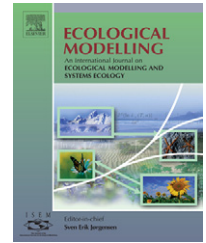


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Immigration events dispersed in space and time: Factors affecting invasion success

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ABSTRACT

Classical models of biological invasions generally assume that introductions consist of single releases of organisms, whereas in nature successful invasions are usually the result of repeated immigration events. A straightforward consequence of such repeated events is that they are likely to increase invasion success. In this article, we consider a less-obvious consequence, namely how repeated immigration events interact with the spatial dispersion of immigration. We construct a spatially explicit model that includes Allee effects and population diffusion, so that repeated introductions must be concentrated in order for the population to exceed the Allee threshold over a critical minimum area and successfully invade. We use this model to show that the spatial dispersion of immigration events is of key importance in determining invasion success. Specifically, invasion risks decline when immigration events are dispersed more widely. Because of this effect, immigration events that occur close to habitat boundaries are likely to lead to higher invasion risks, as dispersing organisms are forced back towards the source of immigrants. These results have important implications for efforts to reduce the risk of aquatic invasions due to discharges of ballast-water by commercial ships. When ballast discharge occurs either far from port, and thus far from habitat boundaries, or far from other ballast discharge events, and thus with wider dispersion, then invasion risks should be greatly reduced. Our work demonstrates the importance of spatial structure for understanding ecological problems, and shows how mathematical models can be useful in guiding environmental management.

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1. Introduction

Invasive species often alter ecological processes (Lodge, 1993; Sala et al., 2000; Stein et al., 2000; Grigorovich et al., 2002), sometimes with important consequences for the economy (Canyon et al., 2002; Pimentel et al., 2002) and for human health (Canyon et al., 2002; Kim, 2002; Lounibos, 2002). Many recent studies have attempted to assess invasion risks by iden-

tifying characteristics that make some species more likely to invade (Baker and Stebbins, 1965; Baker, 1974; O'Connor, 1986; Veltman et al., 1996; Williamson and Fitter, 1996; Schiffman, 1997), or that make some communities more likely to be invaded (Crawley, 1987; Tilman, 1997; Levine and D'Antonio, 1999; Lonsdale, 1999; Richardson et al., 2000). General results, however, have been few (Levine and D'Antonio, 1999; Mack et al., 2000; Veltman et al., 1996; Kolar and Lodge, 2001). Moreover,

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increased human translocation of non-indigenous species is facilitating invasions that otherwise would not have occurred over ecological time scales (Muhlenbach, 1979; Courtenay and Meffe, 1989). These translocations are often independent of inherent dispersal ability (Ashton et al., 1989; Williamson and Fitter, 1996; Smith et al., 1999; Frenot et al., 2001; Ricciardi, 2001). To understand the time evolution of these human-facilitated invasions, we therefore focus on immigration processes (Williamson and Fitter, 1996; Grigorovich et al., 2002) rather than on species characteristics and community properties. An example of particular importance is the incidental release of nonnative zooplankton into aquatic ecosystems during ballast-water discharge from commercial ships (Grigorovich et al., 2002; MacIsaac et al., 2002). Preventing these introductions is far more cost-effective than attempting to eradicate invaders after establishment (Mack et al., 2000). To assist in understanding how to reduce the risk of such invasions, we analyze models of repeated introductions, in which invasion risk is measured in terms of the time it takes for an invasion to be successful. For purposes of comparison, we begin by constructing temporal models of repeated introductions, and then we combine these models with existing spatial-invasion models, to demonstrate how spatial dispersal, dispersal and habitat boundaries affect invasion risks.

Models have played an important role in efforts to understand biological invasions (Murray, 2002), are widely used to analyze invasion data (Lubina and Levin, 1988; Clark et al., 1998), and have been used to guide the management of invasive species (Sharov et al., 2002). Most existing models of species invasions, however, assume that invading populations are founded by single releases of organisms, whereas in nature successful invasions are often the result of repeated colonization events, whether accidental or intentional (Moody and Mack, 1988; Veltman et al., 1996). Recent studies have shown that increases in the frequency and magnitude of immigration events are likely to dramatically increase invasion risks, as one might expect (Drake and Lodge, 2006). The models in question, however, do not include explicit space, whereas in nature, spatial structure often has profound effects on population growth (Tilman and Kareiva, 1997). Moreover, explicit spatial structure is crucial for considering repeated introductions, because both habitat quality (Hanski, 1999) and the initial size of introductions (Kot, 2001) are likely to vary spatially. In this article, we therefore construct a model of repeated introductions that explicitly includes space, and show how the dispersion of introductions in space and time can interact with the number of individuals introduced, their population dynamics, and their movement behavior, to affect invasion success. We use the model to show that it is possible, and practical, to dramatically reduce invasion risk by manipulating the spatial location of introductions. Our results thus have implications for reducing the risk of invasions that result from ballast-water discharge, but our models are general enough that they can be applied to other invasion scenarios as well.

The model that we use is a stochastically perturbed reaction-diffusion equation. Reaction-diffusion equations have a long and successful history in invasion biology because they allow for population growth, dispersal, and explicit spatial structure. To explain our approach, we begin with one of the earliest spatially explicit invasion models, known as

“Fisher’s equation” (Murray, 2002);

$$\frac{\partial N}{\partial t} = rN \left(1 - \frac{N}{K}\right) + D\nabla^2 N. \quad (1)$$

Here N is population size, t is time, and the population undergoes logistic growth, with reproductive rate r and carrying capacity K . The diffusion constant, D , specifies the rate of population spread, and ∇^2 is

$$\nabla^2 N = \left(\frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \right), \quad (2)$$

or in words, the second derivative of population density across space. Eq. (1) therefore says that the change in population size N at spatial location (x, y) with time is due to population growth at that location, as well as to the movement of individuals, which in turn depends on the sign of $\nabla^2 N$ at that location.

For our purposes, two important predictions emerge from Eq. (1). The first is that there is a critical habitat area $\mathcal{A}_{\text{crit}}$ below which the population will go extinct. This occurs because local population decline via diffusion across the relatively large circumference of the patch will dominate population growth within the relatively small area of the patch (Kot, 2001). The critical area,

$$\mathcal{A}_{\text{crit}} = \pi \left(\frac{D}{r} \right)^{1/2}, \quad (3)$$

depends on both local population growth, as governed by r , and on the population spread rate, as governed by D . Note that there is a critical area $\mathcal{A}_{\text{crit}}$ even when population growth is instead exponential (Skellam, 1951; Kierstead and Slobodkin, 1953). The existence of this critical area is an important difference between spatial and non-spatial models of population growth. The second important prediction of the Fisher model is that all initial populations introduced into habitats larger than $\mathcal{A}_{\text{crit}}$ will invade and eventually spread into the remaining habitat at a constant speed $c = 2\sqrt{rD}$. Thus, if this critical area is exceeded, the invasion succeeds deterministically.

Lewis and Kareiva (1993) replaced logistic growth in Fisher’s equation with a growth function that allows for Allee effects, such that, when population densities are below the Allee threshold a , the population growth rate is negative. This model, known as the “Nagumo equation”, is,

$$\frac{\partial n}{\partial t} = rn(1-n)(n-a) + D\nabla^2 n. \quad (4)$$

Here, and hereafter, we have scaled population density N by dividing by the carrying capacity K (i.e., $n = N/K$). The parameters r and D can also be removed by additional rescaling, but they play a key role in determining the invasion criterion, R_{crit} , described below, and so are best retained (Kot, 2001). The scaled population size n therefore ranges from 0 to 1, while the Allee threshold is constrained to $a < (1/2)$ by Eq. (5).

