

Predicting how altering propagule pressure changes establishment rates of biological invaders across species pools

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Abstract. Biological invasions resulting from international trade can cause major environmental and economic impacts. Propagule pressure is perhaps the most important factor influencing establishment, although actual arrival rates of species are rarely recorded. Furthermore, the pool of potential invaders includes many species that vary in their arrival rate and establishment potential. Therefore, we stress that it is essential to consider the size and composition of species pools arriving from source regions when estimating probabilities of establishment and effects of pathway infestation rates. To address this, we developed a novel framework and modeling approach to enable prediction of future establishments in relation to changes in arrival rate across entire species pools. We utilized 13 828 border interception records from the United States and New Zealand for 444 true bark beetle (Scolytinae) and longhorned beetle (Cerambycidae) species detected between 1949 and 2008 as proxies for arrival rates to model the relationship between arrival and establishment rates. Nonlinearity in this relationship implies that measures intended to reduce the unintended transport of potential invaders (such as phytosanitary treatments) must be highly effective in order to substantially reduce the rate of future invasions, particularly if trade volumes continue to increase.

Key words: arrival rate; biological invasions; Cerambycidae; forest insects; interception; modeling; prediction; Scolytinae; trade.

INTRODUCTION

Nonnative, invasive species represent a major threat to biodiversity, environmental stability, and sustainability (Mack et al. 2000). Such invaders can have enormous economic impacts on primary production through management and control actions, loss in amenity values, trade restrictions, and various other costs (Holmes et al. 2008). The consequences of biological invasions are especially grave because they are usually irrevocable. Forest trees have been particularly affected by invasive insects and pathogens, including tree-killing species such as emerald ash borer (*Agrilus planipennis*) and ramorum dieback (*Phytophthora ramorum*; Poland and McCullough 2006, Brasier 2008). Recent establishment records indicate that the unprecedented mixing of the world's biota is still continuing, largely as a result of international trade. In fact, rates of arrival and establishment of nonnative organisms may have even increased in the last few decades (e.g., Brockerhoff et al. 2006, Aukema et al.

2010, Kirkendall and Faccoli 2010), despite the implementation of measures to mitigate biological invasion pathways (e.g., Perrings et al. 2010). This probably results from the ever-expanding volume of international and intercontinental trade (Levine and D'Antonio 2003), which may overwhelm mitigation efforts. However, progress in preventing biological invasions is also hampered by insufficient understanding of key parameters. The relationship between arrival rate (i.e., propagule pressure) and establishment is appreciated (Kolar and Lodge 2001, Leung et al. 2004, Lockwood et al. 2005, Eschtruth and Battles 2011), but with few exceptions (e.g., Duncan 1997), little is known about the earliest stages of actual invasion events, when establishment occurs. Actual arrival rates of organisms are almost never measured, and most invasions go unnoticed until population growth and, potentially, damage have occurred. Moreover, we now know that most arrivals do not result in successful establishments, because some occur in unfavorable habitats, are affected by adverse effects of stochastic dynamics, or experience Allee effects, which can drive very small populations to extinction (Taylor and Hastings 2005, Liebhold and Tobin 2008).

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An advance in our understanding of the role of propagule pressure in invasions was the work by Leung et al. (2004), who used survival analysis and maximum likelihood techniques to model the relationship between propagule pressure and the probability of establishment of populations of individual species. They were able to predict invasions of zebra mussels (*Dreissena polymorpha*) in lakes by using boater traffic as a proxy for arrival rate. Bartell and Nair (2003) provided another model relating probability of establishment of a single species, *Anoplophora glabripennis*, to propagule pressure (although they did not consider Allee effects). These authors illustrated the potential use of such models as a risk reduction framework by estimating the effect of reducing arrival rates on establishment probability. However, a major limitation of such models that focus on individual species is that for virtually every invasion pathway, there is a large pool of potential invader species, of varying arrival rates and establishment potentials, which is not being addressed. Furthermore, the identity of the next invader species to be recruited from that pool is unknown. Therefore, when estimating probabilities of establishment and the effects of pathway volume and mitigation measures, we stress that it is essential not to focus on individual species, but to consider the size and composition of species pools that are moved along those pathways. The importance of considering species pools has been noted in community ecology (de Bello et al. 2012) and in the context of biological invasions (Cassey et al. 2004), but the size of source pools and the relative abundances of species within pools have not been systematically addressed in establishment models.

