Depletion of heterogeneous source species pools predicts future invasion rates

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Summary

1. Predicting how increasing rates of global trade will result in new establishments of potentially damaging invasive species is a question of critical importance to the development of national and international policies aimed at minimizing future invasions. Centuries of historical movement and establishment of invading species may have depleted the supply of species available for future invasions, and it has been suggested that the problem of invasions will diminish as a result of this. However, the extent to which source pool depletion affects future invasions remains unclear.

2. Here we describe a mechanistic model that captures the simultaneous effects of depletion of source species pools along with increases in pathway rates (e.g. imports) to predict future numbers of new invasions. We assume that the distribution of species abundance within invasion pathways is positively skewed, which is modelled using a log-normal distribution. Given their high propagule pressure, the most abundant species are likely to invade first, while the many rare species are likely to invade only under high pathway volumes. We apply this model to the case study of bark beetle, Scolytinae, invasions in the USA.

3. Source species pools in Europe and Asia (225 and 655 species of Scolytinae, respectively) are much larger than numbers that have historically established (16 and 32). Parameterization of the model indicates a highly skewed species abundance distribution in the pathway and this is confirmed by species frequencies in port inspection records, thus explaining why only a small fraction of species has historically invaded.

4. Forecasts from the model indicate that with increasing rates of imports, more species from these regions are likely to invade in the future despite the depletion of the most abundant species from source species pools. Previous statistical models tend to underestimate future establishments in the presence of increasing import rates due to their failure to account for key underlying mechanisms.

5. *Policy implications.* The mechanistic model developed here is widely applicable for predicting future invasions of all taxa and provides insights into how increases in rates of imports counteract the species pool depletion effect, resulting in the continued establishment of new species.

Key-words: biological invasions, forecast, globalization, invasive species, model, pathway, predictions, propagule pressure, Scolytinae, species abundance distribution

Introduction

A key problem that has long vexed invasion biologists is prediction of future invasions. While this problem is sometimes framed around predicting which species will invade (Kolar & Lodge 2001), a more basic question is how many species will invade (Leung, Drake & Lodge 2004). Knowledge of future invasions is critical both for targeting measures to control invasion pathways and evaluation of the benefit of such prevention efforts (Hulme 2009; Leung *et al.* 2014).

Understanding and predicting temporal trends in the accumulation of invading species is complicated by a plethora of interacting factors that drive such trends.

However, the dominant driver of variation in species establishment is propagule pressure. Variation in propagule pressure often explains why some invading populations establish while others fail (Lockwood, Cassey & Blackburn 2005; Simberloff 2009) and temporal variation in propagule pressure is considered the principal driver of temporal variation in rates of alien species establishment (Levine & D'Antonio 2003; Essl *et al.* 2011, 2015). While many different invasion pathways are known as drivers of propagule pressure, the majority of these are associated with international trade. The flow of imported goods has steadily increased in virtually all countries during the last two centuries and invader propagule pressure has similarly increased. At least in some cases, these increases have been counteracted by quarantine measures that have reduced propagule pressure in the face of increasing trade volume (Hulme 2009; Brockerhoff *et al.* 2014). However, in other cases, invasions by early colonizers have decreased habitat resistance to invasions, contributing to acceleration in rates of alien establishments (Ricciardi 2001).

An important question arising when predicting future invasions is whether future establishments are constrained by the historical depletion of potentially new invading species? If the historical establishment of species depletes the invader pool, this could lead to a decrease in future rates of species establishment. Depletion of species pools might seem impossible given that the world's biota is immensely diverse relative to the small fraction of species that have invaded. However, this pool of species may not be unlimited given that only certain species are prone to transport or finding conditions suitable for establishment abroad (Kolar & Lodge 2001).

Indeed the history of invasions by various species guilds is typified by a relatively small group of species that have proved to be effective invaders, independently invading many different parts of the world (e.g. Brockerhoff *et al.* 2006; Miller *et al.* 2007). While historical invasions are drawn from a relatively small fraction of the world's species, this pool of potential invaders may become depleted over time.

Levine & D'Antonio (2003) recognized that successive invasions are analogous to the sampling of field populations. As species are transported to non-native regions, initial transport is likely to bring the most common species, and numbers of new species arriving with subsequent shipments will necessarily decline as only these most common species are depleted via establishment. They modelled this phenomenon by fitting various nonlinear statistical models to data on cumulative numbers of species establishments as functions of cumulative trade volume. Costello *et al.* (2007) also used historical records of trade and species establishments to fit statistical models of species accumulation, accounting for attenuation in establishment rates over time. Their model was unique in that it accounted for both temporal changes in introduction efficiency (shipping speed and technology) as well as

temporal lags between invasive species establishment and discovery.

Levine & D'Antonio (2003) and Costello *et al.* (2007) used these statistical models to predict numbers of invasions in the future as a function of projected trade volume. However, the ways in which their models account for the attenuation of species establishments over time are purely statistical and therefore may be limited in their ability to explain and make predictions under variable conditions (Cuddington *et al.* 2013). Specifically, the attenuation is accounted for simply by shape functions that do not capture the underlying depletion of the species pool in a mechanistic way. Such statistical approaches also do not account for information that may exist about particular species pools. As an alternative, we propose here a more mechanistic model of species pool depletion resulting from successive invasions. This model accounts both for specific species pool estimates that exist for certain species groups and for the highly skewed nature of species abundance distributions within finite species pools to simulate the depletion of the most abundant species through time.

