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

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Abstract

International trade continues to drive biological invasions. We investigate the drivers of global non-native 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 non-native ant species worldwide from 1827-2012. 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: Climatic similarity; bridgeheads; invasion; trade.

Running head: Drivers of global ant invasions

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1.0 Introduction

Non-native insect species outnumber all other alien animal species, with nearly 500 non-native insect species established in Japan, over 1,500 in Europe and nearly 4,000 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 non-native insects (Angulo et al., 2022; Holway et al., 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, non-native ants can cause declines in native biodiversity, alter ecosystem processes and trigger declines in ecosystem services such as agricultural production and human health. Non-native ants can lead to substantial economic costs (Angulo et al., 2022). In the United States of America (USA) 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; Liebhold et al., 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 the 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 (Meurisse et al. 2019, Gippet et al. 2019), the connection between imports and insect invasions remains murky.

To address these issues, we analyse 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

65 emphasized in the ecological literature as key drivers of invasion patterns for insects and other

66 taxa (Lester 2005; Jeschke and Strayer, 2006; Sol et al., 2012; Capellini et al., 2015; Hill et al.,

67 2016; Allen et al., 2017). Specifically for ants, several studies have identified ecological traits

68 often associated with invasive species (Lester, 2005; Lloret et al., 2005; Wittenborn and

69 Jeschke, 2011; Fournier et al., 2019). While these studies make clear the important role of

70 biology, they have typically done so in isolation from socioeconomic drivers. Two exceptions

71 within the ecological literature highlight the important role of trade as a key driver, including

72 Westphal et al. (2008) who found it was the most important explanatory variable in a global

73 study of invasions across all taxa and Liebhold et al. (2016) who showed it was more strongly

74 linked to global insect invasions than was the life history of the species involved.

75

76 The economics and environmental management literature has focused on imports as a key

77 driver, highlighting that this risk varies among trading partners (Costello et al. 2007;

78 Dalmazzone and Giaccaria, 2014; Hlasny and Livingstone, 2008, Hume, 2021). Using

79 historical trade data, both Costello et al. (2007) and Essl (2011) showed the importance of prior

80 economic variables (trade and GDP) on current discoveries of biological invasions (in San

81 Francisco, USA and European countries, respectively). Overall, these studies found that

82 imports contribute significantly to biological invasions, however, they mostly focussed on

83 trade and ignored biological drivers such as species characteristics and climatic similarity.

84 However, as we show, these drivers do not operate independently but rather interact with one

85 other.

86

87 An important feature of global invasions that was, until recently, absent from economic and

88 ecological analyses of historical invasions is the so-called "bridgehead effect", where

89 previously invaded regions serve as the source of additional invasions elsewhere through

90 secondary introductions (Lombaert et al. 2010, Bertelsmeier and Keller 2018). Bridgeheads are

91 a form of "spatial" spillover in trade-facilitated invasions, where invasion of a new region

92 creates a spillover risk for their trading partners (Barbier and Shogren, 2004; Zipp et al., 2021).

93 Yet, most analyses ignore the extent of these spatial spillover effects (e.g. Perrings et al., 2000).

94 In the context of marine invasions, Keller et al. (2010) was an early example of research

95 highlighting the role of stepping-stone invasion processes. More recently, Bertelsmeier et al.

96 (2018) showed that bridgehead effects play a major role in ant invasions in the USA and New

97 Zealand. While these studies illustrate the pivotal role of bridgeheads in shaping insect

98 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 (Pauchard et al. 2004, Roura-Pascual et al., 2011; Thuiller et al. 2004; Duncan, 2016). 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 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. 2008; Hlasny and 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 (Perrings et al, 2000; Perrings, 2007; Dalmazzone and Giaccaria, 2014). We address these issues by using a long-run multi-decadal data set for both imports and non-native 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.

