vol. 170, no. 1 the american naturalist july 2007 Ⓔ

Waiting for Invasions: A Framework for the Arrival of Nonindigenous Species

Christopher L. Jerde[1,*] **and Mark A. Lewis**[1,2,†]

1. Centre for Mathematical Biology, Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada;
2. Department of Mathematical and Statistical Sciences, University of Alberta, Edmonton, Alberta T6G 2G1, Canada

Submitted March 14, 2006; Accepted February 5, 2007; Electronically published April 30, 2007

Online enhancements: appendix, tables.

abstract: The process of nonindigenous species (NIS) arrival has received limited theoretical consideration despite importance in predicting and preventing the establishment of NIS. We formulate a mechanistically based hierarchical model of NIS arrival and demonstrate simplifications leading to a marginal distribution of the number of surviving introduced individuals from parameters of survival probability and propagule pressure. The marginal distribution is extended as a stochastic process from which establishment emerges with a waiting time distribution. This provides a probability of NIS establishment within a specified period and may be useful for identifying patterns of successful invaders. However, estimates of both the propagule pressure and the individual survival probability are rarely available for NIS, making estimates of the probability of establishment difficult. Alternatively, researchers are able to measure proportional estimates of propagule pressure through models of NIS transport, such as gravity models, or of survival probability through habitat-matching indexes measuring the similarity between potentially occupied and native NIS ranges. Therefore, we formulate the relative waiting time between two locations and the probability of one location being invaded before the other.

Keywords: nonindigenous species, hierarchical modeling, waiting time, establishment, stochasticity, propagule pressure.

The invasion of nonindigenous species (NIS) into new locations can be divided into three stages: arrival, establishment, and spread (Vermeij 1996; Sakai et al. 2001). The establishment and spread stages garner considerable theoretical attention, but the arrival stage receives proportionally little consideration (Puth and Post 2005), even though it represents a critical phase for preventing the establishment and potential impacts of new invaders (Parker et al. 1999). Arrival is the process by which individuals are transported from a source, through a dispersal pathway, to a destination where the NIS are introduced and attempt to establish (Carlton 1996).

Many studies have attempted to identify the characteristics of successful invaders to predict future invaders (Richardson and Rejmanek 2004), while other studies suggest that propagule pressure is the primary predictor of invasion success (Lockwood et al. 2005), but these studies are often limited to case-by-case assessments of invasion risk (Gilpin 1990; Williamson 1996). Such assessments are effectively tactical approaches for a particular system or a specific species (Godfray and Rees 2002). By way of contrast, strategic models can provide a more general approach indicative of the invasion process rather than a specific case. The absence of a general framework for NIS arrival limits one to a tactical approach to predicting invasion that is potentially insufficient for developing a general foundation for predicting invasions. It has been suggested that by following a tactical approach to NIS arrival, “we are never going to have a scheme to predict the success of invading species” (Gilpin 1990, p. 89), and this is likely one reason why an arrival framework for predicting invasions remains elusive (Carlton 1996). However, Gilpin (1990) advocates a strategic approach to develop a framework that includes stochastic elements for predicting the arrival of NIS. This is the approach we adopt in this article.

Throughout the arrival process, stochasticity influences the eventual establishment success or failure of the NIS. Stochastic events include abiotic changes in the source region, modifying the number of individuals available for transport, establishment of new dispersal pathways, and variable environmental conditions of the destination influencing survival (Carlton 1996). Also, some biological invasions occur with only a few introduced individuals.

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[*] Corresponding author; e-mail: cjerde@ualberta.ca.

[†] E-mail: mlewis@math.ualberta.ca.

Am. Nat. 2007. Vol. 170, pp. 1–9.

Therefore, demographic stochasticity, including Allee effects, is likely a contributor to the establishment or failure of new NIS populations (Shaffer 1981; Lande 1993; Leung et al. 2004). Taken in total, stochasticity leads to uncertainty in our spatial and temporal predictions of invasion (Kolar and Lodge 2001; Drake and Bossenbroek 2004) and is likely one reason why tactical approaches have been emphasized previously (Gilpin 1990; Carlton 1996).

Here we develop a strategic, probabilistic framework for the arrival process of NIS from source to destination. Being a contingent process (Puth and Post 2005), arrival emerges with a hierarchical model. We show that the model can be simplified to a marginal distribution, describing the number of surviving individuals introduced into the destination as a function of the propagule pressure and the individual probability of survival.

