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*Paradigms and perspectives*

# Allee effects, propagule pressure and the probability of establishment: risk analysis for biological invasions

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## Abstract

Colonization is of longstanding interest in theoretical ecology and biogeography, and in the management of weeds and other invasive species, including insect pests and emerging infectious diseases. Due to accelerating invasion rates and widespread economic costs and environmental damages caused by invasive species, colonization theory has lately become a matter of considerable interest. Here we review the concept of propagule pressure to inquire if colonization theory might provide quantitative tools for risk assessment of biological invasions. By formalizing the concept of propagule pressure in terms of stochastic differential equation models of population growth, we seek a synthesis of invasion biology and theoretical population biology. We focus on two components of propagule pressure that affect the chance of invasion: (1) the number of individuals initially introduced, and (2) the rate of subsequent immigration. We also examine how Allee effects, which are expected to be common in newly introduced populations, may inhibit establishment of introduced propagules. We find that the establishment curve (i.e., the chance of invasion as a function of initial population size), can take a variety of shapes depending on immigration rate, carrying capacity, and the severity of Allee effects. Additionally, Allee effects can cause the stationary distribution of population sizes to be bimodal, which we suggest is a possible explanation for time lags commonly observed between the detection of an introduced population and widespread invasion of the landscape.

## Introduction

Species colonization is an important component of global species homogenization (Olden and Poff 2003) and is a driver of long-term biogeographical dynamics (Clark 1998). The processes of colonization are therefore of longstanding interest to both theoretical (Baker and Stebbins 1965; MacArthur and Wilson 1967; Elton 2000) and applied (Cook 1931; Gjullin 1931; Baker 1974) ecologists. Changing patterns of trade have caused increases in invasions (Levine and D'Antonio 2003), raising concern about the widespread accidental distribution of biotic propagules via ships, planes, trains, and aboard other vehicles of personal and commercial transportation. Thus, there is a heightened sense of urgency to understand the factors driving anthropogenic distribution of propagules (Levine and D'Antonio 2003), and biological processes leading to population establishment (Mack et al. 2000; Kolar and Lodge 2001), and a need to develop effective tools for invasion risk assessment (National Research Council 1996, 2002; Hayes 1997; Simberloff and Alexander 1998; Gollasch and Leppäkoski 1999; Mack et al. 2000; Groves et al. 2001; Kolar and Lodge 2001).

Clearly, the availability of suitable habitat is a prerequisite for population establishment, reflected in much recent work in 'environment-matching' (e.g., Peterson and Vieglas 2001; Reichard 2001; Kolar and Lodge 2002; Sutherst 2003; Drake and Bossenbroek 2004). However, because establishment success correlates with propagule pressure, including the number of individuals introduced and the frequency of introduction events (Williamson 1996; Grevstad 1999a; Kolar and Lodge 2001; Colautti et al. in press), it is equally clear that without introductions of adequate size or frequency, no establishment will occur. This statistical relationship between propagule pressure and establishment success is not only an empirical finding of invasion biology, but is also consistent with predictions of theoretical population biology (Richter-Dyn and Goel 1972). This is important because if the causes of introduction failure can be understood in terms of basic population phenomena such as birth and death rates, immigration events, and Allee effects, then risk analysis can hope to provide estimates of the chance of biological invasion from information about the rates of introduction and model parameters.

Below, we consider how a link between theoretical population biology and risk analysis for biological invasions might be made. First, we point to some conceptual similarities between the concept of a dose-response curve and the chance of invasion. Then, we review the relevant theory in population biology, extending existing models to indicate the important conceptual difference between populations that are recurrently supplemented through immigration and introductions that are independent events. Together, these results indicate some general principles that may guide actions to manage risk, even where data are insufficient for precise model parameterization.

## Risk analysis

The need for risk assessment methods for biological invasions is widely appreciated among biologists and policy-makers alike (National Research Council 1996, 2002; Hayes 1997; Simberloff and Alexander 1998; Gollasch and Leppäkoski 1999; Mack et al. 2000; Groves et al. 2001; Kolar and Lodge 2001). The precedent for ecological risk assessment in the United States has been set by the US Environment Protection Agency in the context of radiological and toxicological pollutants, hazards whose consequences are usually simple monotonic functions of exposure rates (Environmental Protection Agency 1998; Kammen and Hassenzahl 1999; Sunstein 2002).