133 Just as multi-decadal invasion dynamics require a long run temporal scale, the global nature of
134 trade and the complexities of bridgeheads motivate a global scale of analysis. Prior studies of
135 invasion drivers have been conducted at various scales, from national (Areal et al., 2008;
136 Levine and D'Antonio, 2003; Lin et al., 2007; Liebhold et al. 2013; Ward et al., 2020) to
137 regional (Hume, 2007; Pysek et al., 2010; Vila and Pujadas, 2001) and global (Bellard et al.,
138 2016; Dalmazzone and Giaccaria, 2014; Lin et al., 2011; Liebhold et al. 2016, 2018; Westphal
139 et al., 2008). Despite the broad spatial coverage of some of these analyses, several are confined
140 to a few species and countries (except Bellard et al., 2016; Dalmazzone and Giaccaria, 2014;
141 Fournier et al., 2019; Liebhold et al. 2018) and examine pathways and species traits in isolation
142 (except Liebhold et al., 2016). To date, most of these drivers are considered separately, with
143 little examination of the interactions between the level of imports and other variables that can
144 also influence biological invasions (Hume, 2021).

145

146 We address limitations surveyed above by estimating a model of ant invasions that incorporates
147 both species traits and trade as well as modulating factors of CS and bridgeheads in a multi-
148 decadal and global analysis. We use a Cox proportional hazards model (Cleves et al., 2016), to
149 estimate the relative role of these drivers in contributing to the "hazard" or likelihood of a non-
150 native species establishing. We model the accumulation of non-native ant species as a hazard
151 function of historical trade-flows while accounting for biogeographic factors such as source
152 native regions, climatic similarity (CS), and species-specific attributes. The model incorporates
153 imports from both native regions and invaded (or bridgehead) countries over a period spanning
154 185 years. Our study addresses the following questions: (1) How much do imports increase the
155 risk of the introduction of non-native ant species globally? (2) How does invasion risk change
156 over time and vary by different trading regions? (3) How significant are imports, species
157 attributes and CS as drivers of ant species invasions? (4) Is the bridgehead effect important in
158 explaining historical ant invasions?

159

160 Our study offers four contributions relative to the existing literature. First, it unifies two strands
161 of models which are more narrowly focused on establishment risk from either: (A) species
162 attributes and CS, or (B) trade. Our approach integrates these static and dynamic factors and
163 allows assessment of the significance of each to forecast invasion risk. Second, it expands the
164 scope and scale of analysis by utilizing global bilateral imports data spanning 185 years (1827-
165 2012) and using individual species-level establishment records (rather than simple cumulative
166 counts). Third, the model accounts for invasions from both the native range and from

167 previously invaded regions (i.e., bridgehead regions). Fourth, we incorporate CS between
168 source country and recipient country. No previous studies of species invasions have integrated
169 data on species attributes, CS and dynamic propagule pressure (trade) at a global scale. We
170 show that CS interacted with cumulative imports during the 20 years prior to a species
171 discovery in any given year is an important predictor of establishment, consistent with a delay
172 between initial species establishment and discovery. Ultimately, our results can be used to
173 target biosecurity efforts to prevent new ant establishments, while the methods are easily
174 generalizable to other taxa that hitchhike through international trade pathways.

175

176 **2.0 Methods**

177 *2.1 Econometric model*

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

190

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

195

196 $$d_{tik} = h_0(t) exp\big(f(\widetilde{M}_{tik}, \overline{CS}_{ik}|\alpha) + \beta Z_k + \varphi_l + \varphi_j\big), \tag{1}$$

197

198 where $h_0(t)$ is the baseline hazard, Z_k is a vector of species attributes, *l* is region in which
199 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 $f(\widetilde{M}_{tik}, \overline{CS}_{ik}|\alpha)$ specifies the way in which imports ($\widetilde{M}_{tik}$) and climate similarity ($\overline{CS}_{ik}$) 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, e.g. $M_{tijk}^{t-9,t}$, 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).[2]

We define J_{tk} 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_{tk} relevant countries in J_{tk} for species k and take the natural log: $\widetilde{M}_{tik} = log(\sum_{j \in J_{tk}} M_{tijk})$. CS_{ij} is an index of climatic similarity between source and receiving countries. The average CS across the n_{tk} relevant countries is given by $\overline{CS}_{tik} = (1/n_{tk}) \sum_{j \in \tilde{J}_{tk}} CS_{ij}$.[3] Our "full" specification is given by direct and interacted import and climate similarity terms in the imports-CS function:

$$f(\widetilde{M}_{tik}, \overline{CS}_i|\alpha) = \alpha_0 \widetilde{M}_{tik} + \alpha_1 \overline{CS}_{ik} + \alpha_2 \overline{CS}_{ik} \widetilde{M}_{tik}. \qquad (2)$$

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[2] We 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.

