypothesis is that policy variables such as investment in invasive species prevention and control could also play a role. It has been shown that inspection efforts can reduce invasibility (Hill et al., 2016; Surkov et al., 2008). Another explanation is the fact that low-income countries tend to have less effective regulations thereby increasing the risk of invasions (Perrings, 2007). A related factor is the heterogeneity in the level of biosecurity expenditures globally, with Australia, New Zealand, the United States and the United Kingdom as the countries with the largest investment in prevention policies (0.076%–0.001% of GDP) (Convention on Biological Diversity [CBD], 2012).

Our preferred model in Table 3 integrates two strands of existing models, which are more narrowly either (1) a “trade-focused” model without species attributes (e.g., Costello et al., 2007; Dalmazzone & Giaccaria, 2014; Hlasny & Livingston, 2008), or (2) a “species-focused” model with only species attributes and CS as an independent variable but without an indicator of propagule pressure like imports (e.g., Allen et al., 2017; Sol et al., 2012). In Table 3 we show estimates from implementing both of these typical, more narrow approaches. In the trade-focused model, we use total imports from all countries instead of imports from only native and bridgehead countries (for each species) to be more comprehensively naïve on the species dimension. One caveat here is that the species-focused model presented here indirectly and partially accounts for imports via the region dummy variables, which will loosely account for regional differences on average imports.

Surprisingly, we do not find that either narrower model leads to substantial bias in hazard ratio estimates for terms shared with the comprehensive (preferred) model. In addition, for the trade-focused model, cumulative imports have the expected positive impact on species discoveries. In the species-focused model, the hazard ratios on species attributes remain statistically significant and in the expected direction of impact as in the previous models. Thus, while both “incomplete” models miss important drivers, in our case the estimates they do provide are not misleading. As before, we evaluated the overall fit of the alternative models using Cox–Snell residuals. In Supporting Information: Figure A6, we observe a lack of fit for both of the limited models (trade-focused and species-focused). Note that the first subplot is the same as the first subplot in Supporting Information: Figure A4 (i.e., the preferred model). The comprehensive model shows the best overall fit, indicating that both the biological and economic factors should be incorporated for accurate prediction of invasions.

We further explore the role of CS using the full specification of the imports-CS function (model 4B) in Equation (2). Supporting Information: Appendix 4 provides a detailed analysis and results of

varying the level of CS on establishment risk. These results have several important implications. First, they demonstrate that accurate estimates of the impacts of trade on establishments require information on both trade and CS. Models that include only trade provide a good estimate of the hazard of trade for countries with average CS. But trade-only models will overestimate the hazard for countries that are climatically dissimilar and underestimate the hazard for more similar country pairs. Second, these results imply that it may be desirable to vary the intensity of biosecurity effort focused on imports from different countries. Trade between countries that have more similar climates presents a higher hazard. The results indicate that risk of ant invasions is lowest between country pairs with the lowest 15% of CS values and that above this threshold CS has a strong impact on risk.

Finally, we estimated the fitted hazard function, which shows that the hazard rate is increasing over time and varies across exporter regions (Supporting Information: Figure A7). We also conducted several robustness checks to test and evaluate the model fit (Supporting Information: Appendix 6–8). Overall, we fail to find evidence of problems with the assumption of proportional hazards (see Supporting Information: Appendix 6).

4 | CONCLUSIONS

In this study, we assessed the socioeconomic and ecological drivers of ant invasions globally by fitting a Cox proportional hazard model. Our key results highlight the importance of bridgehead imports in explaining invasion risk. This indicates that such spatial spillover effects are important temporal and dynamic drivers of biological invasions. We also find that expanding the historical horizon over which cumulative imports are considered from one decade to two decades improves explanatory power. Our preferred model incorporates CS as an interaction of imports (the likely pathway of species introduction) rather than as a standalone factor. We find that a model including only trade (and excluding species-specific factors) can still provide a reasonable estimate of the hazard of trade for countries with average CS. But trade-only models will over-estimate the hazard for countries that are climatically dissimilar and vice versa.

When we compare estimates of individual effects of key variables from our comprehensive model to those obtained from a less-complete (trade- or species-focused model) surprisingly we find little bias in these less-complete model effect estimates. However, when we turn our attention from individual drivers to prediction of risk, the comprehensive model shows a much better fit overall. As expected, we found that the relative risk of establishment also varies by species attributes, native regions of a species, and by importing region.

There are also limitations to this study. As previously stated, the data on trade flows is highly aggregated and does not allow us to identify how establishment risk may differ by product type or time of year. A limitation to our study of the role of CS is that this measure was calculated at the country scale to match the scale of the establishment and import data. We would expect CS to show even greater explanatory power should future resolution of data make it possible to pinpoint the subnational location of species establishment, allowing for tighter connections between that localized climate and the source region climate. While we accounted for regional fixed effects as well as establishments, trade and CS at the country level, there may be other important sources of within-region heterogeneity that are not represented. Finally, while international trade is likely responsible for the increased spread of ant invasions, it is not the only factor here at stake and knowledge of ant taxonomy and biogeography, ease of identifications, and increased sampling efforts in particular habitats and regions are important cofactors. While this approach in this paper is novel in its integration of both trade flows over time and species attributes, additional integration in further research would be fruitful. Specifically, recent studies have identified climate change, and land-use change as important factors in biological invasions (Epanchin-Niell et al., 2021; Robinson et al., 2020; Roura-Pascual et al., 2021).

These results provide useful information for informing biosecurity policies that facilitate international trade while minimizing future invasions. Our results provide support to allocating substantial resources for mitigating invasive species at the introduction stage through policy instruments such as trade inspections. Several economic studies have shown that allocating resources for the prevention of introductions of invasive species can be more cost-effective than control and eradication (Born et al., 2005; Leung et al., 2002, 2005). Our results show that global ant invasions are driven by international trade and suggest that essentially all countries should be implementing one or more of the trade policy instruments available to address invasive species—targeted inspections (Surkov et al., 2008), tariffs (Lichtenberg & Olson, 2020; Margolis et al., 2005; Perrings et al., 2005) and tradable risk permits (Horan & Lupi, 2005)—to address this market failure. There is also potential to use insights from our analysis to improve surveillance and early warning systems for the management of biological invasions. Our findings on the importance of bridgeheads emphasize the importance of countries with deep experience and expertise in preventing trade-driven invasion risk working to disseminate that knowledge to other countries. In addition, our model can be applied to other taxa for which accidental transport through trade is the primary pathway and where there is data on the year individual nonnative species were discovered to have invaded individual countries or regions, for example, bark beetles, termites, and other insects.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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

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