# Forecasting Biological Invasions with Increasing International Trade

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**Abstract:** *We used historical data to parameterize species-accumulation models relating international trade to the establishment rates of nonindigenous species in the United States over the past century. We then coupled these relationships with published trade forecasts to predict future invasion rates for insects, plant pathogens, and mollusks. Relationships between the accumulation of non-native species and merchandise imports were reasonably described by log-log and log-linear species-area models and Michaelis-Menten accumulation functions. However, the latter two models produced markedly better fits. When coupled with projected trade forecasts, the log-linear species-area model predicted 16–24% taxon-specific increases in the number of nonindigenous species established in the United States from 2000 to 2020. The Michaelis-Menten model predicted much lower 3–6% increases, but even this meant 115 new insect species and 5 new plant pathogens. These results suggest that the ecological and economic costs associated with human-caused biological invasions may continue to rise substantially over the coming decades.*

Predicción de las Invasiones Biológicas con el Incremento del Comercio Internacional

**Resumen:** *Empleamos datos históricos para parametrizar modelos de acumulación de especies relacionando el comercio internacional con las tasas de establecimiento de especies no-indígenas en los Estados Unidos a lo largo del siglo pasado. Posteriormente acoplamos estas relaciones con predicciones de mercado publicadas para determinar las tasas futuras de invasión para insectos, patógenos de plantas y moluscos. Las relaciones entre la acumulación de especies no nativas y las mercancías de importación fue razonablemente descrita por modelos de especies-áreas log-log y log-lineal y las funciones de acumulación de Michaelis-Menten. Sin embargo, estos últimos dos modelos produjeron ajustes notablemente mejores. Cuando se acoplaron con predicciones de mercado proyectadas, los modelos de especie-área logarítmicas-lineales predijeron incrementos específicos de taxón del 16-24% en el número de especies no indígenas establecidas en los Estados Unidos del 2000 al 2020. El modelo de Michaelis-Menten predijo incrementos mucho menores del 3-6%, pero aún esto representa 115 nuevas especies de insectos y 5 nuevas especies de patógenos de plantas. Estos resultados sugieren que los costos ecológicos y económicos asociados con las invasiones biológicas causadas por humanos podrían continuar incrementándose sustancialmente a lo largo de las siguientes décadas.*

## Introduction

Nonindigenous species rank second only to habitat degradation as a source of species endangerment (Miller 1989; Wilcove et al. 1998) and cost the U.S. economy over $100 billion per year in losses, damages, and control (Pimentel et al. 2000). The often irreversible ecological effects of invasive species, the enormous financial costs attributed to them, and the potential for even more biotic exchange with the move toward reduced trade barriers mandate quantitative predictions of how many exotic species will accumulate in the United States over the coming decades.

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It is widely recognized that most harmful nonindigenous species arrive in their new locations as a result of trade (Office of Technology Assessment 1993; Daehler & Carino 1999; U.S. Department of Agriculture 1999; Perings et al. 2000; Convention on Biological Diversity 2002). For example, commodities transport was the source of 81% of introduced weeds intercepted by U.S. federal authorities in the late 1980s (Office of Technology Assessment 1993). Furthermore, over the next 20 years, the volume of trade entering the United States is forecasted to grow exponentially at an average rate of roughly 6% per year (University of California Anderson Forecast 1999). Relating trade to the number of new introductions is complicated, however, because the expected relationship is nonlinear. Each new container ship does not bring with it a whole new set of species; instead, each ship brings samples from regions already sampled by previous ships. Thus, as import volume increases, the per-ship probability of transporting a new introduction declines.

We hypothesized that this is similar to the classic ecological problems faced when species richness is estimated from a series of samples. When a meadow is sampled, for example, each new plot added to the area already sampled contains some species that were present in previous samples plus new ones. Thus cumulative species richness does not scale linearly with the number of plots sampled (Rosenzweig 1995). For this reason, ecologists have developed a number of alternative species-accumulation models that relate species richness to sampling intensity (reviewed by Colwell & Coddington 1994). From these models, the species richness of larger samples can be extrapolated (Palmer 1990; Colwell & Coddington 1994; Keating & Quinn 1998).

Given that estimating the number of exotic species with increasing imports is similar to estimating species richness from a series of samples, we related past merchandise trade to the accumulated number of biological invasions with species-accumulation models. Here, we present these relationships for insects, plant pathogens, and mollusks and couple them with projected trade forecasts to produce the first quantitative forecasts of future rates of biological invasion.

## Methods

We obtained historical numbers of established exotic insects from Sailer (1983) and data for plant pathogens and mollusks from the Office of Technology Assessment (1993). For trade data, we used U.S. Department of Commerce statistics of merchandise imports from 1800 onwards, converted to 1999 U.S. dollars. We then calculated cumulative imports to 1920, 1930, 1940, . . . 1990. Although other taxonomic groups were available for study (e.g., mammals), we restricted our analysis to those continuing to enter the United States as accidental introductions with trade.