[3] Instead 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.

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

230

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

234

235 $$f\left(\widetilde{M}_{tik}, \overline{CS}_{ik} \middle| \alpha\right) = \sum_{I \in L} \alpha_I \cdot 1(\overline{CS}_{ik} \in \overline{CS}_I) \cdot \widetilde{M}_{tik}. \tag{3}$$

236

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

243

244 We estimated multiple versions of the Cox model, which differ in three ways. First, we
245 considered two approaches to the scope of imports to include: imports from countries within
246 the native range of each species only versus combined imports from native range *plus*
247 bridgehead (previously invaded) countries. Second, we allowed for CS to enter as a standalone
248 variable and/or interacting with imports, or not included at all.[4] Third, we allowed for the length
249 of recent import history driving discovery likelihood each year to be either the past 10 years or
250 20 years (including the current year). We included a set of dummy variables for each native
251 region and each importing biogeographic region in the model. The omitted reference region
252 (for both native and importing region) was selected to be Asia. These fixed effects capture non-
253 time varying factors such as the underlying invasibility of the destination region, and properties
254 associated with the invasiveness of species from different source regions. This would include
255 the persistent effect of export or import commodity mix, shipping technology, and policy-

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[4] As a robustness check we considered additional specifications for CS, which are discussed in the online appendix.

256 related variables including implementation of sanitary and phytosanitary standards (SPS) that
257 are specific to either native or destination regions (Lichtenberg and Olson, 2018).

258

259 *2.2 Data*

260 For estimation, we merged economic and ecological data listed in Table 1. Information on the
261 year that each established non-native ant species was first discovered in each country represents
262 the core outcome data. These were compiled by Bertelsmeier et al. (2017) from different
263 sources including public online databases, scientific publications, books and personal
264 collections. The dataset contains historical first records for the 36 most widespread alien ant
265 species across the world (1793-2012) for which dates of first observation at the country level
266 were available from the literature (Bertelsmeier et al., 2017). For each ant species included, the
267 dataset specifies native regions as well as each country outside of its native region where it has
268 been discovered and the year it was first reported there. We also compiled two key life-history
269 traits for each species that have previously been associated with invasiveness (Bertelsmeier et
270 al., 2017): (i) Gyny, indicating whether the species typically has single or multiple queens (0,1;
271 0=monogynous, 1= polygynous), and (ii) Habitat generalism, indicating the number of
272 different habitat types in which the species occurs (integers, 1:8).[5] This dataset was compiled
273 by Bertelsmeier et al. (2013) using the Antprofiler database, which leveraged expert opinion
274 from professional ecologists. We combined ecological data with global bilateral import value
275 data obtained from the TRADHIST database (Fouquin and Hugot, 2017). [6] The data set
276 contains nominal trade flows for 197 countries from 1827 to 2014, converted to real values
277 (2019 US$).

278

279 Many studies have shown that CS between a species' native range and a new environment is a
280 major determinant of the probability of species establishment (Pauchard et al. 2004, Roura-
281 Pascual et al., 2011; Thuiller et al. 2004). We calculated CS for each country pair as follows.
282 First, we quantified the land area of each of the 32 Köppen-Geiger Climatic subgroups in each
283 country (Kottek et al., 2006). Then, we specified a distance measure between each Köppen-
284 Geiger climate using 19 bioclimatic variables sourced from the WorldClim Global Climate
285 Database at a resolution of 5 arc-minutes globally (Hijmans *et al.*, 2005). Finally, we took the
286 proportion of land area falling in each Köppen-Geiger subgroup land area for each country pair

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[5] Habitats include: tropical rain forest, tropical dry forest, temperate forest, boreal forest (taiga), tundra, grasslands, scrubland, riparian zones, desert, coastland, urban areas and agricultural areas.
[6] Available at: http://www.cepii.fr/CEPII/en/welcome.asp

287   and weighted it by the distance measure between each subgroup category. After normalizing

288   values to the unit interval and subtracting from 1 we arrived at a CS index spanning from 0 (no

289   similarity) and 1 (identical) (see Appendix). In the online appendix Figure A1, we show the

290   distribution of CS index levels for the full set of country pairs. The CS index is relatively low

291   for country pairs that are distant in terms of climatic conditions (for example Canada-Brazil,

292    $CS_{ij} = 0.36$) and relatively high for climatically similar countries (for example Canada-USA,

293    $CS_{ij} = 0.78$).

