

ECOLOGY

Hidden patterns of insect establishment risk revealed from two centuries of alien species discoveries

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Understanding the socioeconomic drivers of biological invasion informs policy development for curtailing future invasions. While early 20th-century plant trade expansions preceded increased establishments of plant pests in Northern America, increased establishments did not follow accelerating imports later that century. To explore this puzzle, we estimate the historical establishment of plant-feeding Hemiptera in Northern America as a function of historical U.S. imports of live plants from seven world regions. Delays between establishment and discovery are modeled using a previously unused proxy for dynamic discovery effort. By recovering the timing of pest arrivals from their historical discoveries, we disentangle the joint establishment-discovery process. We estimate long delays to discovery, which are partially attributable to the low detectability of less economically important insect species. We estimate that many introduced species remain undiscovered, ranging from around one-fifth for Eurasian regions to two-fifths for Central and South America.

INTRODUCTION

The unintentional transport of living organisms is an undesirable side effect of otherwise principally beneficial international commerce (1). Trade agreements have greatly increased economic connectedness over the past century (2). While trade connects producers with geographically distant consumers—mutually improving aggregate welfare (3, 4)—it also facilitates the introduction of organisms inadvertently transported with cargo. These introductions can result in species establishing outside of their native ranges. Many invading organisms alter ecosystem processes substantially and detrimentally affect agricultural productivity, forestry, fisheries, human health, property values, and outdoor recreation (5, 6).

Inadvertent movements of organisms with cargo are not rare. For example, between 2003 and 2010, insect pests or plant pathogens were found by inspectors on 22,267 shipments (2.6% of all shipments) of plants entering the United States (7). Imports of plants have been identified as the dominant pathway by which non-native plant pests have been historically transported to new habitats around the world. The insect order that is most frequently transported with imported plants is the Hemiptera—a typically inconspicuous, mostly plant-feeding (phytophagous) group of insects that comprises one of the largest fractions of all invading species (7–10). Of the 3500 species of non-native insects that have established in Northern America (the contiguous United States, Alaska, and Canada), about 27% are Hemiptera (11), with many of these considered serious pests.

Here, we examine the relationship between imports and discoveries of Hemiptera from the 1800s to the present with emphasis on a central puzzle: Despite rapid expansion of plant imports since the 1960s—greater than 400%—new Hemiptera establishments have remained relatively steady. In Fig. 1A, we show historical imports of plant material into the United States during 158 years (1854–2012) disaggregated across seven ecological source regions (see map).

Figure 1B displays the historical first discoveries of non-native phytophagous Hemiptera species from various regions established in Northern America.

The dominance of the European and Asian Palearctic regions in imports and species discoveries has—for both of these series—diminished in recent decades, with increasing roles played by the Neotropic and Indomalaya regions (see Fig. 1). But most notable overall is the lack of an observed tight coupling between rapidly growing trade and discoveries in recent decades. We evaluate the dynamics behind this counterintuitive relationship. This evaluation includes exploration of whether there is attenuation in establishment risk from imports over time and, if so, whether this is associated with the cumulative history of imports [e.g., due to source species pool depletion (12)] or other time-varying factors (e.g., changes in the commodities imported or phytosanitary measures).

Dynamic-regional modeling of the import-establishment-discovery process

We use maximum likelihood estimation to fit a model of Hemiptera establishment and subsequent discovery in Northern America that accounts for exporter region differences, changes in import levels, and other dynamic factors (see Methods). There are several reasons to expect establishment risk from cargo to differ across exporting regions. Source regions vary in their export type and volume and the composition of their indigenous and non-native insect populations. Imports from areas with an abundance of species capable of establishment and adapted to environmental conditions in new regions pose greater establishment risk, although identifying the risk associated with individual species can be challenging (13, 14).

Threats associated with various sources of trade are also dynamic: Successive establishments may reduce or amplify the source pool of potential invaders, and the likelihood of a unit of imports introducing a novel species might decrease given either successive establishments reducing the source pool of potential invaders (12, 15, 16) or increased application of phytosanitary measures (17–20). Conversely, this risk per unit of imports may increase if phytosanitary measures are eased or if the sourcing or type of imports diversifies in ways that connect additional species in source regions with trade pathways.