Conventional human health and ecological risk analysis is concerned with quantifying the chance of an undesirable effect as a function of exposure to some quantity of a stressor (Environmental Protection Agency 1998; Kammen and Hassenzahl 1999). The dose–response curve describes the relationship between the probability of the undesirable effect and the magnitude of acute or chronic exposure to the stressor. For risk analysis of biological invasions, the invasion of an undesirable species is clearly the hazard, while the propagule pressure to an ecosystem is analogous to the stressor. We think that the *establishment curve*, which relates the chance of invasion to propagule pressure, is analogous to toxicological dose–response curves and can be used in similar ways in setting risk management objectives. Moreover, when establishment curves are derived from invasion theory, all terms in the models are given biological interpretations. Such a mechanistic understanding of establishment curves will be extremely useful for identifying and predicting the effectiveness of possible interventions.

Although at present, no formal policies or guidelines require that specific techniques be used to obtain probabilities of establishment, several authors have suggested that stochastic models of population growth could be used to estimate the chance of establishment, if establishment probability is defined as the complement of extinction probability (Goel and Richter-Dyn 1974; Haccou and Iwasa 1996; Wilson 2000; National Research Council 2002; Drake 2003, 2004). Extinction probabilities have been well studied in the theoretical literature and are common in conservation applications. Surprisingly therefore, although the ideas that follow are not without precedent, especially in the theoretical literature, current applications to invasions are few (e.g., Drake 2004).

Two statistics commonly used in population viability analysis are the chance of extinction and the mean time to extinction. It is natural therefore to suppose that their 'opposites' – one minus the chance of extinction and the inverse of mean time to extinction – might be good metrics of invasion risk, as we and others have suggested (MacArthur and Wilson 1967; Goel and Richter-Dyn 1974; Drake 2003). Unfortunately, these metrics are only useful in limited situations. For example, only populations that are permitted to grow indefinitely do not eventually go extinct. In contrast, all real populations are bound by carrying capacity and will eventually go extinct, given enough time. Thus, the chance of extinction for finite populations is (trivially) one. The mean time to extinction is a more general metric, but is not useful for populations supplemented by immigration, where the population eventually settles to a stationary distribution of population sizes and any extinction will quickly be rescued by the arrival of additional propagules. These limitations suggest that three criteria for more desirable statistics are that:

1. they should be meaningful for populations both with and without recurrent immigration;
2. they should be valid for bounded population growth; and
3. their interpretation should be intuitive and relevant to policy and management decisions.

Such an alternative metric is readily available. It is the first passage probability of attaining a large, 'nuisance' population size before going extinct (Gardiner 1985), which we designate by $n_{\text{inv}}$. Arguably, the choice of any precise number for $n_{\text{inv}}$ can be disputed. For practical purposes, however the exact choice of $n_{\text{inv}}$ will not matter, so long as it is greater than the population sizes at which Allee effects are severe. We must also consider a quasi-extinction threshold $n_{\text{ext}}$, below which the population is of no concern. Then, for any introduced population size $n$, the question is which population size will be attained first, $n_{\text{inv}}$ or $n_{\text{ext}}$. The probability of attaining $n_{\text{inv}}$ before attaining $n_{\text{ext}}$ is the first passage probability ($\xi$), and can be obtained numerically for many situations of interest, including models of immigration and Allee effects. Moreover, the first passage probability meets all three of the criteria above. It tells us precisely the probability that an introduced population will become a nuisance rather than simply go extinct.