The addition of Allee effects is important because it introduces a new criterion for invasion success (Lewis and Kareiva, 1993; Kot et al., 1996). Specifically, invasion success in model (4) requires the current population size to be at or near the carrying capacity over some minimum area. Under the sim-

plifying assumption that the area is circular, the radius R_{crit} of this minimum area is,

$$R_{crit} = \left(\frac{D}{2r}\right)^{1/2} \left(\frac{1}{(1/2) - a}\right). \tag{5}$$

This expression shows that increasing values of r reduce the critical invasion area, while increasing values of the dispersal parameter D or the Allee threshold a instead increase the critical invasion area. Notice in particular that initial areas with radius $R < R_{crit}$ fail deterministically.

For studies of invasion risks, the spatial spread model (4) thus includes the useful feature that there can be immigration events that do not lead to invasion success, even if the habitat patch is large enough. Populations that occupy areas with radius less than R_{crit} do not disappear instantaneously, however, and so may linger long enough to be rescued from extinction by later arrivals, the so-called “rescue effect” (Brown and Kodrick-Brown, 1977). Indeed, although most reaction-diffusion equations assume that populations are closed to immigration, allowing for deterministic, density-dependent immigration can lead to persistence even when the habitat patch is smaller than the critical area (Skellam, 1951; Kierstead and Slobodkin, 1953). Similarly, allowing for multiple immigration events dramatically increases the speed of range expansions by creating patchy invasion fronts (Shigesada and Kawasaki, 1997; Lewis, 1997). Useful models of invasions thus require both repeated, stochastic immigration events, and spatial structure, and here we construct such a model.

2. Methods

2.1. Modeling repeated immigration events

To build a spatially explicit model with repeated immigration, we add a stochastic perturbation term to Eq. (4). Because to our knowledge models of repeated immigration have not previously been considered, we begin by constructing temporal models of repeated immigration that clarify how it affects invasion risks in well-mixed, spatially homogeneous systems. In the absence of any population dynamics, repeated immigration can be modeled as a compound Poisson process of the form (Parzen, 1962),

$$X(t) = \sum_{n=1}^{N(t)} Y_n. \tag{6}$$

Here $\{Y_n\}$ is a sequence of independent, identically distributed random variables, each representing the number of individuals added by the n th introduction event, so that $X(t)$ is the sum of all the individuals introduced by time t . For this model, the expected number of individuals at time t is then,

$$E[X(t)] = \lambda t E[Y]. \tag{7}$$

where λ is the mean rate of occurrence of perturbations and $E[Y]$ is the mean number of individuals per introduction. Thus, $E[X(t)]$ can be calculated directly when the distribution of Y is known.

In the context of invasions, we also need to consider the effects of population growth (or decline), that change population size between introductions. In particular, we are interested in the case for which there is an Allee threshold a , so that populations with density below a decline, while those above the threshold increase. Given initial densities of zero, we would then like to calculate the expected time it takes for the population to exceed the threshold $E[T_a]$, given the opposing effects of introductions and population decline. To describe this process mathematically, we use the so-called “shot noise process”, which is essentially a modification of Eq. (6) to include negative exponential interarrival dynamics (Cox and Miller, 1965; Cox and Isham, 1980). Thus, we use a shot noise process to describe the case for which the number of organisms is initially zero, the number introduced at each event follows an exponential distribution, and for which population dynamics consist of exponential decline between arrivals. For such processes, Laio et al. (2001) showed that, starting from 0, the expected time $E[T_a]$ at which the population size first crosses the threshold a , known as the mean first passage time or “MFPT”, is

$$E[T_a(0)] = \frac{1}{\lambda} + \frac{\gamma a}{\lambda} \sum_{k=0}^{\infty} \frac{(\gamma a)^k \Gamma(1 + (\lambda/\beta))}{(k+1)\Gamma(1 + (\lambda/\beta) + k)} \tag{8}$$

Here λ is the Poisson rate parameter governing the average interarrival time, γ the inverse of the mean introduction size, β is the linearly increasing change in the rate of exponential population decline as population density increases, and $\Gamma(\cdot)$ is the gamma function. Because population growth is always positive after the Allee threshold a is exceeded at time T_a , $E[T_a]$ is effectively the expected invasion time in this nonspatial process. Here, we have assumed that sub-threshold Allee dynamics are described by exponential decay and in that case, Eq. (8) provides a useful summary of the underlying stochastic process, and serves as a simple case to which we can compare more realistic models. In particular, when $\lambda \ll \beta$, so that arrivals are very infrequent compared to the rate of population decline, we have the approximation,

$$E[T_a(0)] \approx \frac{(e^{a\gamma} - a\gamma)}{\lambda}. \tag{9}$$

In words, Eq. (9) says that starting from population size 0, the mean invasion time grows linearly with mean interarrival time ($1/\lambda$), but grows exponentially with decreases in mean introduction size ($1/\gamma$) and threshold size a . Conversely, as the product $a\gamma$ approaches 0, the mean invasion time approaches the constant ($1/\lambda$). As we will show, these results are qualitatively consistent with more realistic models.

2.2. Including more realistic population dynamics and spatial structure

Although these simple approximations are useful in guiding our intuition, invasions in nature are likely to involve additional complexities. In our more realistic models, we therefore consider Allee dynamics that change smoothly as we cross the Allee threshold, lognormally distributed introduction magnitudes, and spatial structure. Nevertheless, the underlying

model retains the shot noise process that we introduced above. Symbolically, we represent our spatial model as the randomly perturbed partial-differential equation,

$$\frac{\partial n}{\partial t} = rn(1-n)(n-a) + D\nabla^2 n + \sum_i h_{(x,y,i)}\delta(t-\tau_i) \quad (10)$$

with $n = (N/K)$ again being the population size scaled by the carrying capacity and $\delta(\cdot)$ being the Dirac delta function. The first two terms on the right-hand side of Eq. (10) are thus the same as in the deterministic Nagumo Eq. (4). The third term, involving the random variable $h_{(x,y,i)}$, which is also scaled by K , represents our triply stochastic immigration process. Specifically, like the compound Poisson process (6), introductions occur according to a Poisson process with rate parameter λ so that the interarrival times, τ_i , between successive immigration events are exponentially distributed with mean $(1/\lambda)$ (Ross, 1996). Consequently, the delta function ensures that population size is perturbed by introductions only at the random, exponentially distributed times, τ_i . Second, the magnitude of each immigration event h_t , where t is the introduction time, is a lognormal random variable, such that $\log h_t$ is a normal random variate with mean μ and variance σ^2 . Finally, the location \bar{x} at which an immigration event occurs is also a random variable, drawn from distributions that are discussed below. The introductions h_t are thus independent and identically distributed. Moreover, the magnitudes of the immigration events are independent of the Poisson process that determines when they occur, and of the spatial locations where they occur, making the magnitude, timing, and location of releases independent of each other.

For clarity we assume that initial population density is zero everywhere, so that the initial condition of Eq. (10) is $n(x, y; 0) = 0$. Also, because we are interested in the effects of reflecting (i.e., uncrossable) boundary conditions, we assume that individuals cannot leave the habitat. Mathematically, we write these conditions as

$$\frac{\partial n}{\partial x}(x_{\min}, y; t) = 0, \quad (11a)$$

$$\frac{\partial n}{\partial x}(x_{\max}, y; t) = 0, \quad (11b)$$

$$\frac{\partial n}{\partial y}(x, y_{\min}; t) = 0, \quad (11c)$$

$$\frac{\partial n}{\partial y}(x, y_{\max}; t) = 0. \quad (11d)$$

We have thus added stochastic immigration to Eq. (4), in the form of a term that prescribes the stochastic, multiple arrivals that are typical of invasion processes. Because we assume that dispersal is diffusive and that there is an Allee effect, and because Allee effects are best-known to be caused by an inability to find mates at low density, our model is perhaps most immediately applicable to sexually reproducing plankton or insects, organisms for which diffusion often provides a good description of dispersal (Okubo, 1980). For aquatic organisms in particular, we are essentially assuming that the organisms have little control over their dispersal and that diffusion and turbulence strongly influence spatial location (Koehl, 1991).