As a case study, we fit the new model to data on historical establishments of non-native tree-feeding Scolytinae (bark and ambrosia beetles) in the USA introduced from Asia and Europe and make predictions of establishments in the future. This analysis documents the skewed distribution of species abundance in pathways and demonstrates how this distribution leads to attenuation of future establishments that can only be counteracted by increases in future pathway (import) volumes.

Materials and methods

SPECIES POOL MODEL

We assume that species are transported from one continent to another at a rate that is proportional to total pathway volume (e.g. import volume), which may vary through time. In the source region, there exists a finite number n of species that potentially could be transported in the pathway. However within this pool of species, there exists variation among species in both their abundance within their native habitats and their probability of association with invasion pathways. For simplicity, we combine both of these features that affect the probability of a species being transported and simply refer to it as the abundance N_i of species i in a pathway. It should be noted however that this abundance in a pathway is affected by a multitude of species characteristics, including not only abundance in native regions but also their behaviour and their spatial distribution, both of which affect their likelihood of being transported in the pathway.

Ecologists have long recognized that for any community, there exists an underlying distribution that describes the relative abundance of species in that community (Magurran 2004). One of the most universal observations in ecology is that within any community, there are a few very abundant species and many rare species (McGill *et al.* 2007) implying that species abundance distributions must always be strongly positively skewed. Mathematical models that are commonly used to quantify this property include the

log-normal and gamma distributions (Magurran 2004). Here, we assume an underlying log-normal distribution of species abundance (Hubbell 2001).

When using the log-normal species abundance distribution in simulations, we assumed that the abundance of each species falls at even probability intervals across the distribution. Therefore, the number of individuals N_i for the ith ranked species was calculated using:

$$N_i = \exp\left(\Phi^{-1}\left(1 - \frac{\text{rank}_i}{n} + \frac{1}{2n}\right)\Big|\mu, \sigma^2\right) \qquad \text{eqn 1}$$

where n is the total number of species, and $\Phi^{-1}(P|\mu,\sigma^2)$ is the inverse of the cumulative normal distribution function with mean μ and variance σ^2, these being the mean and variance assumed for the log-transformed species numbers from the species abundance distribution. The value of the mean μ was chosen such that $N_1 = 1$, meaning that the abundance of each species was expressed relative to the most abundant species.

The second component of the species pool model links variation among species in their abundance with their probability of establishment. The link between propagule pressure and establishment is well known (Lockwood, Cassey & Blackburn 2005; Simberloff 2009), but only a few attempts have been made to model the relationship (e.g. Leung, Drake & Lodge 2004; Drake & Lodge 2006). We modelled the probability of a species establishing within any given year as a Weibull function of its relative abundance (Leung, Drake & Lodge 2004; Brockerhoff *et al.* 2014):

$$P_i = 1 - (1 - p)^{N_i^c} \qquad \text{eqn 2}$$

where P_i, the probability of establishment of the ith species, is a function of N_i, the relative abundance of that species. The parameter p is the probability of the most abundant species (i.e. the species with relative abundance $N_1 = 1$) establishing within any given year. The parameter c is the Weibull shape parameter. When $c = 1$, this model is the 'Independence', or 'Non-Allee' model, in which every entry event has an equal probability of leading to establishment. When $c > 1$, the model incorporates an Allee effect, with the probability of establishment increasing disproportionately to N_i (Taylor & Hastings 2005). When $c < 1$, the probability of establishment increases with N_i, but at a decreasing rate.

The probability of the ith species establishing during a period of t successive years can be estimated as:

$$P_{t,i} = 1 - \left((1 - p)^{N_i^c}\right)^t \qquad \text{eqn 3}$$

The above estimate of establishment probability assumes a constant rate of propagule pressure among years. However, in most parts of the world, there has been a pattern of increasing rates of imports that can be expected to translate into increasing pathway rates. In the species pool model, we allowed for temporally variable rates of pathway volume (identically across all species in the pathway) using a parameter W_j which connotes pathway volume in year j. Incorporating this effect, the probability of species i establishing over t years is:

$$P_{t,i} = 1 - \prod_{j=1}^{t} (1 - p)^{(W_j N_i)^c} \qquad \text{eqn 4}$$

Note that in this revised model, the parameter p represents the probability of the most abundant species establishing during a year with a pathway volume of $W_j = 1$.

The expected number of species establishing during the period of t successive years can now be estimated as the sum of the establishment probabilities for each species:

$$S_t = \sum_{i=1}^{n} P_{t,i} = \sum_{i=1}^{n}\left[1 - \prod_{j=1}^{t}(1 - p)^{(W_j N_i)^c}\right] \qquad \text{eqn 5}$$

In order to understand the behaviour of the species pool model, we simulated the accumulation of species establishments over 300 time steps (years) given four different values for the log-normal standard deviation σ, the shape parameter c of the Weibull propagule pressure model and n, the total number of species in the species pool. These simulations were performed assuming a constant time series of pathway rates W_j (imports). We then tested the effects of pathway rates increasing both linearly and exponentially. All simulations were calibrated (by adjusting parameter p) to produce 50 species establishing between years 0 and 200 with further species establishments 'forecast' from years 200 to 300.