The objective of the present study was to develop a novel framework and modeling approach to determine the relationship between the probability of species establishment in a new region and each species' arrival rate in that region, across an entire pool of potential invading species. Specifically, we utilized longhorned beetles (order Coleoptera, family Cerambycidae) and true bark beetles (order Coleoptera, family Curculionidae, subfamily Scolytinae, hereafter referred to as bark beetles) as model systems because these groups include many damaging forest insects with well documented, successful establishments (Brockerhoff et al. 2006, Haack 2006, Aukema et al. 2010, Haack et al. 2010, Kirkendall and Faccoli 2010). We used extensive records of entry across borders based on interception records by customs officers in several countries (e.g., Brockerhoff et al. 2006, Haack 2006). It has been shown that, for individual species, border interception rate is a useful proxy for arrival rate, and that this is correlated with establishment probability (Brockerhoff et al. 2006). Our approach of modeling the relationship between probability of establishment and arrival rate, as it applies to entire species pools of potential invaders, allows the prediction of future rates of establishment in response to changes (increases or decreases) in arrival rate due to

increases in global trade or the effects of quarantine treatments and phytosanitary regulations (IPPC 2011). The model developed here can easily be adapted to predict invasion rates of other invader taxa. Such models capture the inherent nonlinearity of the arrival–establishment relationship, and are thus critical for predicting the consequences of changes in propagule pressure on the rate of future species establishment.

METHODS

Interception and establishment data.—To determine the relationship between the probability of a species becoming established in a new location and arrival rate, a model was derived for predicting the probability of a species having become established within the last 100 yr (i.e., from ca. 1909 to 2008), based on its border interception frequency, as a proxy for arrival rate. We used data in which each distinct interception of a single bark beetle or longhorned beetle species was considered a single observation. All species in this data set had either been intercepted at United States border entry points (e.g., seaports, airports) during routine cargo inspections, or recorded as being established in the United States, or both. In order to examine a larger data set, we also modeled the relationship between interceptions in either the United States or New Zealand (which collectively provided a better global overview of beetles arriving from all countries) and establishments in any country worldwide. Species native to the United States were excluded from the analysis when we examined relationships between establishment in the United States and arrival rate. For our analysis of establishments in the United States, we defined the United States as the continental states (including Alaska), but excluding Hawaii. United States interception records from 1949 to 2008 were collected by the United States Department of Agriculture. Interceptions recorded in New Zealand were obtained from Scion (New Zealand Forest Research Institute). Details on the source of interception records are provided in Appendix A. Interception data are summarized in Appendix B: Table B1. Data on establishment of bark beetles and longhorned beetles outside their native ranges were assembled based on published records (see Appendix B: Table B1).

Establishment model.—The statistical approach to modeling the relationship between probability of establishment and arrival rate was similar to that used by Leung et al. (2004), and utilized the Weibull function. The basic form of this model is as follows:

$$P_i = 1 - q^{N_i^c} \quad (1)$$

where P_i , the probability of establishment within a given year of the i th species, is a function of N_i , the annual frequency of entry (i.e., arrival rate) of that species. The model has two parameters, a calibration parameter q , and a shape parameter c . 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 . When $c < 1$, the probability of establishment increases with N_i , but at a decreasing rate.