## Population biology

### *A brief history of time to extinction*

At least since the 1930s, biostatisticians have been aware of novel behaviors that emerge when the deterministic assumptions of classical population growth models are relaxed and probabilities are built directly into dynamic model structures (Feller 1939; Kendall 1949; Bartlett 1960; Bailey 1964). Though some of these models are decades old, new results continue to be discovered (Rand and Wilson 1991; Henson et al. 2003). One classical result is that when one state is an 'absorbing' boundary (such as extinction) there is a positive chance of reaching it, while the existence of finite carrying capacities for real populations implies that all will eventually go extinct. A second classical result is that when vital rates fluctuate (i.e., growth rate is stochastic), as they almost always do in real populations, the average realized population growth can be considerably reduced from the mean of instantaneous growth rates over time (Lewontin and Cohen 1969; Lande et al. 2003). Because these phenomena have especially severe consequences for the growth of small populations, the theory of stochastic population growth was developed largely with applications to the conservation of endangered populations (Shaffer 1981; Soulé 1987; Lande and Orzack 1988), though early theoretical work perceived the importance to colonization theory too (MacArthur and Wilson 1967; Goel and Richter-Dyn 1974).

In the context of increasing concern about species' extinctions, Shaffer (1981) introduced the idea of the *minimum viable population*: a population with a predicted probability of extinction that is acceptably low within the time frame under management considerations. Subsequently, *population viability analysis* (PVA) was developed to facilitate risk analysis, decision-making, and planning for management activities to curb the extinction of endangered populations (Beissinger and McCullough 2002; Morris and Doak 2002). Though controversial (Fieburg and Ellner 2000; Brook et al. 2002; McCarthy et al. 2003), many conservation biologists are optimistic that through careful model specification and proper interpretation, these techniques will yield considerable benefits for conservation planning (Beissinger and McCullough 2002; Morris and Doak 2002; McCarthy et al. 2003). Even so, the idea that stochastic population growth models can be used to study the probability of establishment has only been recently re-introduced into the literature about invasive species (Haccou and Iwasa 1996; Wilson 2000; National Research Council 2002).

Rather than focus on the intricacies of particular modeling frameworks (for details see Tier and Hanson 1981; Lande and Orzack 1988; Tuljapurkar 1990; Dennis et al. 1991; Mangel and Tier 1993; Ludwig 1996; Beissinger and McCullough 2002; Morris and Doak 2002; Lande et al. 2003), we will focus on two important conceptual distinctions that pertain to the invasion process and relate to the concept of propagule pressure in general ways: (1) the difference between closed populations, in which introductions are isolated events, and open populations in which introductions are recurrent, potentially inducing rescue effects (Brown and Kodric-Brown 1977); and (2) populations that exhibit Allee effects *versus* those that do not (Dennis 2002). An important difference between open and closed populations is that finite, closed populations eventually go extinct with a probability of one. In contrast, open populations converge to a stationary probability distribution of population sizes, since arriving immigrants can restore locally extirpated populations.

Density-dependence in small populations is commonly exhibited in two forms: (1) regulation of populations by carrying capacity, and (2) depensation in populations exhibiting Allee effects, which we define in demographic terms as diminished per capita population growth rates at low densities (Dennis 1989, 2002; Lewis and Kareiva 1993; Grevstad 1999b; Berggren 2001; Boukal and Berec 2002; Drake 2004). While depensation is relatively rarely documented compared with other forms of density dependence (See Courchamp et al. 1999 for a review), many species should be expected to exhibit Allee effects at low densities, including all sexually reproducing species where mate-finding can limit reproductive success (McCarthy 1997). When severe, Allee effects typically exhibit a critical density or population size, $n^*$. In deterministic models, this is an unstable equilibrium. In stochastic models, this is usually manifest as an inflection point in the time to extinction: populations that are smaller than $n^*$ have an accelerating time to extinction as they decline (Dennis 2002). Though the characteristics of particular models of Allee effects have been less studied than those of carrying capacity, this is an active area of research (Boukal and Berec 2002). Additionally, in populations where Allee effects are large relative to carrying capacity, these two forms of density dependence can interact and affect the theoretical chance of establishment.

Below, we use the theory of stochastic differential equations to explore the effects of demographic stochasticity on populations with and without continuous immigration and populations with and without Allee effects (Tier and Hanson 1981). Incorporating environmental variability is a straightforward extension of these models that we do not consider further here (Tier and Hanson 1981; Dennis 2002). Dennis (2002) has studied the Allee effect with logistic regulation and others have studied linear and nonlinear birth-death-immigration processes (Bailey 1964; Renshaw 1991; Matis and Kiffe 2000). However, to our knowledge the analysis below of a model for population growth with immigration, Allee effects, and logistic regulation is new, and offers important insights into the colonization process.