The ecological literature contains a number of species-accumulation curves that could also model relationships between exotic-species richness and trade. Even in their application to ecological sampling, however, there is little consensus about which model is best (Palmer 1990; Colwell & Coddington 1994; Keating & Quinn 1998). Thus, for each species group we fitted three commonly used models to the accumulated number of exotic species with imports from 1920 onward: the log-log species-area model, the log-linear species-area model, and the Michaelis-Menten model. All have been used to relate some measure of sampling intensity (area or number of samples) to cumulative species richness. In our use of these models to relate trade to the number of exotic species invasions, we replaced sampling intensity with cumulative imports.

### Log-Log Species-Area Model

Analogous to the nested form of Arrhenius' (1923) species-area model (Rosenzweig 1995), one hypothetical relationship between exotic-species richness and trade takes the form $S = cI^z$, where $S$ is species richness, $I$ is cumulative imports, $c$ is a constant, and $z$ describes the rate at which the species richness accumulates with increasing trade. Because the relationship between $\log S$ and $\log I$ is linear with slope $z$, we used linear regression to estimate $z$ and $c$.

### Log-Linear Species-Area Model

Based on an alternative form of the species-area curve, proposed by Gleason (1922), another model for the relationship between trade and the accumulated number of exotic species is $S = \log I^z + c$ (or $S = \log bI^z$, where $b = 10^c$). For this model, parameters can be determined from linear regression of $S$ against $\log I$.

### Michaelis-Menten Model

Relationships between the cumulative number of samples ($n$) and the cumulative number of species ($S$) are also commonly described by the Michaelis-Menten equation for enzyme kinetics (Colwell & Coddington 1994; Keating & Quinn 1998). Replacing the number of samples with quantity of imports yields

$$S = \frac{S_{max} I}{B + I},$$

where $S_{max}$ and $B$ are constants. We used Raaijmakers (1987) maximum-likelihood estimators to calculate $S_{max}$ and $B$ because linear regression on transformations of this equation reportedly yield biased parameter estimates (Raaijmakers 1987; Colwell & Coddington 1994). Unlike the two species-area models, the Michaelis-Menten model has an upper bound ($S_{max}$).

To obtain an overall description of fit comparable across all models, we calculated an $R^2$ for each model as the sum of the squared deviations of each data point from the model prediction, divided by the total sum of squares (untransformed axes). The associated $p$ values are not presented because significance tests are inappropriate with double-cumulative data.

Lastly, we coupled the parameterized models with historical trade volumes (U.S. Department of Commerce 1975) and projected trade volumes (University of California Anderson School 1999) to estimate the number of exotic species that will be established in the United States between 2000 and 2020 (21.795 and 66.606 trillion dollars of cumulative imports, respectively).

## Results

The species-import curves obtained for the invasion of various taxonomic groups since 1920 were reasonably described by all three models (Fig. 1), supporting the hypothesis that the accumulation of exotic species with trade can be modeled with species-accumulation curves. However, the log-log species-area model described the historical data least accurately (Table 1). The Michaelis-Menten model produced the best fits, although its superiority to the log-linear species-area model was substantial only for exotic plant pathogens. For all species, the relationships supported the hypothesis that the per-ship probability of transporting a new introduction declines with increasing imports. Nonetheless, future invasion rates also depend on the forecasted changes in trade volume.

Despite each model reasonably describing historical data, the forecasted increases in exotic-species richness between 2000 and 2020 differed markedly (Table 1). The Michaelis-Menten model predicted only 3–6% increases over this 20-year period, whereas the log-log species-area predictions ranged from 27% to 61%. Although the latter predictions are suspect based on the relatively poor fit of the log-log species-area model to historical data, even the log-linear species-area model predicted 16–24% increases. These predictions may still seem high, but the 492 new exotic insects, for example, represent less than twice the number observed over the 20- year period between 1960 and 1980, a period over which imports were 10% of the amount forecasted for the next 20 years. Changing the forecasted trade volume by 30% changed the number of new species by a comparable amount for both species-area models and by roughly 15% for the Michaelis-Menten predictions.

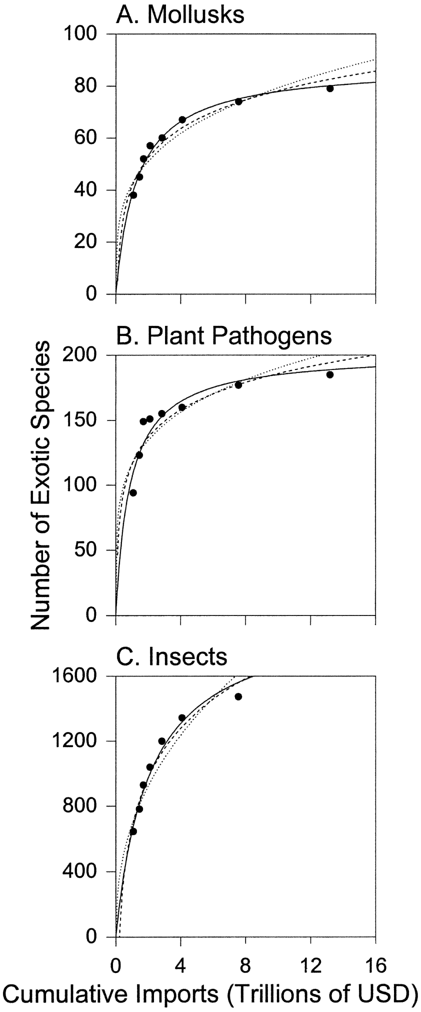


*Figure 1. Relationship between U.S. merchandise imports and the accumulation of exotic (a) mollusks, (b) plant pathogens, and (c) insects since 1920 (10-year increments). Lines show the different species-accumulation models in Table 1 (dotted, log-log species-area; dashed, log-linear species-area; solid, Michaelis Menten). USD are 1999 U.S. dollars.*