Assuming the probability of establishment in each year is independent, P_{Yi} , the probability of establishment of the i th species over a period of Y years is

$$P_{Yi} = 1 - (q^{N_i})^Y = 1 - q^{YN_i}. \quad (2)$$

In practice, annual frequency of entry of each species is unknown. However, in order to test the model in Eq. 1 across a group of species, it is only necessary that the relative entry frequencies among the species are known. For example, if a proxy n_i proportional to N_i is known (i.e., $N_i = k \times n_i$ where k is some unknown constant), the following relationship must hold:

$$P_{Yi} = 1 - q^{Ykn_i} = 1 - r^{n_i}. \quad (3)$$

This model is the same form as that in Eq. 1, with the parameter r replacing q to account for the differences in the dependent and independent variables.

In this study, we used border interception records as a proxy for entry frequency, based on the assumption that interceptions are approximately proportional to entry frequency. Specifically, we used a combined United States and New Zealand interception frequency for each species. The log of the expected interception frequency of the i th species in the j th country, I_{ij} , (United States value $j=1$; New Zealand value $j=2$) was fit to a Poisson regression model (or log-linear model) using the SAS GENMOD procedure

$$\log(E(I_{ij})) = s_i + c_j \quad (4)$$

where $E()$ is the expectation operator, s_i represents the effect of the i th species, and c_j is a country effect (in practice, GENMOD sets c_2 to zero so that c_1 is the effect of United States relative to New Zealand). As is standard in Poisson regression, it was assumed that the variance of I_{ij} equaled $\phi E(I_{ij})$, where ϕ is a scaling coefficient estimated from the data.

The next step was to fit the Weibull model using $n_i = \exp(s_i)$, estimated from the Poisson regression model, as the independent variable. The dependent variable was E_i , coded one if the i th species established within any new location worldwide during the previous 100 yr (from ca. 1909 to 2008), and coded zero otherwise. This model was fitted using the SAS NLMIXED procedure (SAS Institute 2004), with the residual errors e_i assumed to follow a binary error function

$$E_i = 1 - r^{n_i} + e_i. \quad (5)$$

This model was fit for worldwide establishments and interceptions (i.e., United States and/or New Zealand), and also for United States establishments using United States interceptions. The model was fit separately for the two beetle groups, and also fit for the combined bark

beetle and longhorned beetle data using a common c parameter, but different r parameters for each group.

It is important to point out that n_i , the interception estimate for the i th species derived from the United States and New Zealand interception series, represents only a fraction of the actual, but unknown, entry frequencies, as inspectors are only able to inspect a small proportion of commodities at ports (Haack 2006, McCullough et al. 2006). Because we do not know the true value of entry frequencies, the independent variable of the regression procedure suffers from measurement error, which can affect analyses. Measurement error in an independent variable can cause bias in the parameter estimates, and loss of power (Carroll et al. 2006), making detection of relationships between variables more difficult. Specifically, in this case, measurement error would be expected to introduce a negative bias in the Weibull c parameter estimate. We refer to this biased estimate as the naïve estimate. The SIMEX method (Carroll et al. 2006) was used to model the unbiased establishment probability accounting for measurement error in arrival rate (Appendix C).

For worldwide establishments, we not only knew whether a species had established at a new location, but also whether it had established independently at more than one location. We attempted to model this information using a multinomial Weibull model. For this purpose, the world was divided into the following geographically discrete regions: United States, Canada, Central America, western South America, eastern South America, Europe, East Asia, Middle East, Indian Ocean islands, New Zealand, Australia, Hawaii, and Africa. The dependent variable, E_{ij} , was coded one if the i th species established in the j th location, and zero otherwise. The following multinomial model was then fitted using the NLMIXED procedure

$$E_{ij} = 1 - r^{n_i} + e_{ij}. \quad (6)$$

Jackknife estimates of the standard error of the parameter c were obtained for this model using the SAS %JACK macro (SAS Institute 2004). The SIMEX procedure was also applied to this model.