### *Stochastic differential equations*

Stochastic differential equation (SDE) representations of population growth are stochastic generalizations of the familiar deterministic models of population growth (ordinary differential equations – ODEs) obtained by the addition of a term for random perturbations (Allen 2003). Equivalently, SDEs can be derived as continuous approximations to a (possibly density-dependent) branching process (Tier and Hanson 1981; Ludwig 1996). As described above, stochasticity can result from demographic stochasticity (the random sequence of births and deaths in the population or fluctuations in sex ratio) or as random fluctuations in the vital rates caused by changes in the organism's environment. SDEs are also commonly known as diffusion approximations and are completely specified by a model for the infinitesimal mean and infinitesimal variance, which we designate $m(n)$ and $v(n)$, respectively. Typically, $m(n)$ will be identical to the ODE representation of the deterministic population growth process. The form of $v(n)$ depends on the source of stochasticity (Tier and Hanson 1981; Allen 2003; Lande et al. 2003).

### *Allee effects and immigration*

As a basic model, we assume $m(n)$ can be represented by the logistic growth process:

$$\frac{dn}{dt} = rn - \frac{r}{k}n^2, \tag{1}$$

where $n$ and $k$ are positive constants representing growth rate and carrying capacity. Following Dennis (1989, 2002), Allee effects are incorporated by the addition of a term $[n/(\theta+n)]$ representing mate limitation. The mean process of the Allee-logistic model becomes

$$\frac{dn}{dt} = rn - \frac{r}{k}n^2 - \frac{\lambda\theta}{\theta+n}n, \tag{2}$$

where $\lambda$ and $\theta$ are positive constants representing birth rate and the effect of mate limitation.

Models of the Allee effect often exhibit a critical density ($n^*$) below which (in deterministic models) the population declines to extinction. For Equation (2), the critical density can be obtained as the lower of up to two equilibria after defining the new variables $a = -r/k$, $b = r(k - \theta)/k$, and $c = \theta(r-\lambda)$ from the quadratic formula $n* = (-b \pm \sqrt{b^2 - 4ac})/2a$ (Dennis 2002). Immigration is added to Equations (1) and (2) by the addition of a constant immigration rate $\iota$, resulting in

$$\frac{dn}{dt} = rn - \frac{r}{k}n^2 + \iota, \tag{3}$$

and

$$\frac{dn}{dt} = rn - \frac{r}{k}n^2 - \frac{\lambda\theta}{\theta+n}n + \iota, \tag{4}$$

respectively. Clearly, Equations (1) and (2) are just special cases of Equations (3) and (4), with $\iota = 0$. Additionally, Equation (2) reduces to Equation (1) and Equation (4) reduces to Equation (3) at $\theta = 0$, i.e. when the Allee effect is absent. Because here we are interested mostly in the effect of $m(n)$ on the chance of invasion, we assume throughout that $v(n) = \alpha n$ (Tier and Hanson 1981; Dennis 2002), accounting for demographic stochasticity, not environmental fluctuations.

### *First passage probabilities*

Above, we argued that the most useful metric of invasion risk is the first-passage probability of attaining a large (nuisance) population size $n_{\text{inv}}$ before going extinct. Using the notation of Dennis (2002), the chance of attaining $n_{\text{inv}}$ before $n_{\text{ext}}$ is given by

$$\xi(n; n_{\text{ext}}, n_{\text{inv}}) = 1 - \frac{\int_{n}^{n_{\text{inv}}} \exp[-\phi(x)]dx}{\int_{n_{\text{ext}}}^{n_{\text{inv}}} \exp[-\phi(x)]dx} \tag{5}$$