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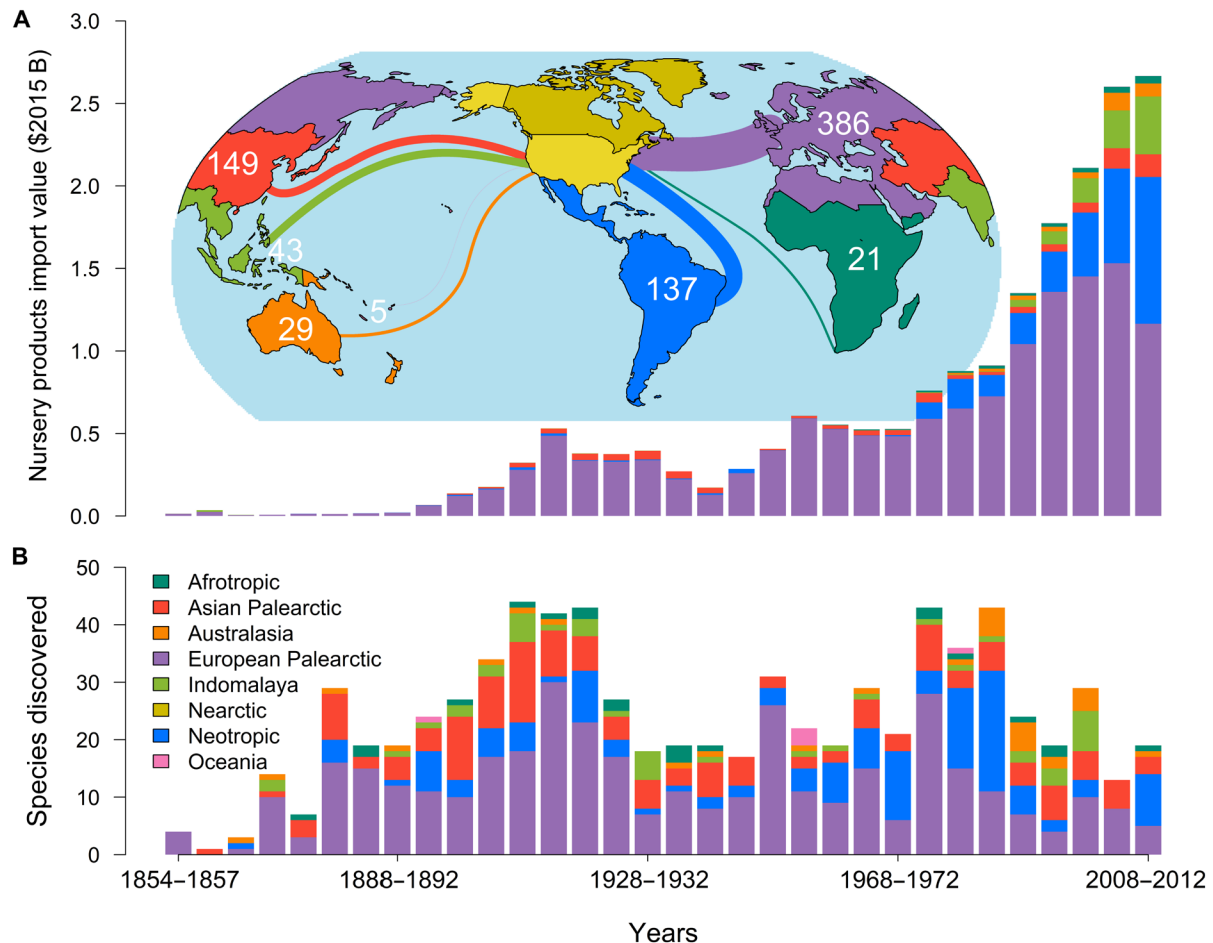


Fig. 1. Value of live plants imported into the United States and established non-native Hemiptera species discoveries in Northern America by biogeographic region of origin. The map illustrates biogeographic regions that are the source for both annual plant material imports (A) and non-native plant-feeding Hemiptera species discovered (B) from 1854 to 2012. The widths of lines drawn from each region to the Nearctic region are scaled to cumulative live plant imports, and the map numbers in white indicate the cumulative non-native Hemiptera species from the region from 1800 to 2012. Values are disaggregated by source region shown in 5-year increments (except the first increment, 1854–1857). Data sources are described in section S1.

The value of imports shifts with economic development and trade policies. By accounting for current and historical imports, and other dynamics of the system, we quantify the establishment risk posed by imports from distinct biogeographic regions and how these risks have changed with the accumulation of trade history and time.

We build on an estimation approach from the economic literature (15) that combines a model of import-driven non-native species establishment with a probabilistic model of discovery as detailed in Fig. 2. We make two important advancements. First, we substantially expand the geographic scope by modeling establishments for Northern America versus a single customs district. Second, we improve the modeling of the delay between species establishment (at time t) and discovery (at time $t \leq u$). We follow existing models that allow the probability of discovering a species (after establishment) to grow with time ($u - t$) as the species spread. But there is no reason to expect—as commonly assumed for lack of data—that search effort for novel species has been constant over the horizon considered, here the past two centuries. We address this gap with analysis of taxonomic data to construct a measure of search intensity for native Hemiptera in Northern America to serve as a proxy for

time-varying biodiversity survey effort leading to the discovery of non-native Hemiptera (z_u).

Species discovery data are available through the beginning of the 19th century, but consistent data on regional import values before 1854 are not. Rather than drop establishments from 1800 to 1853, we include these observations and estimate a simple constant species establishment rate per year over this early time frame (see Methods).

RESULTS

In Fig. 3A, we show the time series of cumulative observed discoveries of non-native phytophagous Hemiptera species in Northern America between 1800 and 2012. Fitted discoveries and unobserved establishments, estimated using a Poisson regression model, are also depicted (see Methods). The estimated establishment debt level—the number of established species that have not yet been discovered (21)—has been relatively constant since the late 1800s, with the number of discovered and estimated established species growing at similar rates. For the final year (2012), we show the total number of observed discoveries (770) and the estimated establishment debt