The hierarchical structure is suitable to estimate the probability of establishment for one time step. The time step formulation is flexible and may consider seasonal or yearly patterns of arrival. The increasing number of established invaders is likely linked to repeated introductions (Cohen and Carlton 1998), so we examine the marginal distribution of establishment as a stochastic process (time-to-event model) and produce invasion waiting time distributions. The results of the hierarchical modeling and the time-to-event modeling produce the probability of establishment at the next time step and the probability of establishment within a defined period of time, respectively. While providing a theoretical framework from which to study the arrival process, the framework is also directly related to ecological risk assessment for NIS (Suter 1993). We demonstrate how to estimate the waiting time risk (probability) and relative risk (odds) of two locations being invaded.

The Arrival Process

Conceptualizations of the arrival stage of the invasion process take many forms (Wonham et al. 2000; Sakai et al. 2001; Lockwood et al. 2005). Here we adopt Carlton's (1996) description of source, dispersal, and destination pools (fig. 1). All parameters and variables are defined in table 1. Throughout, we refer to individuals, populations, and pools for a single species unless otherwise noted. First, individuals at the source site are subject to environmental conditions such that the source population, N_s, is a random variable. The individuals are then transported from the source, N_s, to the dispersal pool, N_{dp}. Transported NIS constitute a dispersal pool of individuals. From the dispersal pool, individuals are then introduced into the destination. The process from source to destination represents one unique pathway of introduction. However, as the box in figure 1 demonstrates, there are likely many pathways, such as multiple ships (Drake and Lodge 2004). The input of individuals to a destination from all pathways is the propagule pressure (ΣN_d) of a species to a destination (Lockwood et al. 2005). Last, we consider survival of the introduced individuals (p_s). This does not capture the growth and spread but simply the physiological tolerance of the organism to the new environment (Spidle et al. 1995), also called inoculant survival (Smith et al. 1999). Additionally, p_s includes properties of habitat invasibility. Biotic and abiotic interactions at any new location have the potential to increase or decrease the probability of surviving and establishing (Jules et al. 2002; Von Holle 2005).

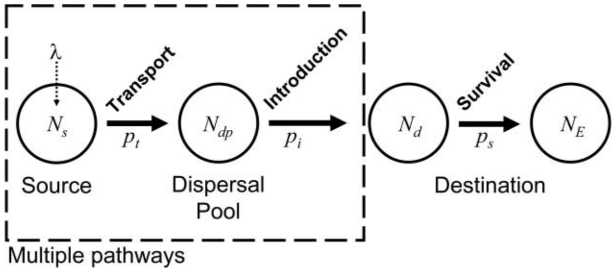

Figure 1: Flow diagram of the arrival process from source to destination. Variables and parameters are defined in table 1.

The entire arrival process, from all pathways, occurs over time. For example, the arrival of aquatic NIS may be the number of introductions occurring over 1 year or the arrival of seeds into a location during a particular season. Generally, we refer to the period of time considered in the arrival model as a time step. Hereafter, "establishment" refers to the event of an organism surviving in the new system beyond the arrival time step. More complexity, such as source population dynamics, population dynamics during transport, or different types of release mechanisms, may be significant for a given species or pathway, but our simplified process is a reasonable, strategic skeleton of arrival.

A Hierarchical Model of NIS Arrival

The usefulness of hierarchical modeling comes by reducing the larger process to a collection of simple processes. In its simplest form, a hierarchical model is a random variable with a distribution that is conditional on a random variable (Casella and Berger 2002; Clark 2003). We assume that individuals act independently from each other, and by following individuals, the model captures demographic stochasticity (Shaffer 1981; Lande 1993). In a probabilistic framework, an individual has a Bernoulli trial of being transported from one pool to another (such as being trans-