Viewed in this light, Eq. (4) can be thought of as a deterministic approximation to models that allow for stochastic variability in movement and population growth among individuals (Andow et al., 1993). There is, however, a key difference in the stochasticity that we introduce in Eq. (10). Specifically, the shot noise process represents changes at larger scales of time, space and density than the scales for stochastic population growth and dispersal that are approximated by Eq. (4). In other words, immigration events are assumed to be large relative to the instantaneous changes in population density that stem from continuous population growth and diffusive spread. Nevertheless, we are still interested in perturbations that are smaller than the Allee threshold, and so the immigration events in our model generally occur at population densities $h_t < a$ and initially occupy areas less than the threshold area R_{crit} . We are therefore interested in arrival densities that are smaller than the single propagules that MacArthur and Wilson (1967) defined as the minimum number of individuals required to successfully establish a population, but which can nevertheless accumulate in spatio-temporal patterns governed by Eqs. (10) and (11), and sometimes, eventually lead to invasion. Below, we explore how the components of the stochastic arrival process combine to influence the speed of the latter.

2.3. Simulating the models

Adding the repeated immigration process to the spatial model means that we must resort to simulation to analyze the model. Because our intent is to understand invasion risks, it is important to realize that the probability of invasion is not a useful metric, because invasions are certain over the long run, and so the probability of invasion is always 1. To quantify invasion risks, we therefore instead use \log_{10} of the time to invasion success, T_I as our dependent variable (Renshaw, 1991). In practice, we first specify the frequency, magnitude and dispersion of arrivals, and then we use the model to compute the expected (or mean) time to invasion success $E(T_I)$, read as, “the expected time to invade”, where the mean is calculated across stochastic realizations. We can then conclude that a given frequency, magnitude and dispersion of releases increases invasion risk if it leads to lower values of $E(T_I)$. In summary, we use frequency, magnitude and variability around the mean release location (\bar{x}, \bar{y}) as our independent variables, $E(T_I)$ as our dependent variable and Eq. (5) for the critical radius R_{crit} as our criterion for invasion success.

We solved Eq. (10) using standard numerical techniques for partial differential equation models (Press et al., 2002), Poisson processes in time (Renshaw, 1991) and generation of random variates (Evans et al., 2000). We solved the model for $T_{\text{max}} = 10^4$ time steps, with an integration time step of 0.01, or until the area occupied by the portion of the invading population that was within 5% of carrying capacity exceeded R_{crit} , whichever occurred first. Empirical tests of this cut-off rule showed that in every case, once R_{crit} was achieved, the invasion was self-sustaining and the organism went on to fully invade the space. In each computer simulation, we simulated the full model Eq. (10) 60 times for each parameter combination (see Table 1) and we report \log_{10} of the average invasion time $E(T_I)$ across the

Table 1 – Parameters, their descriptions and values used in our stochastic spread model, Eq. (10)

Type	Parameter	Meaning	Range
Deterministic	r	Population growth	1.6
	D	Diffusivity	0.1
	a	Allee threshold	0.01
	dt	Time step	0.01
Stochastic	x, y	Spatial coordinates	0–139
	$\sigma^2_{(x,y)}$	Variance in space	0.05–0.5
	μ	Mean introduction size	0.01–0.3
	σ^2	Variance in intro size	0.1
	λ	Introduction rate	0.01–0.3

Parameters that were varied are shown with the range of variation.

60 replicate invasions. We then explored how $E(\tau_i)$ changed with different parameterizations of Eq. (10). In addition, to explore how invasion risk varies with distance from a reflecting boundary, we explored how expected invasion time $E(\tau_i)$ varied as we changed the mean introduction point from the center of the plane, to near the edge of the plane, and finally to the corner of the plane. We use these latter simulations to consider how distance from a harbor affects the risk of invasion because of ballast-water discharge, on the reasonable assumption

that harbor edges represent impenetrable boundaries for aquatic organisms.

To show how frequencies and magnitudes of introductions affect invasion risks, we quantified invasion risk for 30 different frequencies of immigration events, as determined by the Poisson rate parameter λ , crossed with 30 different introduction magnitudes, as determined by the median immigration magnitude μ , for a total of 900 parameter combinations. λ , the rate of our Poisson process, ranged from 0.01 to 0.3. These values correspond to immigration events that occur, on average, once every 100 to once every three time steps, respectively. Median immigration magnitudes μ ranged from 0.01 to 0.3, thus representing 1–30% of carrying capacity K , or alternatively, in terms of the Allee threshold, a through $30a$. To generate interarrival times, we followed the algorithm presented by Renshaw, (1991, p. 38). Specifically, for each time unit in the simulation, we compared the elapsed time t since the last introduction to a random draw of the interarrival time τ . If $t \geq \tau$, we generated a new introduction with magnitude drawn from a lognormal distribution with median μ and shape parameter $\sigma = 0.1$. This density was then added to the population at a random location chosen from one of three different probability density functions, which are shown in Fig. 1 b–d. Each of these functions represents a different

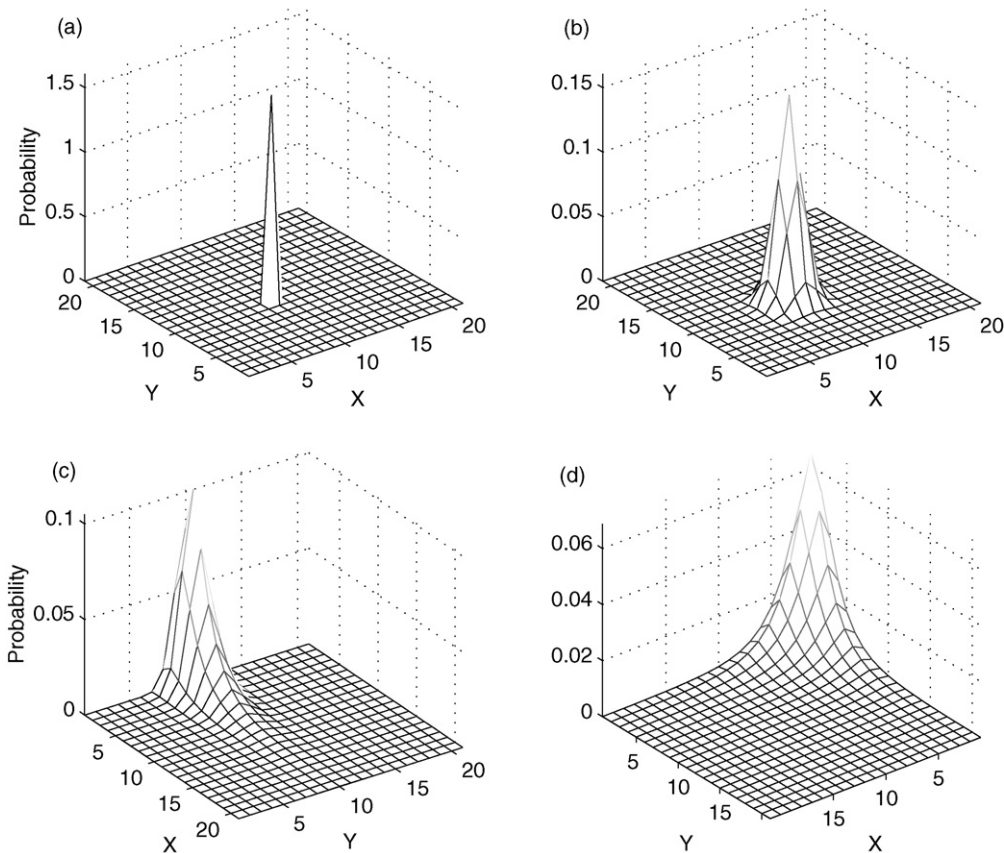


Fig. 1 – Illustration of bivariate pdfs for probabilities of releases in various regions of the plane. Note: actual simulation areas were 140×140 . (a) traditional central point release at (\bar{x}, \bar{y}) . Note that the variance around the release point is zero. In contrast, the cases that we considered incorporate non-zero variance, as follows. (b) central release, bivariate normal. (c) edge release, normal \times lognormal. (d) corner release, lognormal \times lognormal. For each figure, the normal variance was $\sigma^2 = 0.5$ and thus the lognormal shape parameter was $\sqrt{\sigma^2} = 0.7071$.