The above model-fitting was performed using species intercepted on at least one occasion in either the United States or New Zealand. There will, however, be many species that are never intercepted because they arrive in small numbers, but some may nevertheless establish. Although the number of these establishments is known, the total number of non-intercepted species that did not establish is unknown. To explore the potential effect of non-intercepted species on the model, varying numbers of non-intercepted species were added to the data set, along with their recorded number of establishments, and SIMEX estimates of c obtained in each case. A value for n_i equal to half the minimum obtained for intercepted species was assumed for all non-intercepted species.

Having obtained estimates of the Weibull c parameter, it was possible to use this information to calculate

the effect of reducing or increasing the frequency of entry on the likely number of establishments over a defined period of time within the United States. First, the number of species recorded as having established over the previous 100 yr in the United States was used to calibrate the model to the United States by estimating the r parameter. This was found by iteratively solving for r such that the following relationship was satisfied:

$$E = S - \sum_{i=1}^S r^{100n_i^c} \quad (7)$$

where E is the number of establishments in the United States over the previous 100 yr, S is the total number of species, and n_i is a proxy assumed to be proportional to the number of entries of the i th species as described above. A 95% jackknife confidence interval (CI) for r was obtained using the SAS %JACK macro. The number of establishments (E_{YK}) expected to occur over a period of Y years when entry frequencies have increased or decreased by the factor K can then be calculated

$$E_{YK} = S - \sum_{i=1}^S r^{Y(Kn_i)^c}. \quad (8)$$

RESULTS

We used interception and establishment data for 138 species of true bark beetles and 306 species of longhorned beetles to compare the frequency of interception in the United States and New Zealand (as described by n_i estimated from the Poisson regression model) with the number of establishments (Appendix D: Table D1). The two beetle groups have similar numbers of frequently intercepted species (48 bark beetle and 51 longhorned beetle species have $n_i > 5$), but there are far more rare longhorned beetle species than bark beetle species (152 longhorned beetle species compared with 33 bark beetle species where $n_i < 1$). There is a significant trend of decreasing probability of establishment with declining interception frequency for both beetle groups, with establishment percentages among bark beetles and longhorned beetles, respectively, of 9% and 5% for $n_i < 1$, compared with 78% and 75% for $n_i > 100$. Note that $n_i < 1$ resulted if there was only one interception in either the United States or New Zealand. A few species (six bark beetle and 18 longhorned beetle species), that were never reported as being intercepted, nevertheless were recorded as having established. Because the total number of non-intercepted species is unknown, it is not possible to estimate their establishment percentage. In the following analysis we therefore used only species intercepted at least once in either the United States or New Zealand. We also examined the question of rare species.

Naïve estimates of the Weibull c parameter, obtained by fitting the Weibull function using n_i as the

independent variable, were all very close to 0.50 (Appendix C: Table C1). For both bark beetles and longhorned beetles, naïve estimates of c were significantly greater than zero for both worldwide and United States establishments in all cases, indicating that the probability of establishment increases significantly with interception frequency (noting that a value of c greater than zero implies this result). Also, naïve estimates of c did not differ significantly between the two beetle groups.

When estimation bias is removed using SIMEX, estimates of c are much larger than the naïve estimates, and are generally close to 1.0 (Appendix C: Table C1, Fig. C1). There was no significant difference in c between bark beetles and longhorned beetles. The multinomial model did not improve precision in the estimate of c for the naïve model, and gave poorer estimates when the SIMEX procedure was applied. Therefore, we adopted the estimate of c provided by the combined binary model, 0.96 with 95% CI 0.74–1.18, suggesting that the true value is between 0.74 and 1.18. We assumed that these SIMEX estimates of c apply also to the relationship for the United States analysis.

If the relationship between probability of establishment and interception that was derived using only intercepted species also holds for rare species, there must be a significant number of species which occasionally entered a country, but were never intercepted. In fact, it can be inferred from Appendix D: Table D1 that there are likely large numbers of non-intercepted species, especially among longhorned beetles, where more than half the intercepted species had $n_i < 1$.