Table 1: Definitions for the hierarchical model and arrival waiting time

Parameter or variable	Description
N_E	Number of established nonindigenous species (NIS)
ΣN_d	Propagule pressure into a destination
N_d	Number of introduced NIS into the destination from a single pathway
N_{dp}	Number of NIS in the dispersal pool
N_s	Number of NIS in the source population
λ	Central tendency of the source population
k	Index of introduction pathways
n	Number of introduction pathways
p_s	Probability an individual survives introduction into a destination
p_i	Probability an individual is introduced from the dispersal pool
p_t	Probability an individual is transported
ϕ	Expectation of propagule pressure from k pathways
γ	Probability at least one individual establishes
α	Shape parameter for considering Allee effects
T	Waiting time random variable
$\overline{N}_E$	Expected surviving propagule pressure
c	Constant of proportionality
R	Ratio of expected waiting times for two locations

ported from the source to the dispersal pool). Independent, identically distributed (i.i.d.) Bernoulli trials for a group of individuals yield a binomial or Poisson distribution for the transition (Casella and Berger 2002). Linking the transitions between source and destination with the use of the binomial and Poisson distributions leads to a hierarchical model of the contingent arrival process:

$$N_E \mid N_d \sim \text{binomial}(N_d, p_s), \quad (1)$$

$$N_d \mid N_{dp} \sim \text{binomial}(N_{dp}, p_i), \quad (2)$$

$$N_{dp} \mid N_s \sim \text{binomial}(N_s, p_t), \quad (3)$$

$$N_s \sim \text{Poisson}(\lambda). \quad (4)$$

The Poisson distribution describes the number of individuals entering the arrival pathway, while the binomial distributions are used as transition processes. Future investigations may consider alternative distributions both for the number of individuals entering the system and for the transition processes. The binomial and Poisson distributions follow the probability mass functions found in most statistical texts (e.g., Casella and Berger 2002) and are also found in "Simplifications of the Hierarchial Model" in the appendix in the online edition of the *American Naturalist.*

From the arrival process, we can write a random variable for the population size at the source location (N_s) with a parameter, λ, describing the central tendency (eq. [4]). We use a constant-only model (λ) of the source population dynamics for simplicity, but future considerations may investigate the influence of alternative source population dynamic models such as autoregressive processes. A hierarchy emerges when the random variable for the number of individuals entering the dispersal pool (N_{dp}; eq. [3]) is formulated as a binomial distribution with the parameter p_t, capturing the probability of an individual being transported, and is conditional on the random variable N_s. Similarly, the random variable for the number of individuals being introduced into the destination (N_d; eq. [2]) can be written as a binomial process, with the probability of being introduced (p_i) to a particular source and conditional on the contribution of individuals from the dispersal pool (eq. [2]). Last, the probability of survival (p_s) parameterizes the distribution of the number of individuals introduced into the destination that survive to establish. Again, we model this as a random variable, N_E, conditional on the number of individuals released into the destination (eq. [1]).

Equations (1)–(4) are a hierarchical system describing the transfer of individuals from a single source to a single destination, but for purposes of inference, we are interested in the marginal (unconditional) distribution of N_E and not the mixture distribution of $N_E \mid N_d$ (Casella and Berger 2002). In order to find the marginal distribution of N_E, it is necessary to simplify the process.

Hierarchal processes can sometimes be simplified using conditional probability,

$$\Pr(X = x) = \sum_y \Pr(X = x \mid Y = y) \Pr(Y = y). \quad (5)$$

From our formulation, a hierarchy is the number of transported individuals (eq. [3]) defined by the probability of being transported, p_t, and the number of individuals in the source population, where N_s is a random variable from a Poisson distribution. Using conditional probability, the hierarchical statements can be reduced to a marginal distribution of N_{dp},

$$N_{dp} \sim \text{Poisson}(\lambda p_t). \tag{6}$$

The details of this simplification can be found in "Simplifications of the Hierarchical Model."

Similarly, we can use the marginal distribution of N_{dp} and the conditional statement of the number of introduced individuals (eq. [2]) to formulate the marginal distribution of the number of introduced individuals,

$$N_d \sim \text{Poisson}(\lambda p_t p_i), \tag{7}$$

following the same procedure as demonstrated in "Simplifications of the Hierarchical Model." The marginal distribution of N_d is the number of individuals introduced to the destination from a single source.

To consider n independent pathways, we assume the input of multiple Poisson random variables. A useful mathematical result is that the sum of independent Poisson distributions is also Poisson distributed,

$$\sum N_d \sim \sum_{k=1}^{n} \text{Poisson}(\lambda_k p_{t,k} p_{i,k}) = \text{Poisson}(\phi), \tag{8}$$

where $\sum N_d$ is the distribution of the propagule pressure into the destination from n pathways and $\phi = \sum_{k=1}^{n} \lambda_k p_{t,k} p_{i,k}$ is the expectation of the propagule pressure. The last hierarchical simplification is to collapse the propagule pressure (eq. [8]) into the conditional survival process (eq. [1]) to find the marginal distribution of the number of surviving individuals, N_E. Because the propagule pressure is Poisson distributed, we have the same simplification as observed with both the transport and the introduction hierarchical statements. This leads to

$$N_E \sim \text{Poisson}(p_s \phi). \tag{9}$$

The distribution of N_E captures the process variability of transporting individuals from multiple sources to a single destination and the demographic stochasticity of the individual probability of survival.