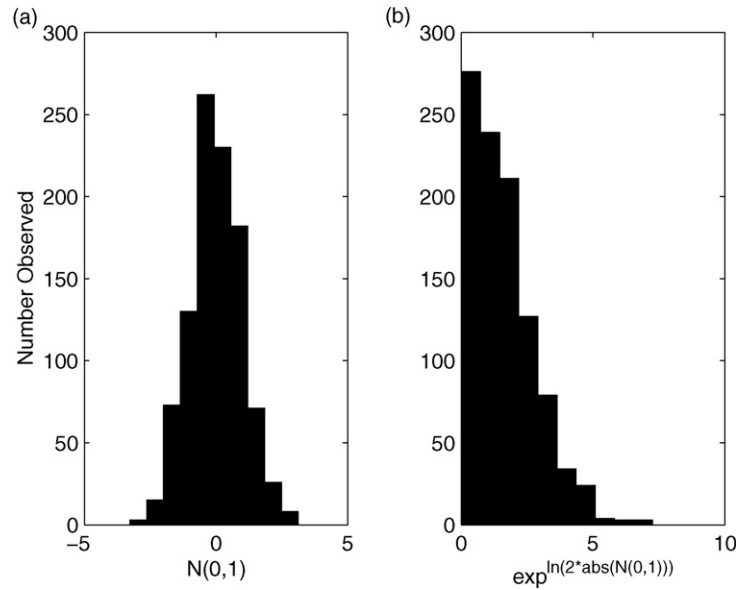


Fig. 2 – Comparison of spatial extent of histogram of realizations from (a) $N(0,1)$ and (b) a lognormal distribution with identical variance. Note that the spatial interval spanned by the two distributions is similar.

assumption about how far away immigration events are likely to occur from habitat boundaries, and how dispersed these events are.

For purposes of comparison, Fig. 1 a shows the typical assumption of previous invasion models, in which all individuals are released at the same time and place, far from any boundaries. Fig. 1 b then shows a case in which release sites are similarly far from boundaries, but for which immigration events are distributed randomly about a central point, such that the locations (x, y) were drawn from a bivariate normal distribution. Fig. 1 c next shows a case in which releases occurred near an edge of the plane, and thus close to one habitat boundary, so that x was chosen from a log-normal distribution, while y was normal as before. Finally, Fig. 1 d shows a distribution in which releases occurred in the corner, and thus close to two habitat boundaries, so that both x and y were chosen independently from a lognormal distribution. The latter two cases are intended to represent situations in which ballast discharge occurs close to a harbor. Because in practice harbor geometry is likely to be quite complex, in the interests of simplicity and generality we consider only the cases in which discharges are close to one or two boundaries of a square habitat, rather than attempting to approximate the true complexity of a particular harbor. In order to compare the effects of variance around (\bar{x}, \bar{y}) , we transformed σ^2 in the lognormal distribution so that, although the positions were all positive, they spanned the same spatial extent as corresponding variates from a normal distribution (see Fig. 2).

Eq. (5) for R_{crit} defines the radius of a circular area over which a potentially invasive population must be at or near carrying capacity K in order to succeed. We therefore used this formula in its original form to measure the area of our simulated populations in the center of the plane. At the edge of the plane, however, it is necessary to transform the formula to represent the radius of a half-circle that covers the same area

Table 2 – Conceptualization of our simulations evaluating the effects of frequency, magnitude and dispersion of introductions on time to invasion

Release frequency	Release sites	Release size
Low	Clustered	Small
	Dispersed	Large
High	Clustered	Small
		Large
	Dispersed	Small
		Large

as a circle of radius R_{crit} ,

$$R_{\text{crit}(1/2)} = \sqrt{2}R_{\text{crit}}. \quad (12)$$

Similarly, the formula for the minimum area of a population invading in the corner of the plane is,

$$R_{\text{crit}(1/4)} = 2R_{\text{crit}}. \quad (13)$$

Table 2 shows a conceptualization of our simulations.

3. Results

3.1. Non-spatial model and approximations

For purposes of comparison, we first consider a non-spatial version of our spread model, Eq. (10), by temporarily assuming that dispersal is so high that spatial structure is of no importance. To understand the results of this model, note first that the deterministic non-spatial Allee-effects model,

$$\frac{dn}{dt} = m(1-n)(n-a) \quad (14)$$

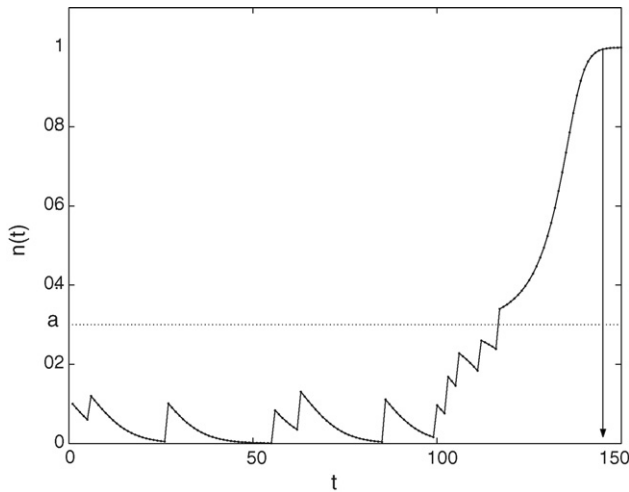


Fig. 3 – Population size $n(t)$ vs. t for a population growing according to Eq. (15) the stochastically perturbed non-spatial Nagumo equation. The Allee threshold was 0.3 (dotted line) and $n(t)$ was scaled so that carrying capacity was 1. Arrivals occurred according to a Poisson process with rate parameter $\lambda = 6$ giving a mean interarrival time of ≈ 17 time units. The arrow marks the time at which the population was within less than 1% of the carrying capacity.

has locally stable equilibria at $n^* = 0,1$ and an unstable equilibrium at $n^* = a$ (Kot, 2001). When we add stochastic immigration to this model, as we did to our spatial model (10), immigration events will move the population away from 0. Incorporating the stochastic process into Eq. (14) gives,

$$\frac{\partial n}{\partial t} = m(1 - n)(n - a) + \sum_i h_i \delta(t - \tau_i) \tag{15}$$

where the details of the stochastic term are identical to those described for Eq. (10), although obviously without the spatial component \bar{x} .

If the immigration events in Eq. (15) are large enough and frequent enough, eventually they push the population density above the Allee threshold a . Fig. 3 illustrates this process for a single realization of this model, starting at $n_0 = 0,1$, below the Allee threshold of $a = 0,3$. Immigration events of random magnitude then occurred at random times, seen as vertical lines in the figure. Until about time 100, however, these perturbations were small enough, and infrequent enough, that the population stayed below the Allee threshold. At around time 100, a series of rapid arrivals overwhelmed negative population growth and pushed the density up near the threshold, and at around time 115, the population size exceeded the threshold and thereafter increased deterministically to the carrying capacity.