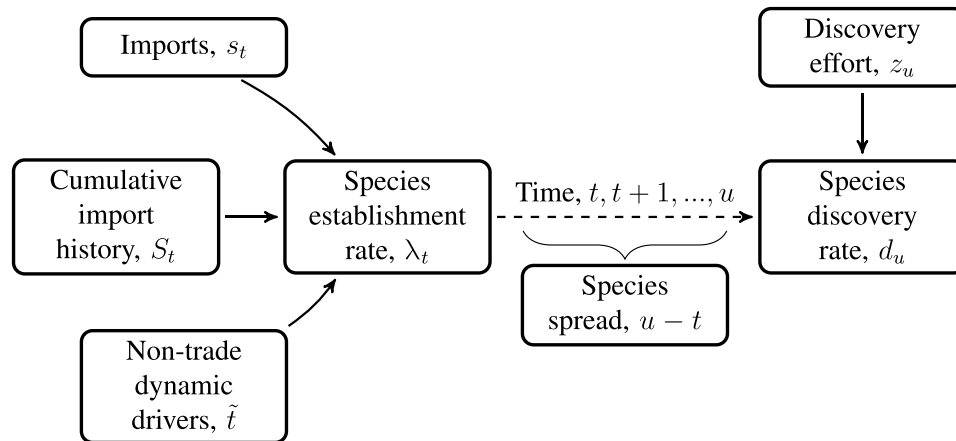


Fig. 2. Schematic of model variables used to estimate the establishment and discovery rates of non-native Hemiptera species over time (years).

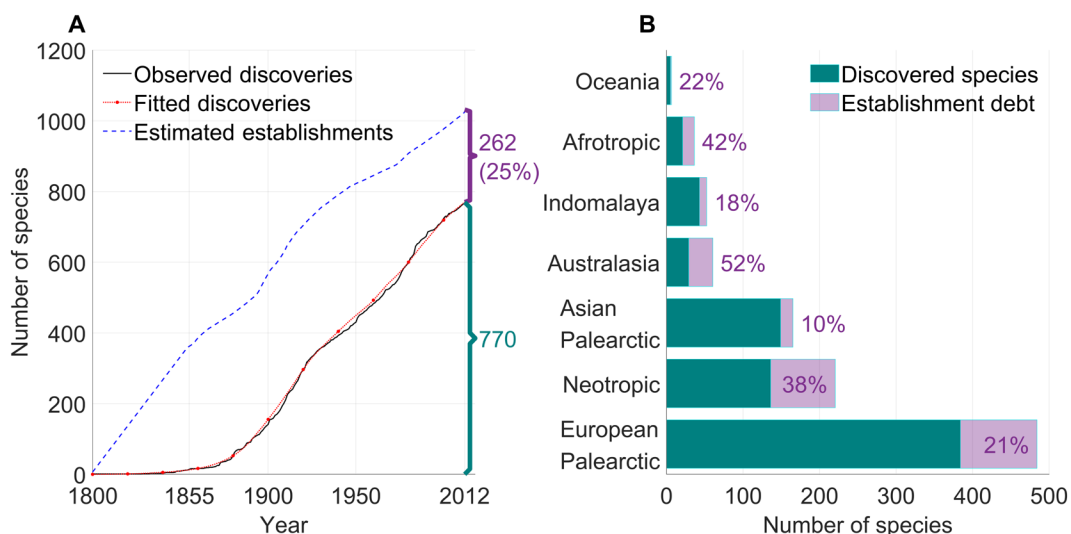


Fig. 3. Non-native species discoveries and estimated establishments over time and by biogeographic region of origin. Cumulative observed discoveries, fitted discoveries, and estimated establishments of non-native Hemiptera species aggregated across regions, 1800–2012 (A). The cumulative observed discoveries and gap between observed discoveries and estimated establishments (“establishment debt”) are reported as both levels and percentages for 2012. The observed discoveries and establishment debt (in levels and percentages) in 2012 are reported by region in (B).

(262), representing approximately 25% of the total established species. The regional disaggregation of these estimates is shown in Fig. 3B. Sustained high levels of imports from the European Palaearctic have resulted in a substantial establishment debt levels. The Afrotropic, Australasia, and Neotropic regions show the highest estimated percentage establishment debt (Fig. 3B) because of relatively recent rapid increases in imports. The greatest raw numbers of established but undiscovered species stem from the European Palaearctic and Neotropic regions. Estimated model parameters used to generate all figures in Results are reported in table S4.

Examination of the import-establishment relationship both (i) among regions and (ii) over time generates useful insight into the puzzle of why the observed discovery and estimated establishment curves in Fig. 3A have remained relatively linear in recent decades despite rapidly growing imports. In Fig. 4, for each region (A to F), we show annual nursery product import values (area plot, log scale),

estimated marginal (establishment) risk per additional \$1 million of imports (dashed blue line), and total establishments (red line).

For all regions, the value of imports has generally increased over time. Despite this increase in imports, we observe a decline in the estimated number of establishments over the past century from the European and Asian Palaearctic regions. Establishments from the Neotropic and Afrotropic regions increased markedly following World War II and remained relatively high after that. After also declining in the first half of the 20th century, Australasia’s estimated establishments have recently increased. Since the 1950s, estimated establishments have remained relatively stable for the Indomalaya region. Thus, the aggregate pattern of establishments in Fig. 3A, where the annual rate is sometimes decreasing and sometimes increasing, emerges from a mix of regionally declining or increasing rates.