Estimating the probability of establishment of NIS may require consideration of the underlying population dynamics at the destination (Drake et al. 2005). Leung et al. (2004) have formulated the establishment process for two models, one that assumes independence in the arriving propagules and one that contains a shape parameter to test for the presence of Allee effects. The independence model of NIS establishment used by Leung et al. (2004) can be formulated from the arrival process modeled here by first considering the probability of not observing an establishment event. Using the marginal distribution for N_E, this is

$$\Pr(N_E = 0) = e^{-p_s \phi}. \tag{10}$$

Its complement, the probability of observing at least one established individual,

$$\gamma = \Pr(N_E \geq 1) = 1 - e^{-p_s \phi}, \tag{11}$$

is similar to the independence model of establishment proposed by Leung et al. (2004).

The difference between the two formulations is that here we have justified a Poisson distributed random variable, N_E, and Leung et al. (2004) used a binomial random variable where $\gamma = \Pr(N_E \geq 1) = 1 - (1 - p_s)^{\phi}$. The Poisson is an approximation of the binomial when ϕ is large and p_s is small (Casella and Berger 2002). The effect of small p_s on γ can be found by expanding e^{-p_s} in equation (11) as $1 - p_s + (p_s^2/2) \ldots$. Keeping the first two terms in this expansion yields γ for the binomial distribution. Thus, the arrival framework resulting from hierarchical modeling is a link to the establishment phase of biological invasions and justifies the independence model of Leung et al. (2004).

Leung et al. (2004) assess the presence of Allee effects by testing for the significance of a shape parameter, α (c in their formulation), on the independence model. Equation (11) of NIS arrival may be modified to include a shape coefficient test developed by Leung et al. (2004), $\gamma = 1 - e^{-(p_s \phi)^{\alpha}}$, but the Allee model formulation for NIS establishment is not further justified here, and we continue our investigation of NIS arrival following the independence model.

Suter (1993) refers to equations (10) and (11) as an endpoint. The endpoint terminology comes from ecological risk assessment and is used to define a formal expression of the environmental values to be protected. In this case, the value to be protected is the absence of the NIS from a particular location (eq. [10]), and the risk (probability) associated with failure of this objective is the complement (eq. [11]). The endpoint is flexible and could be adjusted to monitor for the successful establishment of 10, 100, or more individuals. We use the endpoint defined by equations (10) and (11) hereafter.

Time-to-Event Stochastic Processes

Given that the probability of the event that at least one individual establishes is γ, it is possible to extend the dynamics of this system through time as a series of Bernoulli trials (Taylor and Karlin 1998) to consider the contribution of repeated introductions. This assumes that over discrete time steps, the arrival process can be modeled as an independent Bernoulli random variable. A property of i.i.d. Bernoulli trials is the geometric distribution of the waiting time, T, to the first event (establishment),

$$T \sim \text{geometric}(\gamma),$$

with probability mass function

$$\Pr(T = t) = \gamma(1 - \gamma)^{t-1}, \tag{12}$$

where γ is defined by equation (11). Consider three locations with different propagule pressures ($\phi = 100$, 50, and 10 individuals) and the same probability of survival, $p_s = 0.001$. Equation (11) yields $\gamma = 0.10$, 0.05, and 0.01. The waiting time distributions for the three realizations, following equation (12), are illustrated in figure 2. The geometric distribution has a mean, $1/\gamma$, and a variance, $(1 - \gamma)/\gamma^2$. This results in the property that as the probability of at least one establishing individual becomes small, the mean and variance become large. Thus, by attempting to reduce NIS establishment events, we are increasing the uncertainty of when the NIS will establish. However, there is a trade-off in that we can now accurately state that an invasion is unlikely to occur. Yet, this never precludes the possibility of an invasion occurring in the next time step if $\gamma > 0$. Given the waiting time distribution, we can analytically determine the probability of an establishment by time t according to

$$\begin{aligned} \Pr(\text{establishment by } t) &= \Pr(T \leq t) \\ &= 1 - (1 - \gamma)^t. \end{aligned} \tag{13}$$

Using figure 2 as an example and setting $t = 10$ time steps, we find that the risk of establishment would be the sum, from 1 to 10, of the geometric distributions for $\gamma = 0.10$, 0.05, and 0.01. This results in probabilities of an establishment event (eq. [13]) within the next 10 time steps equal to 0.65, 0.40, and 0.10, respectively.