where $\phi(x) = 2\int(m(x)/v(x))dx$ (Goel and Richter-Dyn 1974; Gardiner 1985). Below, we evaluate this quantity numerically for each of the models discussed above, to explore the effects of immigration and Allee effects on the chance of invasion. Recognizing that the abundance at which a species becomes a nuisance is not well defined, we assign $n_{\text{inv}} = 100$ for our analysis. In fact, here the choice of $n_{\text{inv}}$ is not hugely important as long as $n_{\text{inv}} \gg n^*$ (a condition that would almost always obtain in real ecosystems). Additionally, for simplicity we assume $n_{\text{ext}} = 1$ throughout. Substituting Equation (3) into Equation (5) and for $\iota = (0, 1.5, 3.0, 4.5)$, the chance of invasion rapidly approaches 1 as the introduced population size increases (Figure 1a). For the special case of $\iota = 0$, Equation (3) reduces to Equation (1) representing a single introduction with no opportunity for rescue. The chance of invasion for a population with Allee effects, obtained by substituting Equation (4) into Equation (5), for $\iota = (0, 1.5, 3.0, 4.5)$, shows the dramatic consequence of Allee effects for populations of small size (Figure 1b). In this case, Equation (2) is recovered where $\iota = 0$. Recurrent immigration does not greatly influence the chance

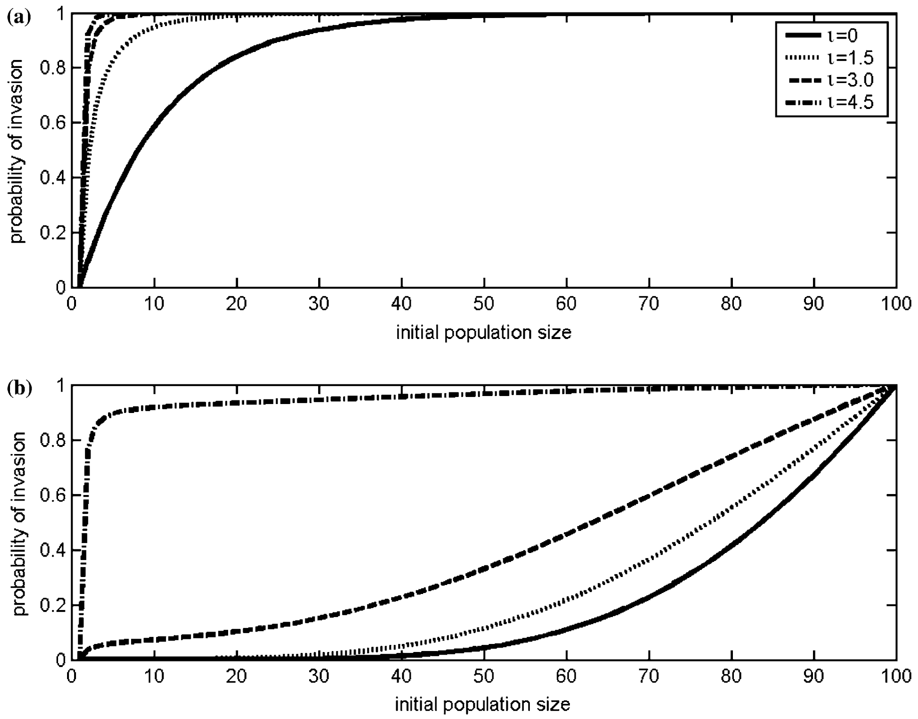

*Figure 1.* Chance of invasion in populations with different rates of immigration and (a) without Allee effects, and (b) with Allee effects. Plots are the first passage probability of reaching $n_{\mathrm{inv}} = 100$ before declining to $n_{\mathrm{ext}} = 1$ given initial population size $n$ ($x$-axis). Other parameters are $r = 0.1$, $\lambda = 0.6$, $\theta = 20$, and $k = 600$.

of invasion where Allee effects are absent (Figure 1a), but can have a strong effect where small populations are ‘rescued’ from depensation (Figure 1b). Where immigration is high (Figure 1b; $\iota = 4.5$), the establishment curve for model defined by Equation (4) appears to qualitatively recapture the shape of the population without Allee effects (Figure 1a). Thus, immigration has the potential to compensate for Allee effects in determining the chance of establishment.