294

295   **3.0 Results and discussion**

296   *3.1 Descriptive statistics*

297   Figure 1 shows the temporal distribution of the year a species was discovered in each country,

298   pooled across importing countries. From 1793-2012, a total of 1,485 discoveries were reported

299   across all countries, giving an average of approximately seven discoveries per year. Recorded

300   invasions increased in the second half of the 19th-century corresponding to the first wave of

301   globalisation (Baldwin and Martin 1999) while the second increase in invasions corresponds

302   to the post World War II second globalisation (Bertelsmeier et al. 2017). Thus, ant invasions

303   have been increasing over time, although with fluctuations due to changes in trade. This is

304   consistent with a more general finding from Bonnamour et al. (2021) that insect and plant

305   invasion rates surged following the two globalization waves. The average number of countries

306   invaded by each of the 36 species is approximately 53. Online appendix A2 shows an example

307   of the geographical distribution of the year of discovery for one selected species, the red

308   imported fire ant, *Solepnosis invicta*.

309

310   In Table 2 we present descriptive statistics of key variables used in the final regressions. The

311   overall dataset spans 197 countries, 36 ant species and about two centuries. In Appendix Figure

312   A3, we show annual imports for seven regions over the last several decades, during which time

313   imports to North America, Asia and Europe have sharply increased. To bridge the slight

314   mismatch between the spans of datasets covering ant discovery (1793-2012) and imports

315   (1827-2014) we truncate to 1827-2012. At the start of the dataset, this means that the two

316   species discovered before 1827 (both in 1793) are treated as being discovered in 1827. We also

317   tested the effect of dropping the two earlier discoveries and found that it had no impact on the

318   model estimates. Figure 1 illustrates that the vast majority of species discoveries occur from

319   1850 onward.

320   *3.2 Cox hazard regression model results*

321   We now turn to the results of the hazard model estimation. The full estimation results are shown

322   in Tables A4-A7 in the online appendix. Our preferred model (3B in appendix Table A1, based

323   on Akaike and Bayesian information criteria) features a cumulative imports over the last 20

324   years (versus 10) and imports interacted with CS (versus uninteracted). In Table 3, we present

325   the full set of hazard ratio estimates for this preferred model (3B). For any country in any year,

326   we estimate that an increase in CS-interacted cumulative imports from the previous 20 years

327   leads to a significant increase in the likelihood of discovering a new species invasion in that

328   year. With respect to the combined impact of CS and imports, these results align with those of

329   Hlasny and Livingstone (2008), Costello et al. (2007), and Westphal et al. (2008) and

330   Dalmazzone and Giaccaria (2014) showing imports to be the major determinant of invasions.

331

332   We also confirmed findings in the literature that species attributes are significant predictors of

333   invasion risk for individual ant species (Table 3, first column). Our results show that species

334   that have a wide habitat range (habitat generalism) present a higher relative risk of invasion.

335   Thus, a unit increase in the habitat range is associated with an 11% increase in the hazard rate.

336   This can be explained by the fact that habitat generalists can exploit many different habitats

337   spanning many countries (Bertelsmeier et al., 2017). The effect of multiple queens per colony

338   (polygyny) was also statistically significant. Polygynous ant species present a 20% higher

339   hazard compared to monogynous species. Our results for these attributes agree with those of

340   Bertelsmeier et al. (2017) who showed that species traits are important for ant establishment.

341   We advance the analysis of Bertelsmeier et al. by considering multiple variables in the

342   regressions simultaneously in a probabilistic fashion. More generally, these results are

343   consistent with existing findings that such species traits are significant predictors of invasion

344   risk for many taxa (Sol et al., 2012, Allen et al., 2017).