The probability of at least one individual establishing in a single time step, γ, and the probability of invasion by time t are two different, albeit closely related, endpoints. When $t = 1$, the two probabilities are equal (i.e., eq. [13] yields γ). Thus, γ provides one-time-step predictions of invasion, while the probability of invasion by time t allows for prediction over a longer time frame.

Patterns of Invasion

There are many reasons why estimating the individual survival probability, p_s, and the propagule pressure, ϕ, may be difficult. It may be economically infeasible to monitor continuously for the introduction of NIS, whose detection is furthermore complicated when only a few individuals are introduced. This is the dilemma community ecologists face when accounting for rare species (Longino and Colwell 1997). Estimating individual survival probabilities faces another set of difficulties in that uninvaded locations likely require not only the standard experimental efforts and logistics (e.g., Von Holle and Simberloff 2005) but also substantial security measures to prevent the experiment from being the source of an NIS establishment event. However, possibly the most limiting factor for all of these estimation considerations is time. Experiments and observations take time to conduct and collect, while inaction in preventing establishment may allow the invasion to occur (Simberloff 2003).

The approach many ecologists have taken is to use relative measures of individual survival or propagule pressure to assess invasion risk in a timely manner. For example, gravity models that describe the movement rates of people with a formulation analogous to Newton's laws of attraction are useful in estimating relative abundance of aquatic NIS transported through recreational boater traffic (Schneider et al. 1998; Bossenbroek et al. 2001; Muirhead and MacIsaac 2005). Relative measures of survival come from habitat matching studies between source and destinations (e.g., Drake and Bossenbroek 2004; Herborg et al. 2007). Therefore, applying relative measures of propagule pressure and survival probability would be useful for uncovering the patterns of successful invasions from

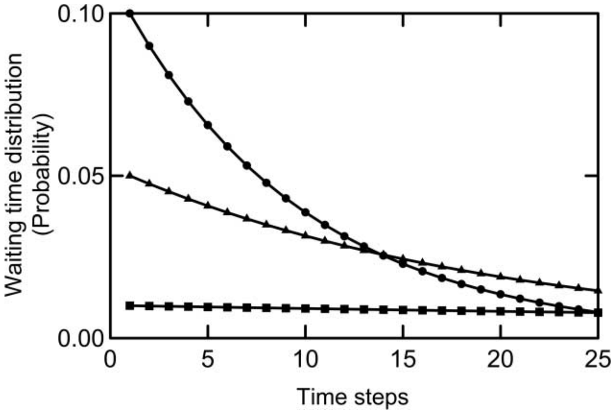

Figure 2: Geometric probability mass function for the time to establishment, where $\gamma = 0.1$ (*circles*), 0.05 (*triangles*), and 0.01 (*squares*). Using the geometric waiting time distribution, as γ goes to 0, the distribution becomes flat. Thus, by reducing the propagule pressure, ϕ, or the survival probability, p_s, we increase the uncertainty of when an invasion will occur. However, there is a reduced probability (eq. [13]) that invasion will occur in the near future (i.e., if $t = 3$).

the arrival framework. The hierarchical model for the arrival process provides a mechanistic basis for comparing invasion waiting times for locations with different propagule pressures and probabilities of survival. Here we show how relative measures can be used to calculate relative waiting times and predict the order of invasion into two locations.

We refer to the expected surviving propagule pressure as $\overline{N}_{\mathrm{E}} = p_s\phi$ (see eq. [9]), and it can be interpreted as the expected number of establishing individuals from the independence model of Leung et al. (2004). Suppose that two locations have different pressures, where we denote $\overline{N}_{\mathrm{E}_A}$ as the expected surviving propagule pressure in location A and $\overline{N}_{\mathrm{E}_B} = c\overline{N}_{\mathrm{E}_A}$ as the expected surviving propagule pressure in location B. Intuitively, we would expect that $c < 1$ would lead to location A, on average, being invaded before location B, as a result of reduced expected surviving propagule pressure, and that $c > 1$ would lead to location B, on average, being invaded before location A, as a result of increased expected surviving propagule pressure in B. These are the arguments used to justify ranked risk assessments of locations found in the gravity model literature (Schneider et al. 1998; Bossenbroek et al. 2001; Leung et al. 2004). However, although ranks may be useful in determining which locations are more likely to be invaded, they do not reveal the probability of invasion (probabilistic risk) or the relative odds that one location will be invaded over another (relative risk).