CASE STUDY: SCOLYTINAE INVASIONS

We applied the species pool model to the accumulation of non-native Scolytinae by decade in the USA. The model was fit to historical records (Haack & Rabaglia 2013) (see Table S1, Supporting Information) of species invading from known European and Asian source species pools (see Table S2). Species native to both Europe and Asia were pooled with European Scolytinae because inspection records (Table S4.1 in Appendix S1) indicated they mostly entered from Europe. The parameterized model was used to make predictions of future establishments 2010–2100.

When applying the model, we assumed a value of 0·96 for the shape parameter, c, of the Weibull model previously estimated for invading Scolytinae (Brockerhoff *et al.* 2014). Pathway volume, W_j, was quantified from historical statistics on the value of imports from Europe and Asia (US Department of Commerce 1975; US Census Bureau 2015), which were used as proxies for the movement of wood packing material, the primary pathway for invading Scolytinae (Brockerhoff *et al.* 2006; Haack 2006). Imports were expressed in billions of USA dollars per year, adjusted to 2013 values utilizing the Consumer Price Index (US Bureau of Labor Statistics 2015).

The number of species establishing during the kth decade $s(p, \sigma, k)$ can be predicted as a function of the unknown parameters p and σ using eqn (5). Assuming that actual numbers of establishments s_k are independently distributed Poisson variables with means $s(p, \sigma, k)$, maximum likelihood estimates of p and σ can be obtained by maximizing the log likelihood function:

$$l(p, \sigma) = \sum_{k=1}^{K} s_k \ln(s(p, \sigma, k)) - s(p, \sigma, k) \qquad \text{eqn 6}$$

Although an exact solution cannot be obtained, numerical methods can be used to maximize this function. We used the Microsoft Excel Solver add-in (Fylstra *et al.* 1998), which utilizes a generalized reduced gradient algorithm. Models were fit using both separate parameters for European and Asian Scolytinae, and using common parameter estimates. The Akaike information criterion (AIC) was used to compare these two alternative models. It was hypothesized that the same parameters p and σ might apply for both European and Asian Scolytinae. Firstly, empirical studies of log-normal species abundance distributions in natural populations have often shown σ to be similar among different communities and taxa (Hubbell 2001). Secondly, no reason is

evident why the probability of establishment for a given level of propagule pressure represented by the parameter p should vary between European and Asian Scolytinae.

Using the maximum likelihood estimates of p and σ, the species pool model was used to forecast future cumulative numbers of species establishing 2015–2105. These projections used predicted future pathway volumes from Europe and Asia. Imports were projected to increase at a rate derived by regression of $\log_{10}(W_j)$ on year j using historical (1815–2005) import data.

For the purpose of comparison, historical decadal data on cumulative establishments and cumulative imports were also used to estimate the Michaelis–Menten equation, the best of several empirical models tested by Levine & D'Antonio (2003):

$$S_t = \frac{S_{max} I_i}{B + I_i} \qquad \text{eqn 7}$$

where S_t is cumulative number of species established, I_i is cumulative imports and S_{max} and B are estimated parameters. Maximum likelihood estimates of S_{max} and B were obtained from the decadal establishment data using the same approach used for fitting the species pool model. That is, predictions at the start and end of each decade were obtained from eqn (7) to predict establishments per decade, and parameter estimates obtained by maximizing the log likelihood function (eqn 6) using numerical methods. The AIC was used to compare the fit of the Michaelis–Menten model with the species pool model. Using these estimates, and projected future imports, the Michaelis–Menten equation was also used to forecast future establishments by decade 2015–2105. The species pool model and Michaelis–Menten models were both coded in a Microsoft Excel macro-enabled workbook, which is provided as Table S3.

INDEPENDENT ESTIMATION OF THE SPECIES ABUNDANCE DISTRIBUTION

The value of σ estimated for European species by fitting the species pool model to historical cumulative numbers of established species by decade (described above) was compared with an independent estimate of σ estimated from historical port interception data using a modification of the maximum likelihood method described by Bulmer (1974) (see Appendix S1 for details). These data were collected from 1949 to 2008 by USA port inspectors (McCullough *et al.* 2006; Brockerhoff *et al.* 2006, 2014). Port inspections are not random but they do provide an approximate quantification of the relative abundance of each species in the invasion pathway. Previous analyses indicate that there is a strong relationship between propagule pressure, as quantified by historical interception frequency, and the probability of a species' historical establishment (Brockerhoff *et al.* 2006, 2014). Interception records could not be used to estimate the species abundance distribution for Asian species because most intercepted Asian specimens were not identified to the species level.