345

346   As anticipated, the relative risk of invasion varies across native/source regions as well as across

347   importing/receiving regions (Table 3). The omitted region in both groups is Asia, which thus

348   carries an implicit hazard ratio of 1. Compared to Asia, we found that ant species from Africa,

349   Central and South America, and Indo-Pacific regions have decreased risk. For example, ant

350   species from Africa present a 20% lower hazard than species from Asia. Similarly, ant species

351   from Central and South America and Indo-Pacific convey a 36% and 22% lower hazard

352   respectively, compared to species from Asia. This finding is consistent with several studies

353   which suggest that invasion risks from certain regions are higher – although these studies are

354 not for individual species and part of the elevated invasion risk identified in these studies may
355 arise because there may simply be more species, i.e., a larger species pool (Hui et al., 2016;
356 Liebhold et al., 2017). Bellard et al. (2016) reported that most of the invasion of invertebrates
357 and plants into Europe and Central America originated from species native to Asia, especially
358 India, China, and Indonesian islands. Dalmazzone and Giaccaria (2014) reported that countries
359 in Asia are the riskiest trading partners for invasive species. The higher invasion risk that we
360 identified for individual species native to Asia may reflect the inherent greater invasiveness of
361 these species, though it remains unclear what species characteristics may drive such a
362 difference. This result suggests that exports from Asia—and from countries in which Asian
363 species have established bridgehead populations—present a higher-risk source region for ants
364 and should be considered for biosecurity focus.

365

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

378

379 Our preferred model in Table 3 integrates two strands of existing models, which are more
380 narrowly either (1) a "trade-focused" model without species attributes (e.g., Costello et al.,
381 2007; Hlasny and Livingstone, 2008; Dalmazzone and Giaccaria, 2014), or (2) a "species-
382 focused" model with only species attributes and CS as an independent variable but without an
383 indicator of propagule pressure like imports (e.g., Sol et al., 2012; Allen et al., 2017). In Table
384 3 we show estimates from implementing both of these typical, more narrow approaches. In the
385 trade-focused model, we use total imports from all countries instead of imports from only
386 native and bridgehead countries (for each species) to be more comprehensively naïve on the
387 species dimension. One caveat here is that the species-focused model presented here indirectly

388 and partially accounts for imports via the region dummy variables, which will loosely account
389 for regional differences in average imports.

390

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

403

404 We further explore the role of climate similarity (CS) using the full specification of the imports-
405 CS function (model 4B) in Equation (2). Online appendix 4 provides the detailed analysis and
406 results of varying the level of CS on establishment risk. These results have several important
407 implications. First, they demonstrate that accurate estimates of the impacts of trade on
408 establishments require information on both trade and CS. Models that include only trade
409 provide a good estimate of the hazard of trade for countries with average CS. But trade-only
410 models will overestimate the hazard for countries that are climatically dissimilar and under-
411 estimate the hazard for more similar country pairs. Second, these results imply that it may be
412 desirable to vary the intensity of biosecurity effort focused on imports from different countries.
413 Trade between countries that have more similar climates presents a higher hazard. The results
414 indicate that risk of ant invasions is lowest between country pairs with the lowest 15% of CS
415 values and that above this threshold CS has a strong impact on risk.

416

417 Finally, we estimated the fitted hazard function, which shows that the hazard rate is increasing
418 over time and varies across exporter regions (Figure A7). We also conducted several robustness
419 checks to test and evaluate the model fit (online appendix 6-8). Overall, we fail to find evidence
420 of problems with the assumption of proportional hazards (See online appendix 6).

421

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-focused 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 in order 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 sub-national 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 on ant taxonomy and biogeography, ease of identifications, and increased sampling efforts in particular habitats and regions are important co-factors. 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-Niel 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 (Margolis et al., 2005; Lichtenberg and Olson, 2020; Perrings et al., 2005) and tradable risk permits (Horan and 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 emphasizes 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 non-native species were discovered to have invaded individual countries or regions, for example, bark beetles, termites and other insects.

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738   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 and 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)

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740   Table 2: Summary statistics for regression variables.