To examine whether rare species could significantly affect the models described above, we obtained SIMEX estimates of c , using the data sets to which we added varying numbers of non-intercepted species and establishment percentages (Appendix C). The effects of assuming varying establishment percentages among non-intercepted species on the SIMEX estimates of the Weibull c parameter gave similar results for both beetle groups (Appendix C: Fig. C2). The estimate of c did not differ from results obtained using only intercepted species for a non-intercepted species establishment rate of about 1%. If a 5% establishment rate is assumed for non-intercepted species, this implies a value for c of 0.75 (Appendix C: Fig. C2), which is thus the minimum plausible value. However, the establishment rate of non-intercepted species is more likely well below 5%, given the trend of a decreasing percentage of established species visible in Appendix D: Table D1. Assuming the rate is about 1%, there must be ~600 non-intercepted true bark beetle and 1800 non-intercepted longhorned beetle species (see Appendix C for the total number of species in these taxa).

We now consider implications of the model for the United States data. The Weibull q parameter was solved using Eq. 5 and the actual recorded establishments in the United States over the previous 100 yr for a range of c

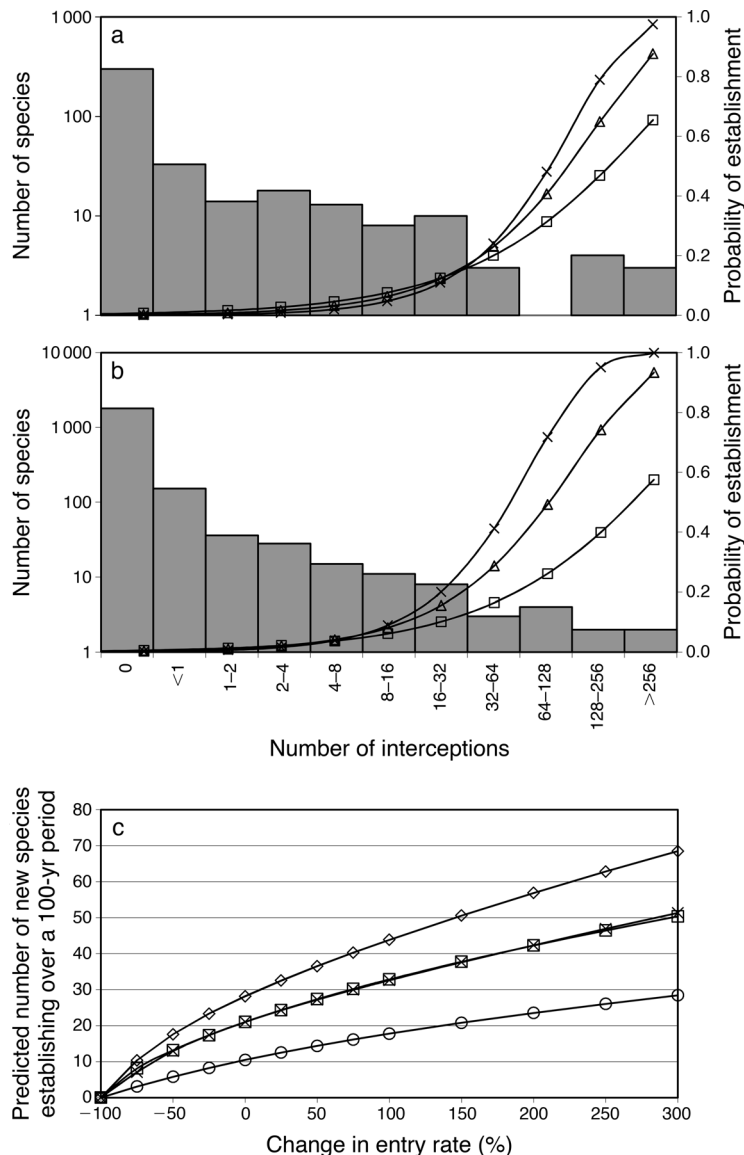


FIG. 1. The distributions of numbers of (a) true bark beetle and (b) longhorned beetle species by frequency of interception (n_i). The distributions include an assumed 300 non-intercepted bark beetle species and 1800 non-intercepted longhorned beetles, and exclude species native to the United States and species established in the United States prior to 1909. Superimposed on the distributions is the probability of establishment in the United States over a 100-yr period for any species in the corresponding interception class, predicted using a Weibull establishment probability model with shape parameter $c = 0.75$ (squares), $c = 1$ (triangles), and $c = 1.25$ (crosses). (c) The resulting predicted number of true bark beetle and longhorned beetle species establishing in the United States over a 100-yr period for varying changes in arrival rate. Predictions were made using Eq. 8 for: $c = 0.75$ and calibration parameter $q = 0.9937$ (squares); $c = 1.25$ and $q = 0.9937$ (crosses); $c = 1$ and $q = 0.9902$ (diamonds); and $c = 1$ and $q = 0.9975$ (circles).

values. The Weibull probability functions of establishment in the United States over the next 100 yr relative to interception frequency (n_i) for the c parameter, varying over its most likely range as discussed (i.e., for c equal to 0.75, 1, and 1.25), are shown along with frequency distributions of interceptions for species nonnative to the United States in Fig. 1a and b. The q parameter estimate for United States establishments varied only slightly between bark beetles and longhorned beetles,