Results

SPECIES POOL MODEL

Simulations using various parameter values demonstrate that depletion of the species pool can produce a trend of decreasing rates of species establishments over time (Fig. 1). This pattern of declining establishment rates is particularly strong when a large fraction of the species
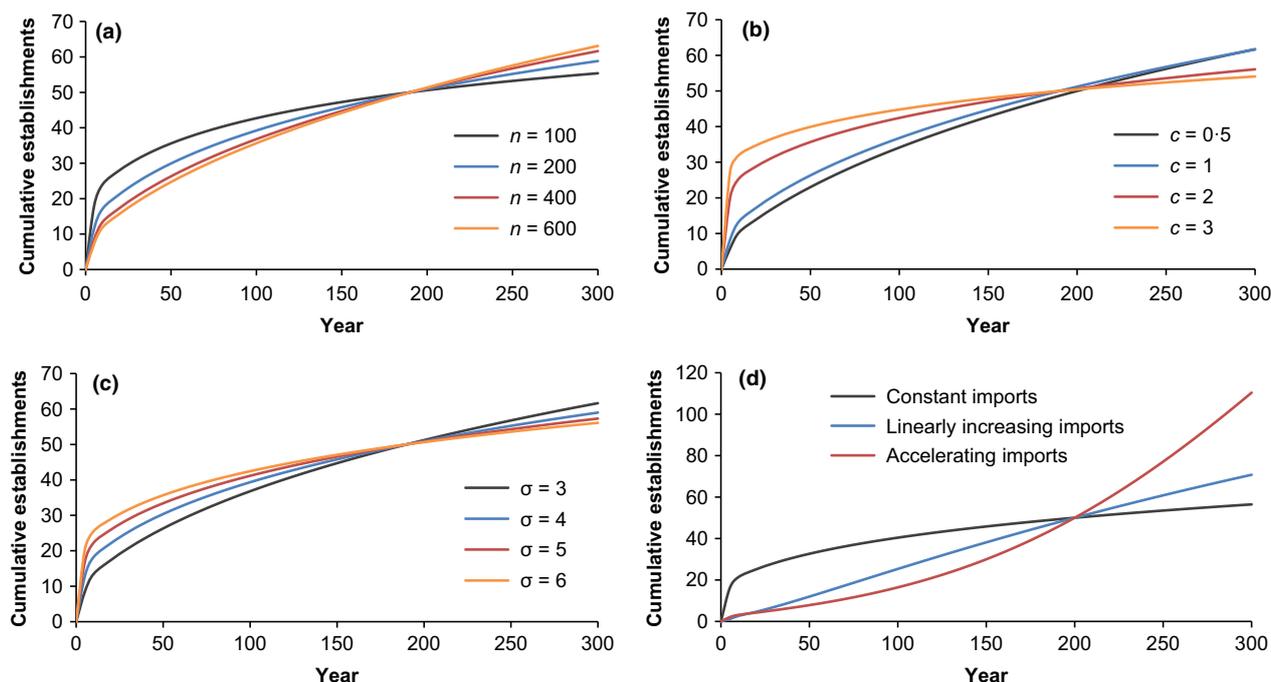

Fig. 1. Simulated accumulation of species establishments given constant pathway rates and calibrated to accumulate 50 species by year 200 for varying source species pools, n (assuming constants $c = 1$ and $\sigma = 3$) (a); varying establishment shape parameter, c, values (assuming constants $\sigma = 3$ and $n = 400$) (b); varying values for the standard deviation, σ, of the log-normal distribution (assuming constants $c = 1$ and $n = 400$) (c); and given either constant import rates, linearly increasing import rates or accelerating import rates, assuming constants $\sigma = 3$, $n = 400$ and $c = 1$ (d).

pool has become exhausted. For example, when 50 of 100 species (50%) establish by the 200th year, the rate of establishment is much slower during years 200–300 than during years 0–100 (Fig. 1a). However, the convex pattern of species establishment is even evident when only 50 of 800 species (6·25%) are depleted by year 200 (Fig. 1a). The reason why establishment rates decline is not simply a matter of total species pool depletion, but it is that the most abundant invaders are depleted early, while the remaining species are less abundant and therefore less likely to establish. In practice, the species abundance distribution model captures not only variation among species in their abundance but also variation in their invasiveness.

The pattern of species pool depletion is strongly affected by the underlying species abundance distribution. For example, when the distribution is only weakly skewed (i.e. low σ), species accumulation proceeds at a nearly constant rate (Fig. 1c). However, in the case of a highly skewed abundance distribution ($\sigma = 9$), accumulation of species distinctly attenuates over time. High values of σ reflect the existence of a very few species that are particularly abundant as well as many species that are very rare. In these situations, the very abundant species quickly become established, but this portion of the species pool becomes depleted and the rate of species accumulation therefore decreases.

The shape parameter c characterizes the relationship of propagule pressure with establishment (Brockerhoff *et al.* 2014) and also influences the pattern of species pool depletion over time. Values of $c > 1$ reflect the existence of an Allee effect which means establishment is much less likely when species arrive at low levels of abundance. The consequence of this is that less abundant species (in the tail of the species abundance distribution) are much less likely to establish. Therefore, for higher values of c, the depletion phenomenon (decline of establishment rates through time) is more pronounced (Fig. 1b). Stronger Allee effects enhance the influence of a skewed species abundance distribution; once the most abundant species are established, the less abundant species are even less likely to establish, thus resulting in a stronger decline in establishment rates over time.

Even though the phenomenon of depletion of abundant species from the source species pool via invasion produces a pattern of declining establishment rates over time, such a pattern is most evident when pathway rates (imports) remain constant (Fig. 1d). However, in reality, import rates to most regions have generally been increasing and this pattern can be expected to continue into the future (Fouré, Bénassy-Quéré & Fontagné 2012). If instead of assuming constant pathway rates, we model monotonically increasing or accelerating pathway rates, this produces a very different pattern of species accumulation in which the rate of species establishment either remains constant or increases over time rather than attenuating (Fig. 1d). In this case, the species pool depletion

phenomenon is still operating, but its effects are overwhelmed by the influence of increasing pathway rates over time.