The process described by Eq. (15) is similar to that of the shot noise process that Laio et al. (2001) used to derive the expected invasion-time Eq. (8). The main differences are first that, for the Nagumo model, the per-capita population growth rate below the Allee threshold declines with distance below the invasion threshold, whereas for the shot noise process, the analogous rate of change is constant below the threshold.

Nevertheless, Fig. 4 a–c shows that exponentially declining population density is a good approximation to the more complex population growth function of the Nagumo model when population density is below m , the density for which population growth rate is at a minimum. Second, for the perturbed Nagumo model, the introduction magnitudes are lognormally distributed, while for the shot noise process they are exponentially distributed. Fig. 4 d shows that an exponential density function is at least a reasonable approximation to a lognormal density function when the standard deviation of the lognormal is near 1, because of structural similarities in the pdf formulae for the two distributions when $\sigma = \sigma^2 = 1$ (see, for example, Hastings and Peacock, 1975). This figure also illustrates, however, that agreement between the two distributions disappears as lognormal variability increases or decreases.

Despite these differences, the expected time to cross the invasion threshold as predicted by Eq. (8) for the shot noise process is often fairly close to the mean time to cross the invasion threshold for the Nagumo model (Fig. 5) when the standard deviation of the lognormal arrival sizes is $\sigma = 1$. To calculate the MFPTs for the Nagumo model, we numerically solved Eq. (15) and averaged the Allee threshold crossing times. The approximation does rather poorly when the mean introduction size is small and the frequency of introductions is low (top left of panel 5a), but is often reasonably accurate for larger introduction sizes (circles and squares in right side of panel 5a) and higher frequencies of introduction (circles and squares in panel 5b). The figure also shows that agreement with the approximation is greatly reduced when variance in the introduction magnitude differs from $\sigma^2 = 1$ (triangles in panels 5a and b). This is apparently because increasing variance leads to a larger number of extremely small arrivals relative to the exponential case, as illustrated in 4d, and thus to an increase in the mean time to invasion.

Another statistic of interest for the arrival process described by Eq. (15) is the number of introductions until the threshold is crossed. Fig. 6 a shows that, as expected, this number decreases as introduction size increases. At first, however, it decreases faster than exponentially, but then slows dramatically. Consequently, the shape of the curve is better fit by a “power-law”-type function than by an exponential. In other words, the effect of increasing introduction size becomes weaker as introduction size increases. This is similar to the predictions of Eq. (9), in which a vanishing magnitude parameter, and hence increasing mean magnitude, led to a constant invasion risk.

3.2. Effects of space

The basic dynamic captured in Fig. 3 is observed in the spatial model as well, but with the added complication that local populations that are initially above the Allee threshold a may nevertheless decline because of diffusion. As a result, the population must be near its carrying capacity over an area of radius at least R_{crit} , as in the single-release model, Eq. (5) (Lewis and Kareiva, 1993). This in turn means that the population may cross the Allee threshold many times before becoming established, whereas in the nonspatial case, the population need only cross the Allee threshold once in order to invade.

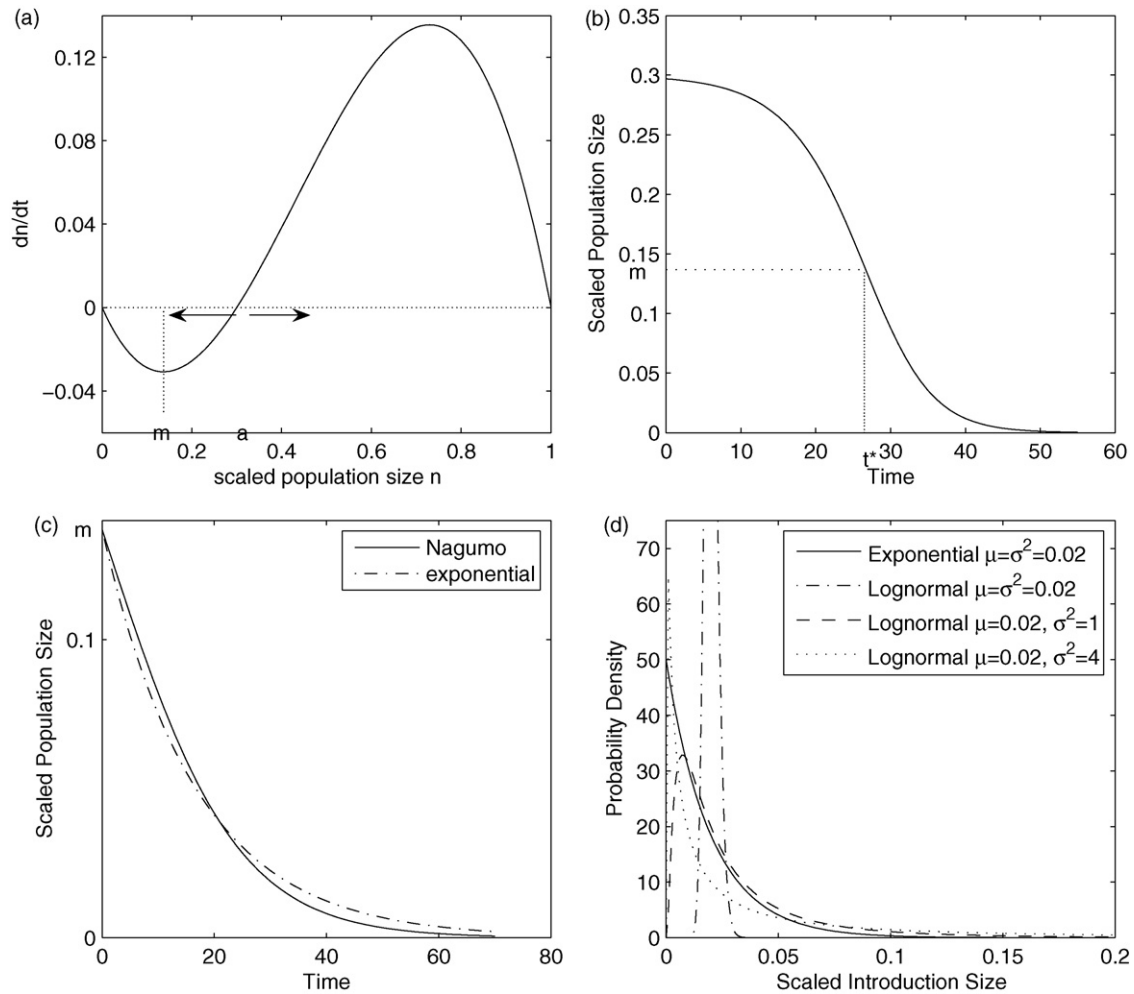


Fig. 4 – (a) Population growth rate vs. population size for the nagumo equation. Notice the unstable equilibrium at a , below which population growth is negative. The point m is an inflection point below which population growth rate decreases at a decreasing rate, because there are fewer individuals on which the rate acts. (b) Population size vs. time for a population started at $0.99a$. Population decline begins slowly, accelerates, reaches a maximum at m , then begins to slow again. Population decline beyond t^* resembles exponential decay used by Laio et al. to describe inter-shot dynamics. (c) Best fit (in the least squares sense) of an exponential decay model fit to our nagumo model with $n_0 = m$, showing that below m , nagumo dynamics can be approximated by exponential decay. (d) Solid line: exponential pdf with equal mean and variance $\mu = \sigma^2 = (1/\gamma) = 0.02$, used to generate the magnitude of shots. Dash-dotted line: lognormal pdf with equal mean and variance $\mu = \sigma^2 = 0.02$. Dotted line: lognormal pdf with mean $\mu = 0.02$ and variance $\sigma^2 = 1$. Dashed line: lognormal pdf with mean $\mu = 0.02$ and variance $\sigma^2 = 2$. Because of similarities in the pdf formulae, lognormal pdfs with $\sigma^2 = 1$ are most similar to exponential pdfs with the same mean.