and in the remainder of the analyses we used common parameter values for both groups. Assuming $c = 1$, the estimated value of q combined across both beetle groups was 0.9937, with 95% CI 0.9902–0.9975. The effects of varying the arrival rate on predicted establishments over the next 100 yr calculated using Eq. 8 for various values of c and q are shown in Fig. 1c and Appendix E: Table E1. This showed that uncertainty in the value of c has only a minor effect on predicted establishments, but

uncertainty in the value of q has a considerable impact. Because establishment of a new species is a comparatively rare event, even with records covering 100 yr, it is not possible to estimate q with a high level of precision. Note that with unchanged arrival rates, the observed total of 21 establishments over the previous 100 yr implies that establishments over any other 100-yr period could vary between 10 and 28 species (95% CI; Fig. 1c). A 50% reduction in arrivals is expected to reduce the number of establishments to between six and 18 species per 100 yr. Even with a 75% reduction in arrivals, between three and 10 species of bark and longhorned beetles are expected to become established.

DISCUSSION

Propagule pressure is perhaps the single most fundamental process driving biological invasions (Lockwood et al. 2005, Simberloff 2009). Most species arriving in an exotic habitat fail to establish, but when such events are sufficiently repeated, they may eventually succeed. Furthermore, low-density populations of most species are prone to extinction, because of stochasticity and Allee effects. Consequently, arrival of a large founding population is more likely to lead to establishment than arrival of small founding populations (Taylor and Hastings 2005, Drake and Lodge 2006). Our analysis provides further support for the relationship between propagule pressure and establishment, as we found a positive association between interception frequency and probability of establishment for both bark beetles and longhorned beetles in the United States and worldwide. These results generally agree with previous studies that have empirically linked propagule pressure with establishment of a single species across space (e.g., Leung et al. 2004), as well as studies that linked variation in propagule pressure among species to establishment (e.g., Duncan 1997). In this study, we used border interception frequency as a proxy for true arrival rate. In most systems, actual arrival rates are difficult to measure directly, but proxies for arrival rate may be sufficiently informative. For example, numbers of boaters proved useful as a measure of zebra mussel propagule pressure, as pleasure boats are known zebra mussel vectors (Leung et al. 2004). Our study is unique and novel in that it considers the propagule pressure–establishment relationship not for a single species, but for an entire pool of species (in fact, thousands of related species). This is critical because it is not possible to predict the precise identity of future invaders among a pool of many potential invading species. The proxy for propagule pressure that we used has some limitations, as indicated. But several mitigating circumstances contribute to the validity of this data set, which is one of the most comprehensive compilations of invertebrate arrival data. For example, our use of data collected over a long period (58 yr) helped overcome interannual variation in sampling intensities.