CASE STUDY: SCOLYTINAE INVASIONS

We identified the source species pool, $n = 225$ for Europe and $n = 655$ for Asia (Table S2). Historically, most Scolytinae invasions in the USA originated from Asia (32 species, 4·9% of source pool) compared with Europe (16 species, 7·1% of source pool) (Fig. 2a). Prior to 1935, Europe was the largest source of species, but by about 1950, Asia had become the dominant source. Accumulation of European species was slightly attenuated from 1875 to 1975 but from 1985 to 2005 it accelerated again.

Of the various model forms tested for predicting species establishments, eqn (6) with common σ and p parameters for European and Asian Scolytinae provided the best fit with the lowest AIC (Table 1). No significant improvement in model fit was achieved using separate parameters for European and Asian species. Predictions and forecasts using the model with common parameters were very similar to the model with separate parameters (Fig. 3). The fit of the Michaelis–Menten model was significantly poorer and this model form required separate parameters for European and Asian species.

Future numbers of species accumulating predicted by the species pool model were much higher than those predicted by the Michaelis–Menten equation (Fig. 3). Establishments forecast by the Michaelis–Menten model quickly attenuated and relatively few future establishments were predicted, but with the species pool model, accumulation of species was predicted to continue into the future at an approximately constant rate (Fig. 3a,b). However, when forecasted cumulative establishments were plotted as a function of cumulative imports, attenuation in future establishments was obvious for both models (Fig. 3c,d).

INDEPENDENT ESTIMATION OF THE SPECIES ABUNDANCE DISTRIBUTION

During the period 1949–2012, there were a total of 5888 interceptions of 69 European Scolytinae species (Table S4.1 in Appendix S1; unidentified species not included) at USA ports. Of the 225 known European Scolytinae species (including both species limited to Europe only as well as species with ranges in both Europe and Asia), 69 were intercepted at the border at least once, with the most abundant species (*Pityogenes chalcographus*) intercepted 1140 times. This meant that 156 European species were never intercepted.

The rank abundances of each species in the interception data are shown in Fig. S4.1 in Appendix S1, plotted along with the log-normal distribution estimated under assumptions of both negative binomial and Poisson sampling. The assumption of negative binomial sampling
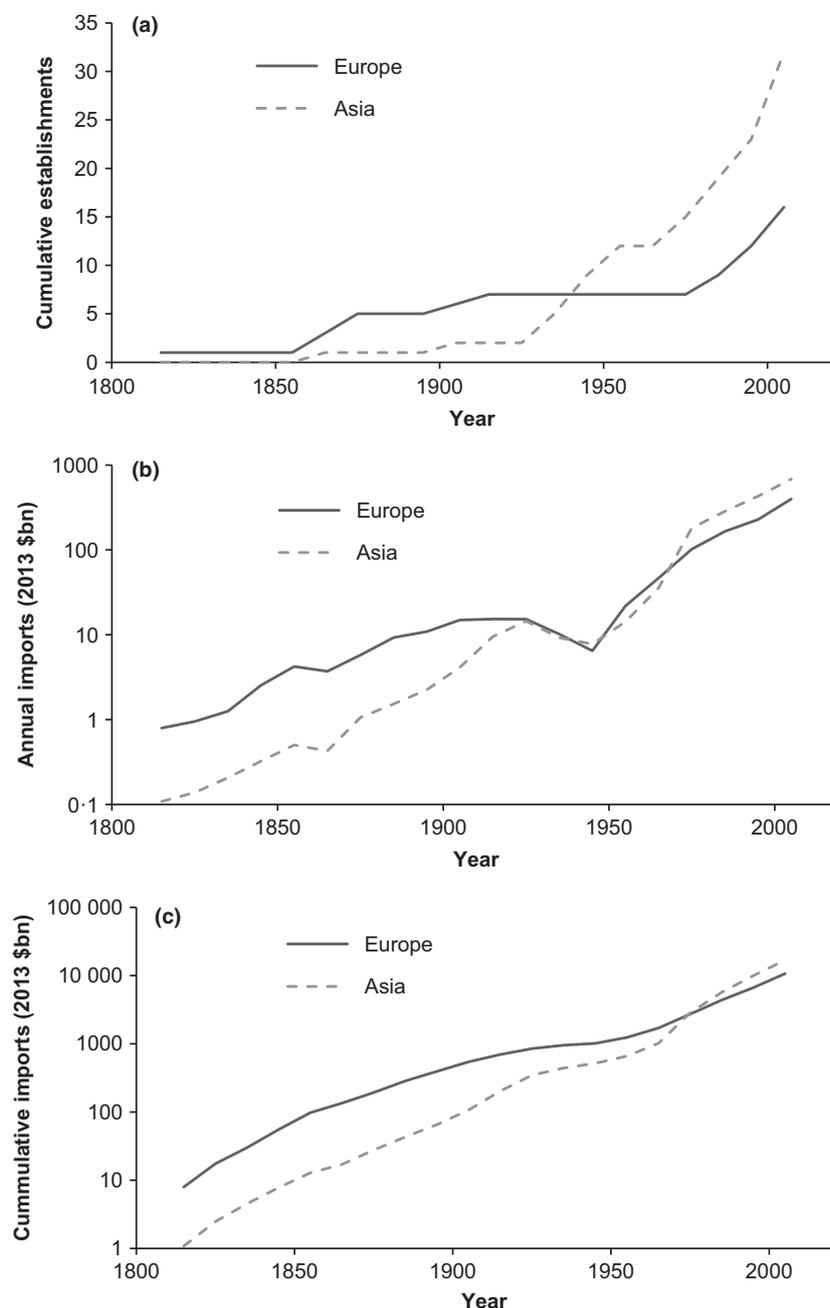
Fig. 2. Historical trends in species accumulation and pathway rates in North America. Decadal cumulative establishments of Scolytinae of species native to Europe and Asia (a). Decadal imports (all goods) from Europe and Asia to the USA expressed in 2013 USD (b). Cumulative decadal imports from Europe and Asia expressed in 2013 USD (c).