To illustrate this effect, Fig. 6 b shows that for a wide range of mean introduction sizes in the spatial model, population levels cross the Allee threshold hundreds of times on average (note the difference in vertical axis scale as compared to panel 6a), only to fall below the threshold again as individuals diffuse away from the release site (dashed lines). Even when introduction magnitudes are sufficiently large that the invasion is eventually successful (solid lines), densities repeatedly fall below the threshold and undergo negative population growth until “rescued” by later arrivals. Thus, the eventual success of the spatial invasion depends to a far larger extent on the rescue effect than does the nonspatial case. This effect is more pronounced when introductions are dispersed (squares)

instead of released at a single location (circles). Indeed, the number of threshold crossings first increases when releases are dispersed as larger release numbers lead to an increase in the number of crossings from below the threshold. As mean introduction size increases further, threshold crossings decrease because arrival magnitudes are sufficient that local populations fall below the threshold from above less often.

Fig. 6 b can be used to illustrate the difference in MFPT between the nonspatial and spatial models. For all the spatial simulations represented in the figure, the Allee threshold $a = 0.01$, which means that the smallest mean introduction size used in our spatial simulations was ten times the threshold. In

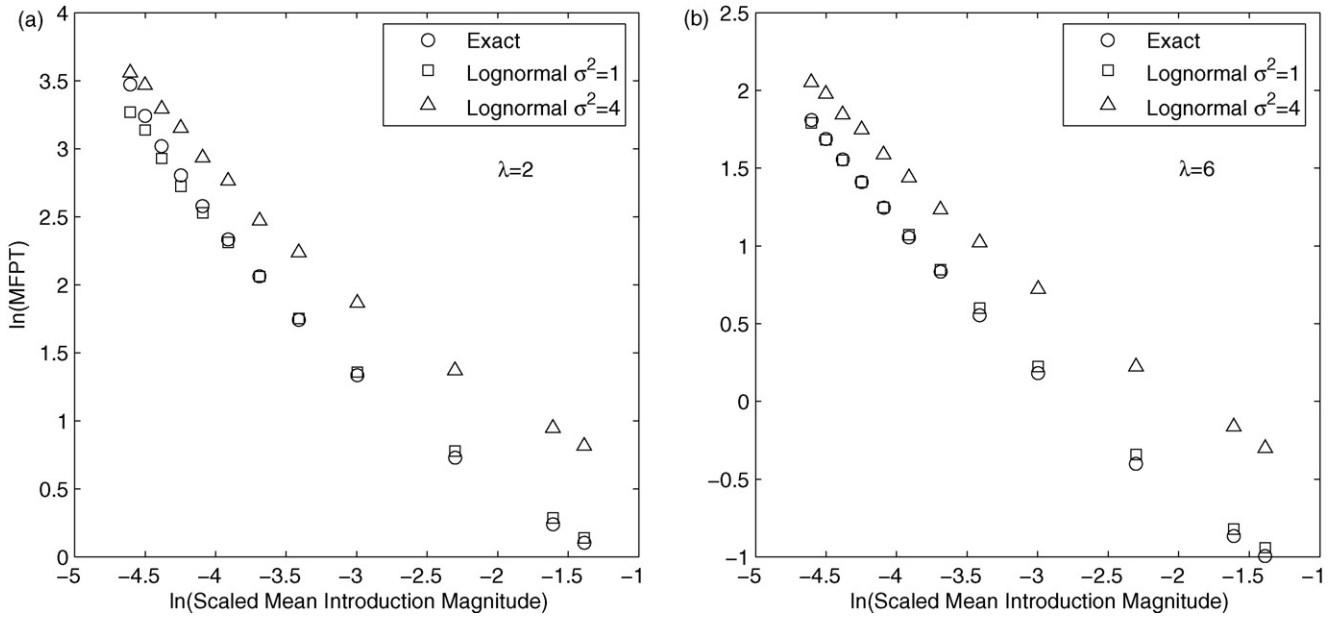


Fig. 5 – Natural logarithm of MFPT vs. mean introduction magnitude. Mean introductions ranged from 0.01 to 0.25, while the first passage threshold was 0.3. (a) $\lambda = 2$ yielding an arrival every 0.5 time units on average. (b) $\lambda = 6$ yielding arrivals every 0.17 time units.

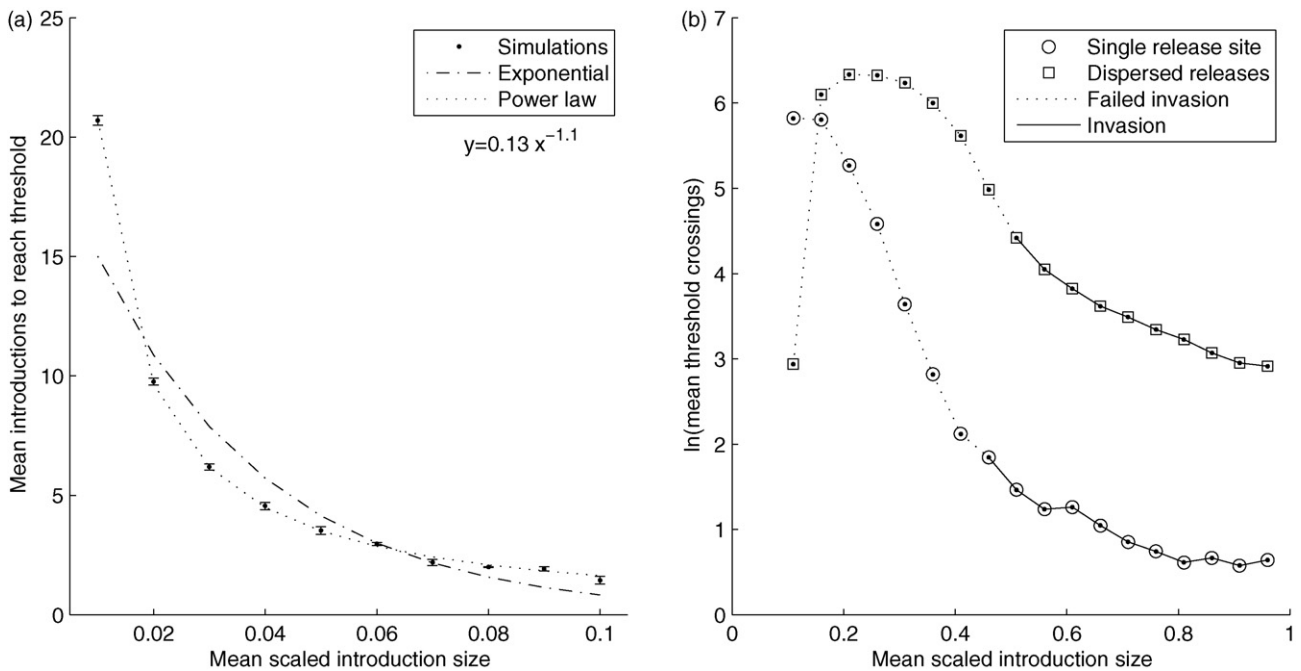


Fig. 6 – (a) Mean number of introductions before crossing the Allee threshold as mean introduction size varies. The dashed line is the best fit exponential approximation to the simulated data while the dotted line is a power law. The decrease in mean introduction number is first faster than exponential, then at high mean introduction level is slower than exponential. Mean introduction number asymptotically approaches 1. (b) Natural logarithm of the number of threshold crossings for the fully spatial model (10) as mean introduction size varies. At relatively small introduction sizes (dotted lines) crossing are numerous, but do not lead to invasion by T_{\max} . As mean introduction size increases, crossings decrease because population density no longer falls below the threshold as often, but diffusion away from introduction sites still prevents successful invasion. These effects are more pronounced when introductions are dispersed (squares) as opposed to focused at a single release site (circles). At high mean introduction sizes, invasions are successful and occur with fewer excursions below the threshold (solid lines).