Import dynamics are an important driver of these patterns. Over the past century, the regions with declining establishments (Fig. 4, B

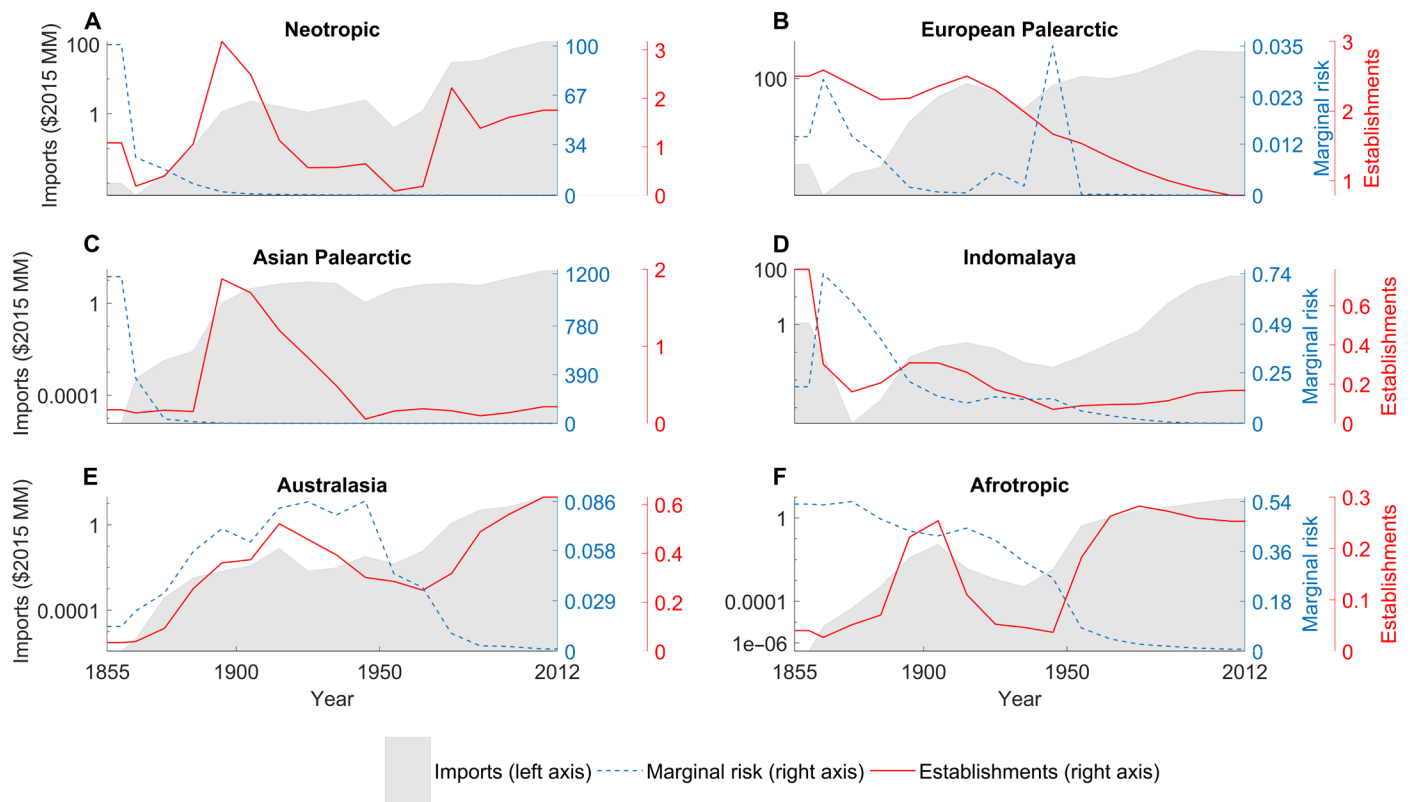


Fig. 4. Imports, estimated establishments, and estimated marginal risk over time in aggregate and for select biogeographic regions of origin. Annual nursery product import values (log scale), estimated marginal (establishment) risk per additional \$1 million (\$2015) of imports, and estimated establishments, by exporting region (A to F) for years 1855–2012. All series are depicted as 10-year averages except for years at the boundaries (1855–1860 and 2008–2012).

and C) have all experienced relatively gradual increases in imports. In recent decades, those regions with relatively steady or increasing establishments (Fig. 4, A and D to F) have each undergone rapid increases in imports.

We find that the coupling between import growth and establishment growth has changed substantially over time. From Fig. 4, we see that, for every region, the first epoch of rapid growth in imports in the late 1800s/early 1900s was associated with increased establishments. However, as summarized above, this coupling did not hold for all regions when imports again spiked in the 1960s. Because species establishment dates are rarely directly observed, the data are not temporally precise enough to pin down the effects of specific factors, such as particular biosecurity policies. However, we do decompose temporal variation in establishment rates into (i) cumulative exposure to imports from a region and (ii) a time trend capturing remaining time-varying effects like changes in shipping and the portfolio of biosecurity practices.

For all regions, estimated marginal establishments—per unit of additional imports—have attenuated because of a combination of increased imports, accumulated imports, and the passage of time. Estimated average establishments—per unit of all imports received in a year—have also declined, between 75.2 and 99.8% for each region from 1962 to 2012. For the Asian Palearctic and Neotropic regions, our estimates indicate that depletion of species pools is a contributing factor (12, 16). We find that dynamic factors other than import volume—as captured by a time trend—are associated with a substantial decline in establishment likelihood for all regions

(see table S4). The higher levels of imports observed in the latter years of our study also are associated with lower marginal risk.

Overall, we find that the risks from substantial growth in imports in the late 20th century have been offset by a combination of attenuation with accumulation of historical trade (e.g., due to exhaustion of species pools) and a mix of non-import factors driving down establishments per unit of imports.