provided a significantly better fit to the data than the assumption of Poisson sampling (likelihood ratio test = 24·87, $P < 0.0001$). The maximum likelihood estimate (±SE) for σ was 2·92 ± 0·21 for negative binomial sampling and 3·67 ± 0·20 for Poisson sampling. These values of σ estimated from port interceptions of European species were less than those estimated by fitting the species pool model to historical establishments (Table 1). If a value of σ = 2·92 is assumed and the species pool model is refitted using maximum likelihood to estimate the parameter p, the model fit is significantly poorer with a higher AIC (Table 1). This model tended to underestimate the number of early establishments, but forecast greater numbers of establishments in future decades (see Fig. S1).

Discussion

Superficial comparison of numbers of invading species with total numbers of species in source regions suggests that the world's supply of invaders has not been substantially depleted. For example, of the ~90 000 insect species native to North America, only 55 have successfully invaded Japan (Yamanaka *et al.* 2015). Despite the seemingly endless supply of species in source regions, there is reason to believe that depletion of species pools has had at least some effect on rates of species establishment. Levine & D'Antonio (2003) plotted cumulative numbers of invading species as a function of cumulative imports and they showed that for insects, mollusks and plant

Table 1. Maximum likelihood parameter estimates (with standard errors shown in parentheses) for the species pool and Michaelis–Menten models. Also shown is the Akaike information criterion (AIC) showing the fit of each model (a smaller value indicates a better fit). Each model was fitted with separate parameters for European and Asian species, and with common parameters fitted for both groups of species

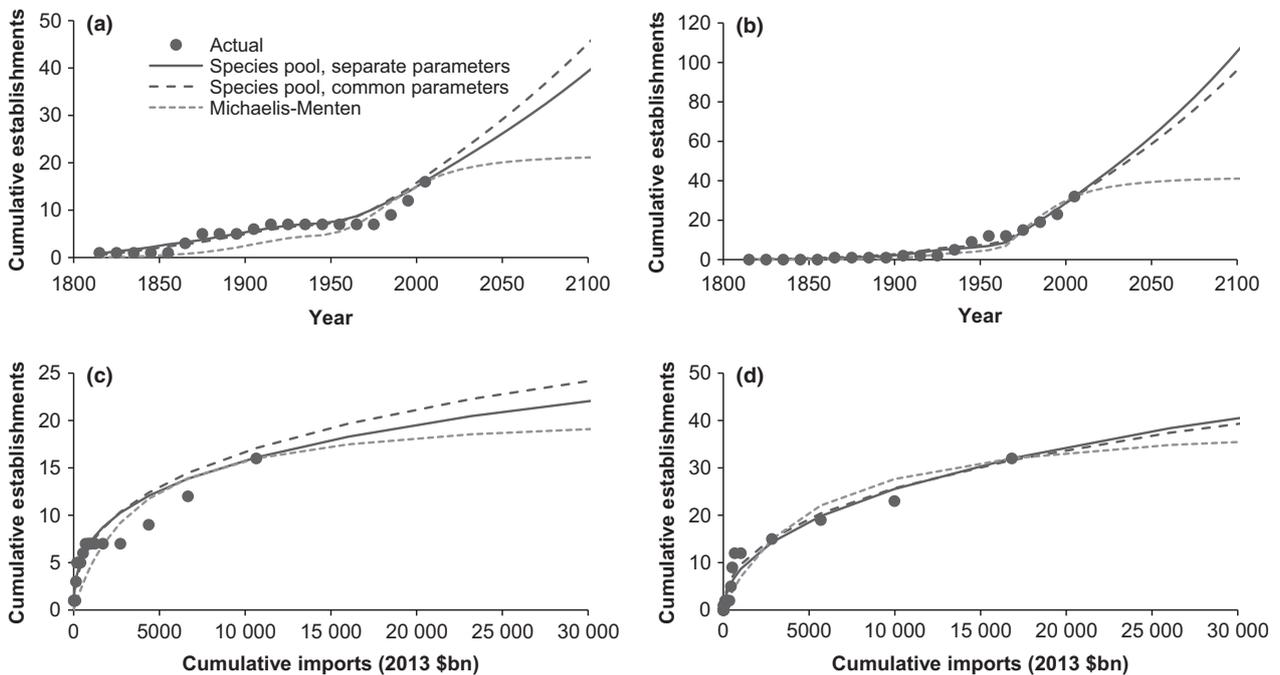| Model	Parameter	European species	Asian species	Combined European and Asian species
Species pool model, σ not fixed	σ	5·84 (0·54)	4·68 (0·26)	5·14 (0·24)
	P	0·112 (0·066)	0·0268 (0·0102)	0·0524 (0·0184)
	AIC		41·39	38·22
Species pool model, σ = 2·92	P	0·00238 (0·00095)	0·00194 (0·00051)	0·00206 (0·00045)
	AIC		48·08	46·27
Michaelis–Menten model	S_{max}	21·4 (5·4)	41·6 (7·3)	23·6 (5·9)
	B	361 (213)	503 (201)	422 (253)
	AIC		56·69	60·43