For $\iota > 0$, the stationary probability density, which can be interpreted as the long-run fraction of time at which a population is any size $n$, is

$$p(n) = \frac{\zeta}{v(n)} \exp[\phi(n) - \phi(n_{\mathrm{ext}})] \tag{6}$$

where $\zeta$ is a normalization constant such that $\int p(n)\mathrm{d}n = 1$ (Gardiner 1985). We also evaluate this quantity, for the case without Allee effects (Figure 2a) and the case with Allee effects (Figure 2b) to examine the effects of immigration and mate limitation on the stationary probability density of population size. Immigration only slightly shifts the stationary distribution of population size when Allee effects are absent (Figure 2a), and the modal population size is around carrying capacity. In contrast, when Allee effects are present, the distribution can exhibit either one or two modes (Figure 2b). The upper mode reflects populations fluctuating around carrying capacity, while the lower mode reflects populations fluctuating near extinction. Additionally, immigration exhibits a much more pronounced effect, changing the shape of the distribution of population sizes, in addition to shifting the distribution to the right (Figure 2b). One consequence is that Allee effects can constrain a continuously supplemented population around zero for a long time. We suggest that this may in part explain the lag time often observed between detection of an introduced species and the subsequent radical increase in population size (Shigesada and Kawasaki 1997).

Of course, these results depend very much on the precise values taken by all of the parameters,

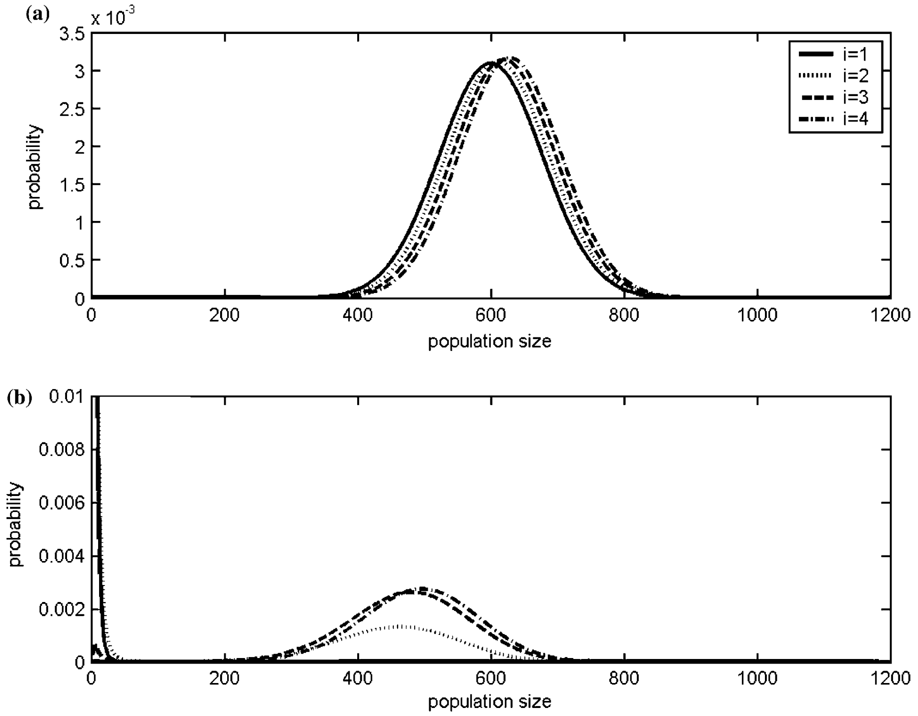

*Figure 2.* Stationary distribution of population sizes for populations with different rates of immigration (a) without Allee effects, and (b) with Allee effects. Other parameters are $r = 0.1$, $\lambda = 0.6$, $\theta = 20$, and $k = 600$.

especially $\theta$ and $k$. Nevertheless, the parameterization in Figure 2b represents only a moderate Allee effect ($\theta = 20$). Increasing the severity of the Allee effect from $\theta = 0$ to $\theta = 30$ for fixed immigration ($\imath = 2$) and carrying capacity ($k = 600$; Figure 3a) shows that when immigration is not great, even an extremely mild Allee effect can cause considerable changes in the shape of the stationary distribution of population size (Figure 3a). This result, however, depends on carrying capacity (Figure 3b). Varying carrying capacity from 500 to 650, while holding all other parameters constant shows that the long run population size is greatly affected by a shift in carrying capacity even over this narrow range relatively far from the critical density $n^*$.