Implications for targeting biosecurity policy

Variation in the risks posed by imports is a critical consideration in the development of policies on biosecurity, such as inspection targeting (22) and import prohibitions (23). While the European Palearctic region has been the largest historical contributor of non-native Hemiptera species, it has also been the largest or second-largest exporter of nursery products to the United States throughout recorded trade. In contrast, the Neotropic region transformed during the trade expansion of the 1960s and 1970s from a relatively small exporter to the second-largest exporter in the period following World War II. The substantial subsequent increase in imports from the Neotropic region has led to a corresponding surge in discoveries of non-native species from this region, even as the rate of estimated establishments stabilized.

The order of relative marginal risk among the Asian Palearctic, Australasia, and Indomalaya regions has changed considerably over the past 150 years. This temporal variation in risk likely reflects changes in the volume of imports. This type of information on changes in risk can inform adaptive approaches to targeting biosecurity resources

toward quarantine, inspection, and other biosecurity practices to specific commodity-country pairs (22).

Discovery process insights

A distinct component of our model is the inclusion of a time-varying proxy for species discovery effort. The estimated coefficient for this term is of the expected sign—more effort increases the probability of discovery—and is statistically significant (see table S4). To illustrate this term in Fig. 5A, we show the probability of discovering a species in the year it was established, π_{uu} , i.e., before any effects of spread. As expected, π_{uu} (driven by search effort) increased in the 20th century, albeit with peaks centered around 1920 and 1965.

As with previous studies, we also find that the probability of a species established in year t being discovered in year $t \leq u$ increases with time $u-t$ (with statistical significance, see table S4) due to, for example, range expansion. In Fig. 5B, we show the probability of a species established in year $t = \{1800, 1850, 1900, 1950\}$ being discovered in years $u = t + \{0, 1, \dots, 100\}$. The probability first increases with the passage of time (spread). However, the probability eventually declines as the probability of having already discovered the species increases. The difference between the curves in Fig. 5B is due to variation in the search effort proxy over time.

From our parameter estimates, we calculated a median delay to discovery of 80 years (95% confidence interval, 24 to 98). This delay is long relative to published observations of the establishment-discovery delay for the few alien Hemiptera species for which both dates are available (8, 15, 24). This difference may reflect that such studies focus on pest species, which are much more likely to be observed and thus discovered sooner. Furthermore, the Hemiptera have been identified as a group for which the efficiency of discovery

of new establishments is particularly low in Northern America, and new establishments remain unreported for long periods (25). Many Hemiptera are small, inconspicuous insects with limited capabilities for dispersal, which may explain, in part, the particularly long discovery lag.

DISCUSSION

A key component of the design of biosecurity policies aimed at excluding establishments of new and potentially damaging species is the characterization of establishment risk among species, pathways, and source regions (1, 20). An informed policy response requires a predictive understanding of how non-native species establishment risk is related to trade, changes over time, and differs among source regions. Unfortunately, the quantification of risk based on historical records of alien species establishments and trade records is obscured by establishment debt (21) stemming from the potentially long delay between alien species establishment and discovery.

Our study applies a unique modeling approach to reveal that the average risk of plant imports to the United States has generally declined over time (Fig. 4), primarily due to gradual technological and policy improvements and, to a lesser extent, past trade experience. For some regions, increasing annual imports were not associated with increasing establishments, perhaps due to both improved biosecurity practices and the progressive depletion of potential invaders from source species pools (12, 16, 26). Regions with recent rapid increases in exports to the United States saw substantial increases in the establishments of Hemiptera species. We estimated that these regions also had a proportionally higher establishment debt of established species that had not been discovered.