Fig. 3. Observed and predicted cumulative Scolytinae species establishments in the USA. Establishment of European species plotted against time (a). Establishment of Asian species plotted against time (b). Establishment of European species plotted against cumulative imports (c). Establishment of Asian species plotted against cumulative imports (d). Predictions are shown for the species pool model with separate and common parameters fitted for European and Asian species, and the Michaelis–Menten model fitted separately for Asian and European species. All model predictions beyond 2010 assume import volumes increase by 34% per decade (rate estimated from historical trends).

pathogens, the rate of establishment of species in these groups declines with increasing cumulative imports. This led them to conclude that the invasion process is analogous to the community ecology problem of estimating diversity through consecutive samples drawn from a finite species pool (Colwell & Coddington 1994; Magurran 2004). In such studies, the number of new species encountered with each additional sample declines over time. Consequently, cumulative species richness does not scale linearly with the number of samples taken but instead takes a curvilinear form approaching an asymptote of total species richness.

A few studies have applied rarefaction to species accumulation curves from port interception data to estimate 'true' numbers of species arriving in specific invasion pathways (Work *et al.* 2005; Miravete *et al.* 2014), but these studies did not attempt to use accumulation curves to predict future invasions. However, Levine & D'Antonio (2003) predicted future species accumulations based on fitting the Michaelis–Menten equation to cumulative species establishments as a function of cumulative trade volume and then used the model to forecast future establishments based upon predicted increases in imports. It can be seen, however, that the Michaelis–Menten

equation provides a relatively poor fit to the historical accumulation of Scolytinae species from Europe and Asia (Table 1) and predicts very few future species establishments (Fig. 3c,d), a prediction that appears unrealistic given that establishments of these species continue at an apparently continuous rate (Table S1).

While the forecast methodologies of Levine & D'Antonio (2003) account for potential depletion of source species pools by sequential invasions, this method is a purely statistical approach with no mechanistic basis. For our forecasting, we adopt a process-based approach that accounts for independent information on the underlying abundance distribution of species within a pathway, independent information about the total number of species within the source species pool and a model relating propagule pressure to establishment probability fit to historical data.

Though the existence of a finite species pool may produce rates of species accumulation that decrease over time, such a trend may not necessarily be observed directly in real species accumulation data. Probably, the most important reason why cumulative establishment curves may not exhibit attenuation is the counteracting trend of increasing pathway volume. Our analysis (Fig. 2) clearly shows that, while the depletion of finite species pools may drive invasion rates to decline under conditions of constant pathway volumes (import rates), species accumulation rates will remain constant or even increase under more realistic patterns of increasing rates of imports.

The other reason why finite source species pools may not produce declining rates of establishment is the tendency of the geographical source of imports to change over time. Data on historical imports (Fig. 2b) illustrate this; prior to 1920, most imports to the USA originated from Europe, but during the following period, imports from Asia increased markedly, ultimately exceeding those from Europe. The consequences of this shift are mirrored in patterns of Scolytinae species accumulation (Fig. 2a). Prior to 1925, the majority of Scolytinae invasions originated from Europe. But after about 1925, invasions from Asia increased markedly and by about 1950, Asia exceeded Europe in terms of cumulative invasions. Though some depletion of the European species pool may have occurred, this was more than offset by the shift of imports from a new region, Asia. In the future, increasing imports from other geographic regions (e.g. Africa and South America) can be expected to open up previously isolated species pools, contributing to increasing rates of establishment and countering trends of source species pool depletion.

Another key aspect of the invader depletion phenomenon captured in the species pool model is the skewed species abundance distribution. Conceptually, consecutive invasions should deplete source species pools, ultimately attenuating future rates of establishment (Levine & D'Antonio 2003). However, data on true source species pools (e.g. Table S2) indicate that historical establishments have had only a minor impact on the pool of remaining potential invaders, which is difficult to reconcile with reports of attenuation in establishment rates (Levine & D'Antonio 2003; Costello *et al.* 2007). The species pool model presented here provides a much more logical perspective on species pools; not all species in these pools are the same, because some are more abundant in invasion pathways than others and consequently much more likely to invade. As a pathway opens, it is the most abundant species that are likely to establish first because of the dominant role of propagule pressure on establishment (Lockwood, Cassey & Blackburn 2005; Simberloff 2009). The skewed nature of observed species distribution functions means that there are many relatively rare species that are less likely to become established. Thus, the observed attenuation of establishment rates relative to cumulative imports can be attributed to the depletion of the most abundant species, which represent only a small fraction of total species pools.