The time-to-event extension of the hierarchical model allows us to forecast probabilities and relative risk associated with the outcomes regarding invasion times for specified locations. We define $T_A \sim \text{geometric}(\gamma_A)$ (see eq. [12]) to be the random variable describing the waiting time that location A is first invaded, where $\gamma_A = 1 - e^{(-\overline{N}_{\mathrm{E}_A})}$ (see eqq. [10], [11]). Likewise, $T_B \sim \text{geometric}(\gamma_B)$ is defined as the random variable describing the waiting time that location B is first invaded, where $\gamma_B = 1 - e^{(-c\overline{N}_{\mathrm{E}_A})}$. The ratio R of expected time for invasion of location B to expected time for invasion of location A is

$$R = \frac{\mathrm{E}[T_B]}{\mathrm{E}[T_A]} = \frac{1/\gamma_B}{1/\gamma_A} = \frac{\gamma_A}{\gamma_B} = \frac{1 - e^{-\overline{N}_{\mathrm{E}_A}}}{1 - e^{-c\overline{N}_{\mathrm{E}_A}}}. \tag{14}$$

If $\gamma_A = 0.4$ and $\gamma_B = 0.1$, then we should expect to wait, on average, $R = 4$ times longer for location B to be invaded than location A. This ratio, R, is a decreasing function of the absolute risk of invasion, as given by the expected surviving propagule pressures $\overline{N}_{\mathrm{E}_A}$ and $\overline{N}_{\mathrm{E}_B} = c\overline{N}_{\mathrm{E}_A}$ when $c < 1$ and an increasing function when $c > 1$ (fig. 3). In the case where γ becomes small, $\overline{N}_{\mathrm{E}_A} \to 0$, and $c > 1$, the ratio of expected times in equation (14) converges to $c^{-1} = \overline{N}_{\mathrm{E}_A}/\overline{N}_{\mathrm{E}_B}$, a measure of relative risk. Hence, relative risk provides a useful measure for the ratio of expected invasion waiting times when the expected surviving propagule pressure is small.

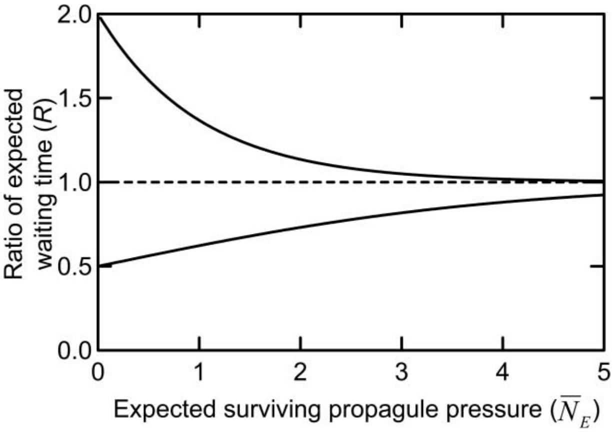

Figure 3: Ratio R of expected time for invasion of location B to expected time for invasion of location A as a function of $\overline{N}_{\mathrm{E}_A}$. The region above the dashed line is for $c < 1$ and the region below for $c > 1$. As $\overline{N}_{\mathrm{E}_A}$ becomes large, the ratio becomes 1. As $\overline{N}_{\mathrm{E}_A}$ goes to 0, the ratio converges to c^{-1}. Two realizations, $c = 2$ and $c = 0.5$, are shown.

Empirical evidence suggests that propagule pressure is often a predictor of invasions (Lockwood et al. 2005; Von Holle and Simberloff 2005). If we compare two locations with the same, but unknown, p_s, then the expected propagule pressure, ϕ, can give estimates of the relative waiting times such that we should, on average, expect to wait $c^{-1} = \phi_A/\phi_B$ times longer for location B to be invaded than location A.