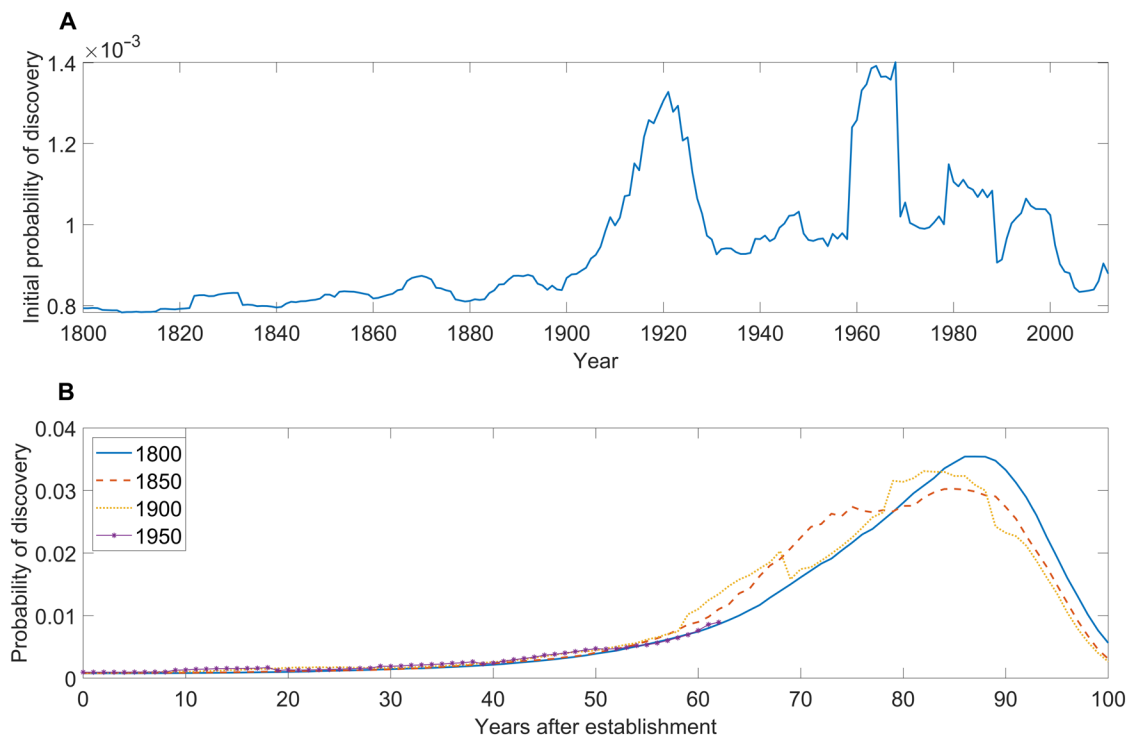


Fig. 5. The probability of discovering a non-native Hemiptera species, 1800–2012. (A) The initial probability of discovery (in the year of establishment) changes with effort. (B) The probability of discovering a species after establishment defers by reference year (legend).

The estimated time-trend—capturing dynamics aside from import volumes—showed decreasing risk, which is consistent with intensified quarantine regulations and inspection efforts. The enactment of the Plant Quarantine Act in 1912 was a profound regulatory event in the history of plant imports to the United States (27), the largest North American importer and most suitable habitat for most Hemiptera species. Just 7 years later, the U.S. Department of Agriculture (USDA) enacted “Quarantine 37,” which, in its initial implementation, largely shut down the practice of importing “plants for planting” in the United States (28). The USDA lifted many of the strongest restrictions on plant imports in the 1950s and 1960s with the movement toward free trade (28), but modern biosecurity practices have been implemented to minimize associated risk (29). Currently, around 5 billion plants are imported to the United States a year, although these imports are highly regulated to reduce overall risk.

Marginal and average risk from imports from all regions (Fig. 4) indicated a consistent downward trend over time. This decline likely reflects, in part, the impact of improved biosecurity measures. Despite this stark decrease in risk per unit of imports, numbers of establishments have remained relatively constant over the past century (Figs. 1A and 3). Decreases in risk from additional imports at the margin were offset by substantial increases in overall import levels and the diversification of the origins of imports across regions, which exposed the United States to new source species pools (Fig. 1B).

In 2011, the USDA implemented a new system to limit commercial imports of plants for which risk information is incomplete (30), but there remain some concerns regarding the risk posed by other plant imports to the United States (31). Our results provide useful context for the current phytosanitary policy debate based on records of imports and discoveries that, superficially, do not provide a clear relationship between trade and the establishment of alien species. First, while the essentially constant rate of accumulation of non-native species in the discovery record suggests a lack of phytosanitary progress, a more optimistic picture emerges from the finding of decreasing marginal establishments (i.e., per additional unit of trade). However, the declines in marginal establishments and average establishments per unit of trade have not been uniform across regions. Thus, our findings have implications for the targeting of biosecurity measures on imports from regions that maintain a higher relative risk. Future research could build on these insights to explore the impacts of historical policy and technological changes on discoveries.

METHODS

Our model of non-native species establishments allows establishment risk to vary by ecological region of imports and over time. We consider imports of nursery products alone because previous case studies indicate that live plants are historically the dominant pathway of introductions of Hemiptera species (7, 9, 10, 17). We model non-native species establishments each year for each region as a Poisson random variable. The mean rate of establishments from region $j \in J = \{1, 2, \dots, 7\}$ in year $t \in T = \{1800, 1801, \dots, 2012\}$ is

$$\lambda_{jt}(\theta_j) = \begin{cases} \exp(\mu + \omega \tilde{t} + \beta_j \ln(s_{jt}) + \gamma_j \ln(S_{jt})), & t \geq 1855 \\ \kappa_j, & t < 1855 \end{cases} \quad (1)$$

where $\theta_j = [\kappa_j, \mu, \omega, \beta_j, \gamma_j]$ is the vector of establishment process parameters. Variables are suppressed in this and all following functions for simplicity. Consistent data on regional import values before 1854

are not available, but species discovery data are available throughout the 19th century (only two species were discovered before 1800 in our data). Thus, we must either ignore the early discovery records until trade measures begin or specify a model in the absence of trade data for early periods. We emphasize the latter approach, assuming that establishments occur from 1800 to 1855 according to a simple constant rate per year (i.e., a homogeneous Poisson process) that differs by region. This vector of early regional establishment rates, κ_j , is jointly estimated with the other parameters of the establishment and discovery processes.

The coefficient μ represents the component of establishment risk that is constant over time and regions. For years $t \in T$, establishments are a function of contemporaneous import value s_{jt} , cumulative import value through the previous year, $S_{jt} = \sum_{\tau=1854}^{t-1} s_{j\tau}$, and a time trend $\omega \tilde{t}$, given the relative year, $\tilde{t} = t - 1855$. The natural log-transformation is a common transformation of time-series data to remove the exponential growth and reduce heteroskedasticity present in the import data. This transformation also decreases the marginal impact of imports when the value of imports is higher when $\beta < 1$, which has a similar effect as the attenuation modeled in previous analyses (15, 24, 32). The coefficient β_j affects the region-specific marginal establishment risk from log-imports, as described in the “Changes in establishments and risk” section.