## Discussion

We suggest that the theory of stochastic population growth, as represented by stochastic differential equations, provides a conceptual framework for risk analysis of biological invasions. This theory provides a risk metric that is analogous to risk analysis in other areas, including human health risk analysis and ecological risk analysis (Kammen and Hassenzahl 1999). These analogies are important, not only for theoretical reasons, but also for exploiting practical and legal precedents in implementing risk analysis for biological invasions. Institutional and government policies already rely on similar frameworks for risk management for other environmental pollutants. Adapting such approaches would provide a partial answer to the US National Management Plan's mandate for the development of more rigorous approaches to risk analysis of invasive species (National Invasive Species Council 2001).

Previous models have indicated that the chance of invasion may be greatly influenced by both immigration and Allee effects. Here, we have shown how these processes operating simultaneously affect the chance of invasion. Two results are especially important for risk analysis. First, consistent with observations (Kolar and Lodge 2001), these models all predict that the probability of establishment after a single introduction

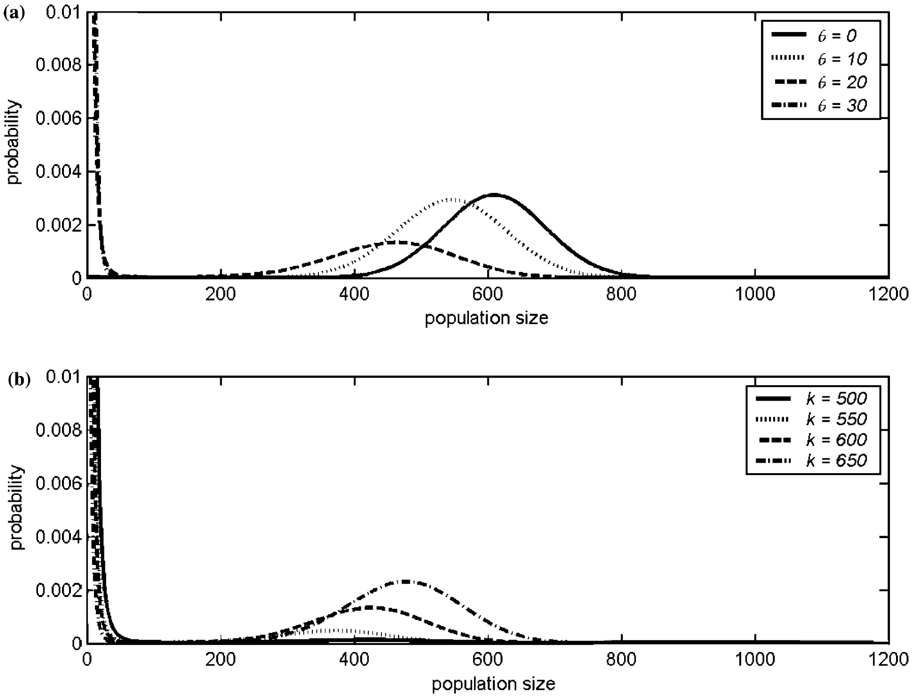

*Figure 3.* Sensitivity of stationary distribution of population sizes to changes in (a) the severity of the Allee effect, and (b) carrying capacity. Other parameters are $r = 0.1$, $\lambda = 0.6$, $\iota = 2$, $k = 600$ (panel a), and $\theta = 20$ (panel b).

will generally be an increasing function of introduction number (Figure 1) [See Drake (2003) for a special case in which this intuitive relationship fails to hold]. Additionally, we have shown that this function may be sublinear or superlinear, depending on rates of immigration and the severity of Allee effects (Figure 1). If the population exhibits Allee effects, steep changes in the probability of invasion are likely to occur in the vicinity of the population's critical density (Figure 1b). Moreover, if the Allee effect is large relative to carrying capacity, these effects can be manifest over the entire range of population sizes (Figure 3b). It follows that determining the severity of Allee effects in real populations of introduced species is an important research goal for risk analysis of invasive species.