In our analysis of Scolytinae invasions, we used frequencies of species interceptions at ports as a proxy for their abundance in pathways, providing an independent estimate of the frequency distribution of species abundance in the invasion pathway. Depending upon the assumptions used in the analysis, the interception data yielded a log-normal distribution with $\sigma = 2{\cdot}92$ or $3{\cdot}67$. By fitting the species pool model to historical cumulative numbers of European and Asian species establishments over time, we estimated even higher values of $\sigma = 5{\cdot}84$ and $4{\cdot}68$, or a combined estimate of $5{\cdot}18$. This higher value of σ provided a better fit of the model to historical establishments (Table 1, Fig. S1). While the smaller values of σ would be more typical of a natural community, it is not unreasonable to believe that the larger value of σ may provide a more realistic distribution in invasion pathways where just a few species are particularly common and most species are very rare. Values of σ may be particularly high as a result of variation in traits that promote establishment. Certain species may be very abundant in pathways but they may possess traits that adversely affect their ability to establish (Goodwin, McAllister & Fahrig 1999; Karatayev *et al.* 2009). An example of this in the Scolytinae is provided by the European spruce bark beetle, *Ips typographus*. It is perhaps the most abundant scolytine in Europe and is frequently intercepted at North American ports (Table S4.1 in Appendix S1); however, it has never become established in North America. The failure of *I. typographus* to establish may be attributed to a strong Allee effect arising from the need for this species to aggregate on hosts in order to successfully colonize them (Kausrud *et al.* 2012). Thus, the fact that values of σ fit to historical establishments exceed those estimated from interception data does not indicate an inherent deficiency of interception data, but instead reflects the importance of trait variation among species, in addition to true variation in abundance in the pathway.

Values of σ estimated from historical establishments were similar for both European and Asian species, and the model using p and σ estimated from both species pools combined provided the best fit (Table 1). This similarity suggests a universality in the establishment process for species from these two world regions. It remains to be seen how applicable the new species pool model is in other biological systems and whether p and σ are similar in such other species pools. Assuming that this process is equivalent, key factors causing differences in species establishment rates among different groups of invading organisms would be total species pool sizes n and pathway volumes W_j. Quantification of invasion pathways may be more difficult in other groups of invading species. Even here for the Scolytinae, the value of imports may be a crude measure of pathway volume since the extent to which cargo is associated with these insects likely has varied over time and among different types of cargo.

One group of invading organisms for which species abundance distribution pathways have previously been quantified before are marine organisms. Studies indicate that species abundance distributions in ballast water vary among taxa and these distributions change during the course of transport (Briski *et al.* 2014; Chan *et al.* 2015). For many marine taxa, source species pools have been quantified and they may be substantially depleted (Samaha, Dohna & Bariche 2016), making these organisms good candidates for application of the species pool model presented here.

The species pool model predicts that future accumulation of European scolytine species (Fig. 3a) will occur at slightly slower rates than accumulation of Asian species (Fig. 3b). There are several reasons for this difference; one of them being higher predicted import rates from Asia. Another reason is the much greater pool of Asian Scolytinae species (655) compared to Europe (Table S2). The European species pool is more depleted (16 of 255 species established) compared to the Asian pool (32 of 655 established). It should be noted that none of these forecasts account for the effects of International Standards for Phytosanitary Measures no. 15 (ISPM 15), an international standard for treatment of wood packing material used in international trade, which was implemented nearly worldwide in the mid-2000s. Haack *et al.* (2014) found that ISPM15 implementation reduced insect propagule pressure in wood packing material by 30–50%. The species pool model could be used to account for ISPM 15 to make predictions about its impacts on future establishments (Brockerhoff *et al.* 2014). Such an analysis would need to incorporate the species model into cost–benefit models (Leung *et al.* 2014). In the scolytine and other invasion systems, there is also a possibility of using the model to explore the benefits of quarantines and phytosanitary treatments that modify species abundance distributions, in addition to affecting the total pathway rates.

As non-native species establish in new regions, this could be considered to cause increases in source species pools. However in our model, species pools represent only the static set of species native to a region; species may invade directly from the native range or indirectly via another region. It should be acknowledged, however, that in many cases, species may become very abundant in invaded regions and thereby elevate the chances that they may invade additional regions (Garnas *et al.* 2016). It should also be noted that true species pools may be larger than indicated in the literature since in some regions, there are likely to be numerous undescribed species. There are many historical examples of invasions by such previously unknown species. However, the European Scolytinae is well catalogued, and it is unlikely that there are many unknown species.

Authors' contributions

A.L. and E.B. conceived of the problem and assembled the data. M.K. led the development of the model. All authors contributed to the interpretation of model results. A.L. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

Data are available from Dryad Digital Repository https://doi.org/10.5061/dryad.v01m0 (Liebhold, Brockerhoff & Kimberley 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Table S1. Year of first detection of non-native Scolytinae in the United States.

Table S2. Species pool sizes.

Table S3. Macro-enabled Excel spreadsheet for running species pool model.

Appendix S1. Independent estimation of the species abundance distribution.

Fig. S1. Observed and predicted Scolytinae establishments using different values of σ.