Establishments may attenuate as cumulative imports grow and exhaust the pool of source non-native species (7, 15). However, this is not assumed or imposed in the model; recent research suggests that past trade may, in some cases, also amplify establishment risk as imported plants provide suitable habitats for invading species (33, 34). Moreover, the trajectory of marginal establishment risk depends on several parameters and variables as characterized in the “Changes in establishments and risk” section. Whether past trade attenuates or amplifies region-specific marginal establishment risk depends on the sign of γ_j .

Initial maximum likelihood estimates returned establishment estimates for Australasia that were implausibly high and occurred almost entirely in a few years. To avoid such an unrealistic solution, we constrained year-on-year increases in the estimated establishment rate, $\Delta \lambda_{jt}$, to below 15 species. This limit is 50% greater than any observed year-on-year increase in recorded discoveries. We applied this restriction across all regions, although only estimates for Australasia were materially influenced.

Post-establishment discovery model

To close the gap between the establishment rate (Eq. 1) and observed discoveries, we use a probabilistic model of the delay from species’ establishment to discovery. This framework generally follows the specification in (35) for modeling the patterns of discovery of non-native species. The probability of observing a species in year $u \in T$ that was introduced in year t is

$$\pi_{tu}(\alpha) = \begin{cases} \frac{1}{1 + \exp(\alpha_0 - \alpha_1(u-t)^2 + \alpha_2 z_u)}, & t \leq u \\ 0, & t > u \end{cases} \quad (2)$$

This probability is a function of the delay to discovery ($u - t$) and our proxy for non-native insect search intensity (z_u) in the discovery year. The delay-to-discovery time component is motivated by a stylized model of radial population establishment spread—the squared exponent is consistent with a constant rate of radial expansion from a point of introduction (36). For our proxy for search intensity,

we take the rate of discovery of native Hemiptera species in the United States over the past two centuries and adjust to account for the declining pool of undiscovered native species, recognizing that more effort is required in later years to discover a species given the shrinking pool of undiscovered species. We detail the construction of this proxy in section S2.

The probability of discovering a previously undiscovered species in year $t \leq u$ is the product of the probability of not observing the species in any of the previous years and the probability that the species will be observed in year u

$$p_{tu}(\boldsymbol{\alpha}) = \begin{cases} \pi_{ut}(\boldsymbol{\alpha}) \prod_{k=t}^{u-1} (1 - \pi_{kt}(\boldsymbol{\alpha})), & t \leq u \\ \pi_{tt}(\boldsymbol{\alpha}), & t = u \\ 0, & t > u \end{cases} \quad (3)$$

Model integration and estimation

Combining Eqs. 1 to 3, the expected number of discoveries from region j in year u is given by the sum of the expected establishments from all previous years through the present, weighted by the probability that they will be discovered in year u

$$d_{ju}(\boldsymbol{\alpha}; \boldsymbol{\theta}_j) = \sum_{t=1800}^u p_{tu}(\boldsymbol{\alpha}) \lambda_{jt}(\boldsymbol{\theta}_j) \quad (4)$$

Assuming that establishments are a Poisson random variable with mean λ_{jt} , then observable discoveries, y_{ju} , are also a Poisson random variable with mean d_{ju} . The likelihood function combines observations and estimates across regions and time and is given by

$$L(\boldsymbol{\alpha}; \boldsymbol{\theta}) = \prod_{j \in J} \prod_{u \in T} \frac{d_{ju}^{y_{ju}}(\boldsymbol{\alpha}; \boldsymbol{\theta}_j) \exp(-d_{ju}(\boldsymbol{\alpha}; \boldsymbol{\theta}_j))}{y_{ju}!} \quad (5)$$

where $\boldsymbol{\theta}$ is the set of establishment parameters, $\boldsymbol{\theta}_j$ for all regions, and the parameter vectors $\boldsymbol{\theta}$ and $\boldsymbol{\alpha}$ are estimated.

For a simpler version of our model, Costello *et al.* (15) use integrated likelihood to overcome challenges of simultaneously estimating the establishment and discovery model (because the two components can trade off together to produce extreme outcomes). Because our extended discovery model does not accommodate an integrated likelihood approach, we estimate the model using maximum pseudo-profile likelihood (MPPL) (37). This approach entails estimating the parameters of λ , represented by $\boldsymbol{\theta}$, given a fixed vector of parameters, $\boldsymbol{\alpha}$. For a given discovery parameter vector, $\boldsymbol{\alpha}$, estimates converge quickly and consistently. We consider a large set ($n = 15,625$) of candidate discovery parameter vectors. For each candidate vector, we obtain parameter estimates of $\boldsymbol{\theta}$ and MPPL value, PL. The presented results are generated from the parameter estimates $\boldsymbol{\theta}^*$ from the vector $\boldsymbol{\alpha}^*$ that are associated with the maximum MPPL value, PL*. More details on the MPPL are presented in section S6.

Parameter estimates are presented in table S4 with 95% likelihood ratio-based confidence intervals. Under the pseudo-profile likelihood approach, the confidence intervals around the parameters of the discovery process ($\boldsymbol{\alpha}$) are evaluated using the profiles developed in the main estimation, which optimizes all parameters, $\boldsymbol{\theta}$. The confidence intervals for each parameter without $\boldsymbol{\theta}$ are found by fixing $\boldsymbol{\alpha}$ at its optimal value and reoptimizing all other parameters in $\boldsymbol{\theta}$.