other words, for every introduction size we simulated with our spatial model, the nonspatial model would deterministically proceed to carrying capacity after the first introduction. In contrast, the models that included spatial dynamics failed to invade until mean introduction sizes were 0.51 when focused at a single release site and 0.56 when dispersed around a central release site. Using the first mean introduction size that allowed successful invasion under all three treatments of space (i.e., none, concentrated and dispersed), 0.56, we can compare the expected time to invade. In the nonspatial model, this is simply the expected time until the first introduction or $(1/\lambda) = 0.17$ scaled time units. The spatial models fell below the threshold repeatedly before finally invading, however, and even then depended on the combination of positive local population growth and subsequent introductions over long periods of time in order to exceed the invasion criterion of Eq. (5). When the introductions occurred at a single location this process involved an average of 3.45 threshold crossings and took 9448 scaled time units. When the introductions were instead scattered around the central location point according to a bivariate normal with mean $\mu = 0$ and variance $\sigma^2 = 1.2$ the process involved 57 threshold crossings and took 9453 time units. Of course, in practice the magnitude of the nonspatial overestimation of MFPT depends on the diffusion constant D in Eq. (10).

To show why spatial dispersion affects invasion time, in Figs. 7 and 8 we show snapshots of single realizations, for the cases when releases occur in the center or on the edge respectively, with the top and bottom rows of each figure representing low and high variance of release location, respectively (note the differences in z-axis scale in each graph). These realizations thus show that increasing the variability around (\bar{x}, \bar{y}) , thereby increasing the dispersion in immigration events, increases the time that it takes for population density to build to high levels. Increasing dispersion thus reduces invasion risk. This effect occurs irrespective of whether the release location is in the center or at an edge, but it is much stronger when releases are far from boundaries. This is because boundaries have an aggregating effect on randomly spreading populations, and so act to reduce dispersion.

Because the model is stochastic, however, single realizations do not adequately represent how quantitative changes in immigration parameters affect invasion times. To systematically illustrate how spatial dispersion and distance from boundaries affect the invasion process, we plotted contours of average invasion time $E(T_I)$ as functions of frequency and magnitude of immigration events, for different variances of immigration events and different average distances from boundaries (Fig. 9). Note that cases for which $E(T_I) = 4$, as in the isobars furthest to the bottom-left in each panel, are equivalent to invasion failure, because the maximum time of any given realization was 4 on a \log_{10} scale. The figure shows that, as one would expect, increases in either the frequency or the magnitude of introductions lead to shorter invasion times. The interesting part of the figure is instead that the effects of frequency and magnitude are strongly affected by changes in the distribution of introduction locations, as in Fig. 8. For example, Fig. 9 a shows the case when releases take place in the center of the plane and the variance around (\bar{x}, \bar{y}) is relatively large, $\sigma^2 = 0.5$, whereas Fig. 9 b shows the corresponding result when

the variance is relatively low, $\sigma^2 = 0.05$. Comparison of the two shows that reducing the variance in release locations leads to dramatic increases in invasion risk. Fig. 9 c and d similarly show edge and corner releases, respectively, both with large variance $\sigma^2 = 0.5$. Comparison of these two panels to panel 9a shows that invasion risks are much higher when introductions occur close to habitat boundaries.

Fig. 10 shows how $E(T_I)$ changes with increases in spatial dispersion of introductions, σ^2 . Fig. 10 a represents center releases, Fig. 10 b represents edge releases and Fig. 10 c represents corner releases. In the center releases, at low (closed circles, hidden by asterisks) and intermediate (asterisks) frequency and magnitude, no invasions occurred before our simulations ended, at $T_{\max} = 10^4$ time units (4 on the \log_{10} scale of our graphs). At the highest frequencies and magnitudes, however, and with extremely low variances, invasions occurred on average at $E(T_I) \approx 3.4$ time units. As the variance was increased, for this level of frequency and magnitude, the log of $E(T_I)$ increased to approximately 3.6, which is equivalent to an increase of about a factor of 1.6. When releases occurred near boundaries, low levels of frequency and magnitude still did not lead to invasion before the simulations ended, but both intermediate and high levels of frequency and magnitude often led to successful invasions. The effect of increasing σ^2 was thus to substantially increase $E(T_I)$, thereby reducing the risk of invasion. At the edge (Fig. 10b), even intermediate frequency and magnitude combinations sometimes failed to lead to invasion, if the dispersion of introductions was large ($\sigma^2 = 0.5$). In the corner (Fig. 10c), all low-valued combinations again failed, but the intermediate and high combinations always led to invasion.

4. Discussion

As in previous work (Drake and Lodge, 2006), our model shows that higher frequencies and magnitudes of immigration events lead to shorter invasion times and thus higher risks of invasion. Reassuringly, invasion rates in nature also increase with increasing frequencies and magnitudes of introductions (Crawley et al., 1989; Veltman et al., 1996; Williamson and Fitter, 1996; Kolar and Lodge, 2001; Marchetti et al., 2004; Cassey et al., 2004). For example, analyses of bird introductions from New Zealand Veltman et al. (1996) and worldwide Cassey et al. (2004) suggest that the probability that a particular species became established increased with the number of introductions and the number of individuals in each introduction. Studies of intentional introductions of economically important organisms have shown similar effects of both frequency and magnitude (Hopper and Roush, 1993; Grevstad, 1999; Shea and Possingham, 2000). Depending on the biology of the species being introduced, successful introduction strategies in such cases may involve many small introductions or a few large introductions, and there are good examples of successful releases using each strategy (Crawley et al., 1989). The near equivalence of these alternatives is in qualitative agreement with the results of our model over a large range of parameters, yet recommendations in the early biological-control literature instead suggested that biocontrol agents should be introduced in the form of a small number of releases