Bossenbroek et al. (2001), using a gravity model of boater traffic, provide estimates of zebra mussel (*Dreissena polymorpha*) dispersal, Q_u, of the relative number of infested boats visiting uninvaded lake u per year. Assuming that the zebra mussel propagule pressure is proportional to infected boater traffic and that the expected surviving propagule pressure, $\overline{N}_{\mathrm{E}}$, for both locations is small, the ratio of boater traffic is an estimate of the relative expected waiting time of invasion. For example, if lake A has $Q_A = 100$ and lake B has $Q_B = 5$, then we should expect to wait, on average, 20 times longer for lake B to be invaded than lake A. Thus, estimates of relative propagule pressure, such as Q_u, provide an estimate of the relative waiting time that is more informative than ranks currently provided.

Additionally, it is possible to estimate the probabilities of ordered invasion into two locations. There are three possible outcomes: location A is invaded before location B, location A and location B are invaded at the same time, and location B is invaded before location A. The derivation of these probabilities are presented in “Order of Invasion–

Derived Distribution" in the appendix in the online edition of the *American Naturalist*, and the results are

$$\begin{aligned}\Pr(B \text{ before } A) &= \frac{\gamma_B - \gamma_A\gamma_B}{\gamma_A + \gamma_B - \gamma_A\gamma_B},\\ \Pr(B \text{ and } A) &= \frac{\gamma_A\gamma_B}{\gamma_A + \gamma_B - \gamma_A\gamma_B},\\ \Pr(A \text{ before } B) &= \frac{\gamma_A - \gamma_A\gamma_B}{\gamma_A + \gamma_B - \gamma_A\gamma_B}.\end{aligned} \tag{15}$$

Again, γ_A and γ_B are the probabilities of at least one individual establishing in location A and location B, respectively, and the γ estimates are functions of the propagule pressure and individual probability of survival (eq. [11]). When the product of the probability of at least one establishing individual for both locations is small ($\gamma_A\gamma_B \rightarrow 0$), the probability of location B being invaded before location A is $1/(1+R)$, and the probability of location A being invaded before location B is $R/(1+R)$ (formulations shown in "Order of Invasion–Derived Distribution"). The probability of both locations being invaded at the same time step is approximately 0.

The waiting time, relative waiting time, and order of invasions are temporal patterns resulting from the hierarchical model of NIS arrival. Therefore, parameters of propagule pressure (λ, p_t, and p_i) and individual probabilities of survival (p_s) will determine these patterns. In "Examples" in the appendix in the online edition of the *American Naturalist*, we provide two examples of parameter estimation and the resulting patterns of invasion. The first is an example of the agricultural nuisance species scentless chamomile (*Matricaria perforata*). This example shows the calculation of γ for two locations with experimentally manipulated levels of propagule pressure. The result of this experiment shows the waiting time distribution and the limitations of using relative formulations (propagule pressure only) on the patterns of invasion. The second example comes from Herborg et al. (2007), regarding the arrival of Chinese mitten crab (*Eriocheir sinensis*). We show how relative waiting times and order of invasion for five U.S. shipping ports can be calculated using relative measures of ballast water discharge. From this formulation, we identify the port of Norfolk, Virginia, as being the most susceptible to mitten crab invasion, while the remaining four ports have probabilities of 0.17, 0.15, 0.05, and 0.03 of being invaded before Norfolk. These probabilities may be useful for designing monitoring and control strategies of mitten crab invasion but are not further developed. The relative formulations presented here are focused on propagule pressure; however, it should be noted that similar relative approaches may be useful for the survival probability.

Discussion

Two approaches have emerged for predicting the arrival and successful establishment of NIS. The first approach emphasizes characteristics of the invader or the location allowing for the NIS to survive and establish (Richardson and Rejmanek 2004). The second approach argues that propagule pressure alone is a sufficient indicator to predict successful invasions (Lockwood et al. 2005). However, neither approach is general enough to move beyond a primarily case-by-case treatment of NIS arrival (Gilpin 1990). The hierarchical probability model highlights the limitation of these approaches for predicting invasions. Consider two species entering a location. The first has $p_s = 0.01$ and $\phi = 10$, while the second has $p_s = 0.0001$ and $\phi = 1{,}000$. Strict adherence to either approach would identify one invader as likely to be more successful than the other, yet γ, and the resulting waiting time for both species, is the same. Therefore, a strategic approach to predicting successful invasions should consider both the propagule pressure and the mechanisms influencing the individual probability of survival.