Neither of the region-specific parameters (β and γ) are statistically significant for four regions. However, using a likelihood ratio test, we reject the null hypothesis that these parameters are zero for

these four regions ($P < 0.01$). Thus, we maintain these parameters in the model while acknowledging the parametric uncertainty associated with our estimates and focusing our discussion on overall estimates of the marginal or average establishment risk.

Changes in establishments and risk

Establishments nonlinearly evolve over time with changes in imports and nontrade factors. The establishment function combines each term within an exponential function, preventing direct interpretation of the parameters. Instead, a total derivative of establishments with respect to time provides an analytical representation of changes in risk for each region

$$\begin{aligned} \frac{d \lambda_{jt}}{d \tilde{t}} &= \frac{\partial \lambda_{jt}}{\partial s_{jt}} \cdot \frac{d s_{jt}}{d \tilde{t}} + \frac{\partial \lambda_{jt}}{\partial S_{jt}} \cdot \frac{d S_{jt}}{d \tilde{t}} + \frac{\partial \lambda_{jt}}{\partial \tilde{t}} \\ &= \frac{\beta_j}{s_{jt}} \cdot \lambda_{jt} \cdot \frac{d s_{jt}}{d \tilde{t}} + \frac{\gamma_j}{S_{jt}} \cdot \lambda_{jt} \cdot \frac{d S_{jt}}{d \tilde{t}} + \omega \cdot \lambda_{jt} \\ &= \lambda_{jt} \left(\frac{\beta_j}{s_{jt}} \cdot \frac{d s_{jt}}{d \tilde{t}} + \frac{\gamma_j}{S_{jt}} \cdot \frac{d S_{jt}}{d \tilde{t}} + \omega \right) \end{aligned} \quad (6)$$

The estimated number of establishments, λ_{jt} , is restricted to be weakly positive. Similarly, contemporaneous and cumulative imports cannot be negative. Cumulative imports monotonically increase ($0 \leq \frac{d S_{jt}}{d \tilde{t}}$). We restrict $0 < \beta_j$. Therefore, how the estimated establishments change over time depends on the signs of γ_j and ω as well as whether contemporaneous imports are increasing.

All else equal, establishments increase (or decrease) as contemporaneous imports increase (or decrease). The effect of cumulative trade is ambiguous and depends on the sign of γ_j . Time can either increase or decrease establishments depending on the sign of ω . We observe a negative relationship between the passage of time and estimated establishments ($\omega < 0$).

We may also evaluate an analytical form for the marginal establishment risk, denoted MER_{jt} , for each region (15).

$$MER_{jt} = \frac{\beta_j}{s_{jt}} \exp(\mu + \omega \tilde{t} + \beta_j \ln(s_{jt}) + \gamma_j \ln(S_{jt})) \quad (7)$$

All else equal, the marginal establishment risk is decreasing in contemporaneous imports over the estimated values of $\beta_j \in [0, 1]$. All of our parameter estimates fall within this interval. The effects of cumulative imports again depend on the sign of γ_j . The establishment risk is generally decreasing over time with nontrade factors (estimated $\omega < 0$).

Rather than displaying the continuous derivative (Eq. 7), Fig. 4 represents the estimated change in establishments for a discrete increase of \$1 million in additional imports. Using a discrete change in imports avoids the very large derivative values that arise as imports approach zero. Very low imports occurred for some regions at the beginning of the series and around World War II.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <https://science.org/doi/10.1126/sciadv.abj1012>

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Acknowledgments: We thank S. Iyer and H. Schrader for contributions to the data collection process and H. Seebens, E. Fenichel, M. Reimao, and E. Brockerhoff for helpful comments on the development of this project. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy. **Funding:** This research was funded by

National Science Foundation grant DEB-1414374 and supported by the National Socio-Environmental Synthesis Center (SESYNC) under funding received from National Science Foundation DBI-1052875 and DBI-1639145. A.M.L. received support from the Czech Operational Programme Research, Development, and Education (EVA4.0; no. CZ.02.1.01/0.0/0.0/16_019/0000803). This research was supported in part by the U.S. Department of Agriculture, Economic Research Service. **Author contributions:** Conceptualization: M.J.M., M.R.S., and A.M.L. Data collection: M.J.M., A.M.L., and T.Y. Methodology and formal analysis: M.J.M. and M.R.S. Funding acquisition: M.R.S., M.J.M., and A.M.L. Investigation: all. Project administration: M.J.M. Visualization: M.J.M. Writing—original draft: M.J.M. and M.R.S. Writing—review and editing: all. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** Import data were provided by the U.S. Department of Agriculture Foreign Agricultural Service's Global Agricultural Trade System (available at <https://apps.fas.usda.gov/gats/default.aspx>) and the U.S. Census Bureau reports (available at <https://catalog.hathitrust.org/Record/001719409>). Data on species discoveries were collated for numerous sources and are available at Github (https://github.com/mjmaclac/NNS_Est_Risk) or Zenodo (<https://zenodo.org/badge/latestdoi/398080863>). All code for generating the results will be made available at Github at https://github.com/mjmaclac/NNS_Est_Risk or Zenodo at <https://zenodo.org/badge/latestdoi/398080863>.

Submitted 20 April 2021

Accepted 3 September 2021

Published 27 October 2021

10.1126/sciadv.abj1012

Citation: M. J. MacLachlan, A. M. Liebhold, T. Yamanaka, M. R. Springborn, Hidden patterns of insect establishment risk revealed from two centuries of alien species discoveries. *Sci. Adv.* **7**, eabj1012 (2021).