Variable	Obs.	Mean	Std. dev.	Min.	Max.
Dependent variable					
Year of discovery (by species and country)	1,485	-	-	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

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744 Table 3: Full Cox regression model hazard ratio results for the preferred model specification, model
745 3B, where imports are from native and bridgehead regions over the past 20 years and are CS-weighted.
746 Alternative limited models (trade- and species-focused) are also presented in the final two columns.
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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)		
Species attributes			
Monogynous	0.80**	-	0.81*
	(-2.60)		(-2.44)
Habitat generalism	1.12***	-	1.12***
	(5.11)		(5.33)
Native region			
Africa	0.80*	0.71***	0.84
	(-2.27)	(-3.74)	(-1.85)
Central and South America	0.65***	0.77*	0.67***
	(-3.71)	(-2.45)	(-3.61)
Indo-Pacific	0.78*	0.75**	0.80*
	(-2.51)	(-3.02)	(-2.31)
Other	0.84	0.84	0.85
	(-1.63)	(-1.65)	(-1.44)
Importer region			
Central and South America	1.03	1.03	
	(0.25)	(0.27)	
Europe	0.68***	0.67***	
	(-3.44)	(-3.68)	
Middle East & North Africa	1.13	1.12	
	(1.02)	(0.93)	
North America	1.38	1.17	
	(1.74)	(0.91)	
Oceania	1.15	1.18	
	(1.01)	(1.20)	
Sub Saharan Africa	0.91	0.94	
	(-0.75)	(-0.46)	
Model statistics			
Chi-square	80.3	42.6	57.3
LL	-4958.5	-4978.8	-4974.5
AIC	9942.9	9979.6	9963.0
BIC	10063.7	10081.8	10028.0
Obs.	79997	79997	79997

748 Notes: Figures in parentheses are t-values; significance levels: * $p<0.05$; ** $p<0.01$; *** $p<0.001$; omitted
749 category for native and importer regions is Asia; LL=log pseudolikelihood.
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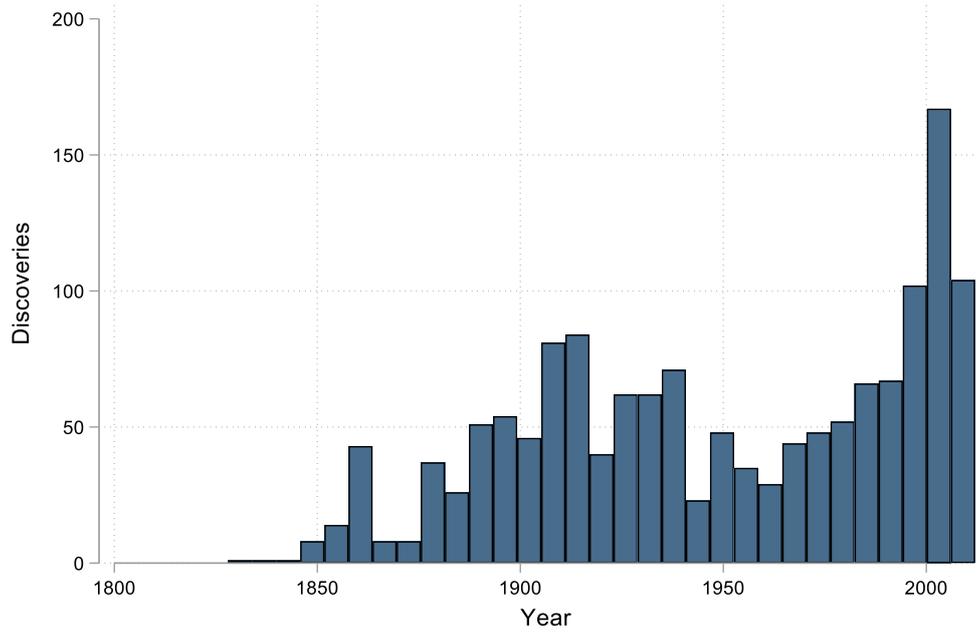
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754 Figure 1: Worldwide non-native ant species discoveries (new species-country combinations) during
755 the period 1793-2012

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