When there is very little propagule pressure and a small probability of survival, the invasion risk is likely negligible, and when there is overwhelming propagule pressure, the invasion dynamics are essentially deterministic. Our results regarding invasion waiting time distributions and order of invasions are applicable to levels of intermediate propagule pressure where there is appreciable invasion risk but uncertainty as to whether and when the invasion will occur. Explicit incorporation of survivorship, p_s, in the expected surviving propagule pressure means that the hierarchical framework allows for investigation of the influences of changes in survivorship on NIS establishment and has the advantage of being connected to the influences of propagule pressure. For example, Simberloff and Von Holle (1999) proposed the concept of invasional meltdown, whereby the presence of NIS in a location increases the p_s for an arriving NIS. Similarly, hypotheses about such issues as the role of fluctuating resources (Davis et al. 2000), enemy release (Keane and Crawley 2002), and biotic resistance (Levine et al. 2004) may also be formulated as a change in p_s leading to increases or decreases in the probabilities of establishment, γ, and the resulting waiting time distributions. Likewise, the natural history of the NIS or the location being invaded may change the individual probability of survival.

Our modeling approach suggests strategies for controlling invasion even when a location is overwhelmed by propagule pressure (Von Holle and Simberloff 2005). Indeed, the arrival of NIS in such abundances that γ approaches 1 essentially guarantees that invasion will occur in the near future. In such cases, attempting to reduce invasion success will consist of evaluating the contribution of parameters λ, p_t, p_i, and p_s to the probability of establishment, γ. It may be that because p_s is large, even a few individuals are enough to overwhelm the system. Alternatively, if p_s is small, then it may take orders of magnitude more propagule pressure to overwhelm the system. In this situation, evaluating the parameters of the arrival process may lead to more effective targeting of management actions, such as reducing the mean abundance of individuals available for transport, λ. Additionally, when comparing the risk of establishment for multiple locations, if p_s is sensitive to difference or changes in biotic and abiotic conditions, then the amount of propagule pressure needed to overwhelm the system will also be sensitive to the biotic and abiotic conditions.

The invasion waiting time is a pattern of the invasion process resulting from the arrival and establishment stages. Strategically, both the propagule pressure and the individual probability of survival will determine the distribution of the waiting time and the order of invaded locations through the parameter γ. However, many tactical approaches to predicting invasion have used relative measures to rank locations most likely to be invaded. Two assumptions should be emphasized that are used to estimate the relative waiting time, R, and the order of invasion for two locations, $R/(1 + R)$ and $1/(1 + R)$. First, $\overline{N}_E$ is assumed to be small. If $\overline{N}_E$ is even moderately large, then both locations are likely overwhelmed by propagule pressure, and both locations are deterministically invaded at the next time step. However, in systems such as that of the Great Lakes zebra mussel, where it is known that individuals have been introduced to inland lakes that remain uninvaded, this assumption seems reasonable (Bossenbroek et al. 2001; Johnson et al. 2001). Second, p_s is assumed to be the same between locations, though unknown. A violation of this assumption would potentially result in a similar misleading conclusion, as demonstrated at the beginning of this discussion, and would influence not only the relative waiting time but also the ranks that are commonly present in the invasion literature.

Tactical approaches to biological invasion are undoubtedly useful for performing risk assessments and making management decisions, but a strategic approach may help us reveal the mechanisms of biological invasions that more generally allow NIS to eventually establish or fail. We believe this framework is a skeleton on which to model the NIS arrival process and strategically identify patterns of successful invasion.

Acknowledgments

We wish to thank C. J. Bampfylde, T. de Camino-Beck, S. R. Lele, H. McKenzie, W. A. Nelson, and the biological invasions work group of the Centre for Mathematical Biology at the University of Alberta for useful suggestions and discussions on earlier drafts of this manuscript. L.-M. Herborg kindly provided the ballast water data for the Chinese mitten crab example. The Alberta Research Council provided experimental plots for the scentless chamomile example. This material is based on work supported by the Integrated Systems for Invasive Species project (D. M. Lodge, P. I.) funded by the National Science Foundation (DEB 02-13698). C.L.J. was supported by a teaching assistantship from the University of Alberta Department of Biological Sciences and research funding from a Natural Sciences and Engineering Research Council (NSERC) Collaborative Research Opportunity grant. M.A.L. was supported by a Canada Research Chair in Mathematical Biology and Discovery grant from NSERC.

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Associate Editor: Nicolas Perrin
Editor: Donald L. DeAngelis