The relationship between propagule pressure and probability of establishment that we modeled here is likely to vary among different groups of organisms, and parameter values fit to our models cannot necessarily be applied to other taxa. Nevertheless, interception data or other proxies are available for other groups, and a model similar to the one described here could be fit to determine propagule pressure–establishment relationships, and to predict the outcome of changes to propagule pressure. These relationships can be expected to vary among taxa, as life history traits can affect both the probability of international transport and the probability that an arriving population of a given size will establish. For example, some bark beetles, such as *Dendroctonus ponderosae*, must colonize host trees in large numbers in order to overcome tree defenses and reproduce; such behavior can be expected to cause an Allee effect that would reduce the probability of establishment (Liebhold and Tobin 2008).

The ultimate objective of this study was to evaluate and predict the consequences of changing propagule pressure on the rate of future establishments. Increasing propagule pressure may result from ever-increasing global trade (Levine and D'Antonio 2003). Conversely, the worldwide adoption of various phytosanitary treatments through international agreements may reduce propagule pressure. For example, the International Standards for Phytosanitary Measures (ISPM) No. 15 prescribes heat treatment and fumigation of wood packaging material (e.g., pallets and crating) used for export (IPPC 2011). Wood packaging has been identified as an important pathway for the introduction of insects and pathogens associated with wood such as bark beetles and longhorned beetles (Brocknerhoff et al. 2006, Haack 2006). Our analysis can be used to assess the likely effects of ISPM No. 15 and other measures on future establishment rates of new species.

One important aspect of our model is that changes in propagule pressure may affect the probability of establishment of different species in very different ways. For the species that exhibit the highest propagule pressure, a fractional change in total propagule pressure (e.g., a 50% increase or decrease) will result in little change in establishment rates. Conversely, the species that arrive least frequently can be expected to exhibit changes in establishment probabilities in response to changes in arrival rate resulting from phytosanitary regulations or changes in trade. Thus, when rates of establishment are considered across an entire species pool, even moderate reductions in arrival rate are expected to lead to reduced establishment rates (primarily for those species that arrive least frequently), whereas more substantial reductions in arrival are needed to achieve effective reductions in establishment for those species with more frequent arrival. Consequently, unless measures intended to reduce arrivals (such as ISPM No. 15) are highly effective, future invasions related to trade will not be prevented entirely,

particularly if trade volumes continue to increase, which could counteract the benefit of such measures.

Predictions about numbers of future invasions that we make here are predicated on the assumption of an unlimited species pool. As the number of species that are transported along invasion pathways are not infinite, and as species vary in their degree of invasiveness, we can expect that the rate of invasions may gradually decline, and that the most successful invaders are likely to establish before other species. However, so far, there is no indication that rates of invasion (i.e., establishments per year) by wood borers and bark beetles are declining (e.g., Aukema et al. 2010). Although trade with Europe has occurred for centuries, many borers that have successfully invaded other countries have not yet become established in the United States (Brockerhoff et al. 2006, Kirkendall and Faccoli 2010). Furthermore, given that trade with Asia, especially China, has greatly expanded, depletion of this and other species pools is not likely to occur in the near future. Nevertheless, this is an important question that requires more attention in order to enable improved prediction of biological invasions and pathway risks.

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SUPPLEMENTAL MATERIAL

Appendix A

Detailed description of inspection methods, recording of interceptions, and sources of information on interceptions (*Ecological Archives* E095-052-A1).

Appendix B

Interception frequency and establishments of longhorned beetles and true bark beetles (*Ecological Archives* E095-052-A2).

Appendix C

Detailed description of the SIMEX method used to improve estimation of the Weibull c parameter, and estimation of effects of rare species (*Ecological Archives* E095-052-A3).

Appendix D

Summary table of the number and percentage of established beetle species by interception frequency (*Ecological Archives* E095-052-A4).

Appendix E

Effects of changes in arrival rate on predicted establishments (*Ecological Archives* E095-052-A5).