## Discussion

Our analysis suggests that trade and exotic-species accumulation are related in a manner similar to classic species-accumulation curves developed for ecological sampling. Our forecasts all suggest that the United States will continue to accumulate exotic species, but the forecasted amount of new introductions varies considerably with different species-accumulation models (Table 1). Nonetheless, even the lowest projection forecasts 115 new insect species and 5 new plant pathogens over the next 20 years. If only 10% of these become harmful (Williamson & Fitter 1996), it will still be a substantial financial burden to add to the costs already associated with

**Table 1. Historical and forecasted increases in the number of exotic species based on three species-accumulation models.**

| Taxonomic group | Log-log species-area: model | $R^2$ | new species, 2000–2020[a] (% increase) | Log-linear species-area: model | $R^2$ | new species, 2000–2020[a] (% increase) | Michaelis-Menten: model | $R^2$ | new species, 2000–2020[a] (% increase) | Observed invasions, 1970–1990[b] |
|---|---|---|---|---|---|---|---|---|---|---|
| Mollusks | $S = 0.0224I^{0.273}$ | 0.89 | 35 (35.7) | $S = \log I^{36.68} - 398.68$ | 0.95 | 18 (19.6) | $S = \frac{88.04I}{1.31 \times 10^{12} + I}$ | 0.99 | 3 (4.0) | 12 |
| Plant pathogens | $S = 0.3139I^{0.214}$ | 0.74 | 61 (27.0) | $S = \log I^{69.86} - 722.40$ | 0.80 | 34 (16.2) | $S = \frac{201.75I}{9.10 \times 10^{11} + I}$ | 0.88 | 5 (2.8) | 25 |
| Insects | $S = 0.0056I^{0.424}$ | 0.88 | 1535 (60.6) | $S = \log I^{1014.08} - 11501.82$ | 0.96 | 492 (24.3) | $S = \frac{1995.52I}{2.11 \times 10^{12} + I}$ | 0.97 | 115 (6.3) | 275 (1960–1980) |

[a] *Forecasts are based on year 2000 and year 2020 cumulative imports totaling 21.795 and 66.606 trillion dollars, respectively. Numbers of new species are rounded to the nearest whole number, and percent increases are the number of new species in 2000–2020 as a percentage of those at 2000.*
[b] *Insect data from 1960–1980 are presented because 1990 data are unavailable for this group.*

nonindigenous species (Miller 1989; Wilcove et al. 1998) and could result in severe ecological changes to U.S. forests and other natural resources.

Determining which model predictions are best is difficult. Although the Michaelis-Menten model produced the highest $R^2$s, similar fit was achieved for mollusks and insects by the log-linear species-area model. Furthermore, Keating and Quinn (1998) caution against using high $R^2$s as justification for extrapolating from Michaelis-Menten accumulation curves. They and others (Palmer 1990; Colwell & Coddington 1994) have demonstrated that this model often underestimates the true richness. Thus, the relatively low increases in exotic-species invasions forecasted by this model (Table 1) are likely to be too low. Meanwhile, the log-log species-area model tends to overestimate richness in larger samples (Palmer 1990), so our log-log species-area predictions are likely too high. The log-linear model tends to be less biased (Palmer 1990). Furthermore, unlike the Michaelis-Menten model, it does not assume an upper boundary to the number of invasions and thus seems more realistic when sampling the worldwide pool of potential invaders.

Our species-accumulation approach makes several important assumptions that qualify our predictions. First, it assumes that past trends in shipping technology, the types of goods being traded, trading partners, and inspection will continue into the future. Some of these assumptions may make our predictions too low (constant inspection per unit of trade), whereas others (the number of trading partners can increase only to a limited extent) may make them too high. They will also be too high if U.S. trading partners lose species as a result of invasions and habitat destruction within their borders or if trade has transported a disproportionate fraction of the best colonizers.

Lastly, our relationships would ideally be derived for the different biogeographic sources of exotic species, but the requisite data were unavailable. For similar reasons, we conducted analyses only for the United States. Nonetheless, our approach should be applicable worldwide. Developing nations, for which international trade will grow even faster, may see increases greater than those for the United States. Despite these and other assumptions, we believe we have developed an important null hypothesis for how invasions should increase with international trade. The application of these methods to other countries and biogeographic regions will further our understanding of how international trade influences species diversity worldwide.

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