Second, immigration interacts with Allee effects, counteracting depensation and escalating the chance of invasion. In contrast to isolated introductions, populations that are continuously supplemented through immigration inevitably invade (in the sense that they eventually obtain the nuisance population size $n_{\mathrm{inv}}$), but not necessarily before they first decline to the quasi-extinction threshold (Figure 1b). Whether invasion or quasi-extinction occurs first depends on the rate of immigration and the severity of the Allee effect (Figure 1). Where Allee effects are absent, immigration has little effect on the chance of invasion (Figure 1a) or the stationary distribution of population size (Figure 2a). This contrasts with the case where species exhibit even mild Allee effects (Figure 3a). For a population with Allee effects, immigration can shift the balance between a sublinear and superlinear establishment curve (Figure 1b). Additionally, the stationary distribution for the model with Allee effects and immigration can exhibit one or two modes, depending on the severity of the Allee effect (Figure 3a). Where immigration is low, the population will mostly fluctuate around zero (Figure 2b). However a small increase in the immigration rate can shift the balance so that the population fluctuates around carrying capacity instead (Figure 2b).

These theoretical results support three important practical recommendations. First, the establishment curve – the relationship between propagule pressure and the chance of invasion – should be adopted as a foundational element of risk analysis for introductions of non-indigenous species. Current US risk analyses for introductions of non-indigenous species of plants and plant pests (under the auspices of the Plant Protection Act of 2000), animals (under the auspices of the Lacey Act), and any organisms delivered in ships' ballast water (under the auspices of the Non-indigenous Species Act of 1996) consider the relationship between propagule pressure and the risk of establishment in qualitative terms at best. In contrast, the National Research Council (2002) recognized that risk analyses for non-indigenous species should be quantitative. The establishment curve provides this quantitative framework.

Second, propagule pressure is the primary control parameter for preventing invasions. In order for risk analysis to usefully inform management interventions, propagule pressure to vulnerable ecosystems must be much more accurately measured. While the Animal and Plant Health Inspection Service of the US Department of Agriculture and other agencies have collected data to estimate propagule pressure from various pathways over many years, these data have not been put to use in this context. If the risk analyses and management responses called for in the US National Management Plan (National Invasive Species Council 2001) are to be implemented, available data on propagule pressure must be made freely available, and previously under-sampled pathways (e.g., ships' ballast water and hull fouling, the live food trade) must be more fully quantified.

Third, ecologists must better measure Allee effects for a diverse reference set of organisms and for invasive species of special concern (e.g., Veit and Lewis 1996). The other parameters in the models reviewed above, such as per capita population growth rate and carrying capacity, are relatively well understood. Although recent studies have estimated the severity of Allee effects in specific populations, especially populations of endangered and declining species (Groom 1998; Courchamp et al. 1999), the prevalence of Allee effects in invasive species is unknown. Liermann and Hilborn (1997) conducted a hierarchical meta-analysis of depensation in four taxonomic groups of fish stocks. In the absence of species-specific information, their results can be used to parameterize models for similar species and indeed permit the relatively sophisticated treatment of uncertainty required for risk analysis to be useful. More studies of this kind are imperative for risk analysis of invasive species to go forward. Thus, there is a central role for population biology to play in risk analysis for introductions of non-indigenous species, which will only be effective if ecologists provide empirical data relevant to estimating the establishment curve for a variety of organisms in a variety of conditions.

Complementary aspects of quantitative risk analysis of non-indigenous species have also advanced rapidly and should be combined with the techniques we have presented for more complete assessments of invasion risk. For example, correlations between species traits and the risk of establishment, spread, and impact have been described for animals (Veltman et al. 1996; Duncan et al. 1999; Kolar and Lodge 2002) and plants (Reichard 2001). Additionally, the combination of non-parametric techniques such as genetic algorithms (Peterson and Vieglais 2001) and neural nets (Lusk et al. 2002) and developments in classical statistical methods like autologistic regression (Augustin et al. 1996) provide increasingly robust tools to identify potential habitats for non-indigenous species. Neither the trait-based or environment-matching approach explicitly considers propagule pressure, however. Therefore, a complete analysis of the risk posed by introductions of potentially invasive species cannot be completed with these methods alone. Ecological theory and practice should fill this void in the risk analysis of non-indigenous species.

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