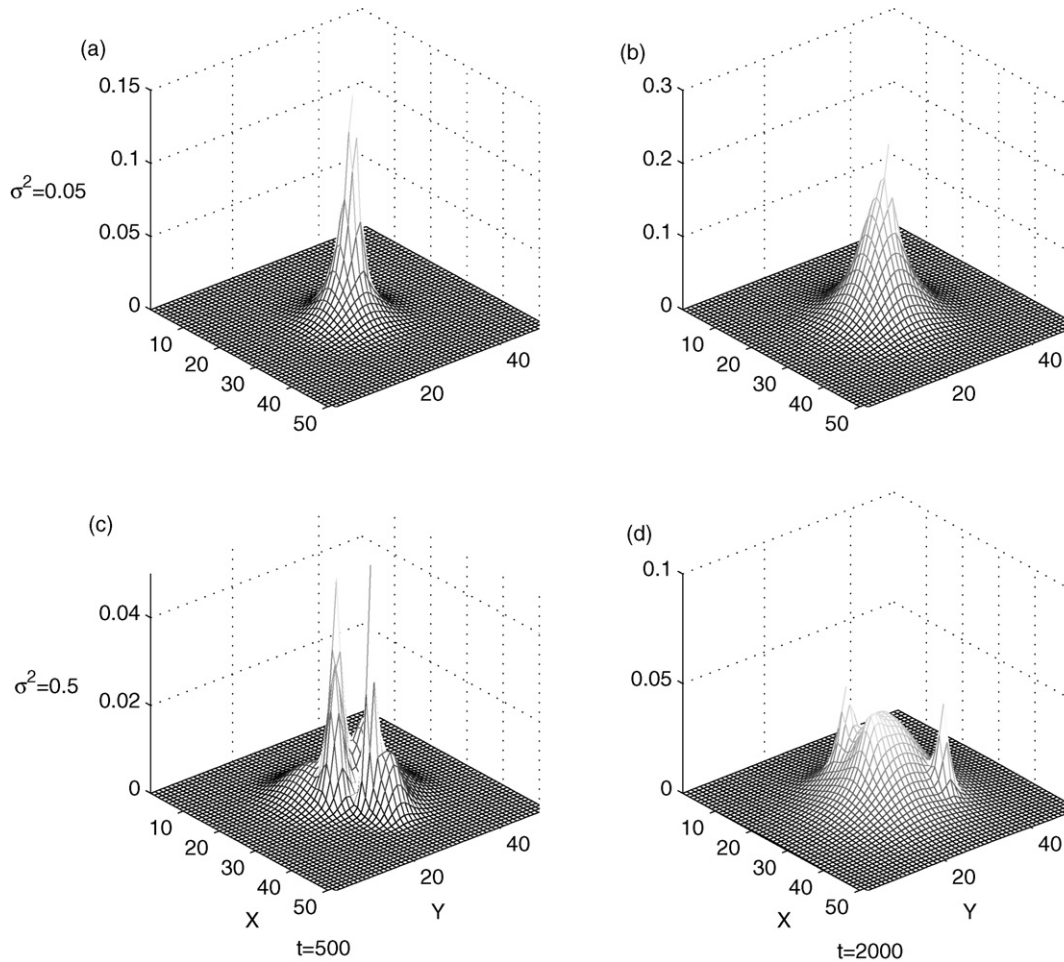


Fig. 7 – Comparison of changes in population density over time for two levels of variability around (\bar{x}, \bar{y}) in center of the plane. (a) and (b) are low variability $\sigma^2 = 0.05$, (c) and (d) are high variability $\sigma^2 = 0.5$. (a) and (c) are results at time $t = 500$. (b) and (d) results from time $t = 2000$. Note the difference in z-axis scale between the top and bottom panels revealing that higher variability leads to slower population accumulations.

of many organisms (DeBach and Bartlett, 1964). Explicit mathematical models can thus provide a useful guide to managing invasions, although additional practical considerations, such as collecting or rearing of organisms, may influence such decisions.

A result that is less obvious without our model, however, is how dramatic an effect spatial structure has on invasion risk. If arrivals occur at high enough frequency and magnitude, then eventually the Allee and invasion thresholds will be exceeded, but only if arrivals occur close together in space. This is because the Allee effect prevents invasions from occurring unless the population is pushed over the Allee threshold in a large enough area, specifically one with radius greater than R_{crit} . Immigrants must arrive in close spatial and temporal proximity because that is the only way for such arrivals to overwhelm the effects of local population decline due to diffusion and negative population growth. In other words, low spatial dispersion increases the strength of the rescue effect (Brown and Kodrick-Brown, 1977). Consideration of spatial structure thus makes clear that the local frequency of introductions is more relevant than the

global frequency, and shows that increases in spatial dispersion can dramatically reduce invasion risks. Our results also show that the location of releases relative to boundaries can have large effects on invasion times. This effect arises through an interaction between diffusion and reflecting boundaries, which causes densities in corner releases to be four times what they are in center releases, and densities in edge releases to be twice what they are in center releases (Rohlf and Schnell, 1971). Reflection of individuals away from boundaries and back toward the population center thus leads to faster invasion times because of reduced spatial dispersion.

These effects suggest a strategy of practical importance for reducing invasion risk from ballast-water discharge. Ballast-water discharges that take place in harbors correspond to releases that occur close to boundaries and close together in space, whereas discharges that take place in open water correspond to releases that occur far from boundaries, and potentially far apart in space. The strong reductions in invasion risk that occur in our model as distances from the boundaries increase and as spatial dispersion increases sug-

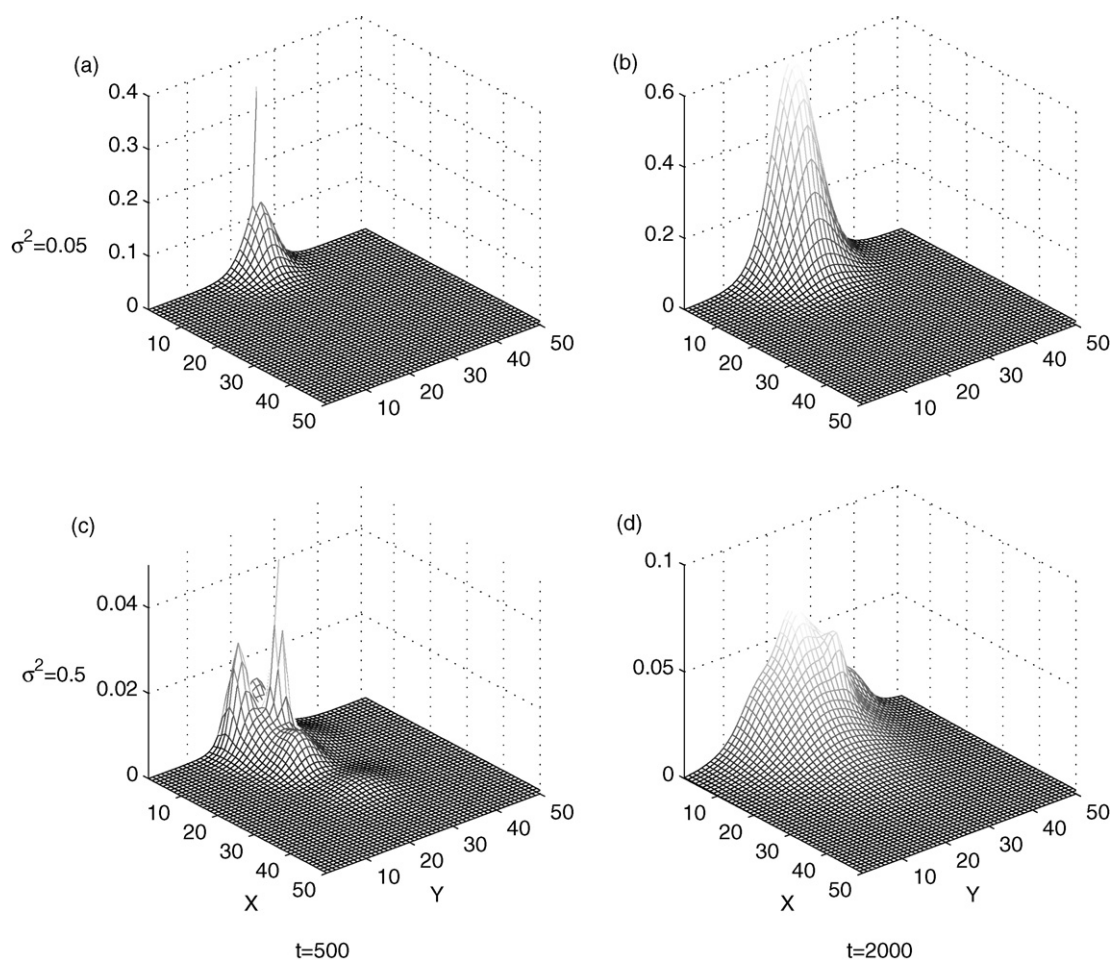


Fig. 8 – Comparison of changes in population density with time for the two levels of variability around (\bar{x}, \bar{y}) near a reflecting boundary. (a) and (b) are low variability $\sigma^2 = 0.05$, (c) and (d) are high variability $\sigma^2 = 0.5$. (a) and (c) results at time $t = 500$. (b) and (d) results from time $t = 2000$. Note differences in z-axis scale.

gest a clear policy for reducing this risk. Specifically, each discharge event should take place as far as possible from harbors and as far as possible from other discharge events. In fact, there is strong empirical evidence that plankton aggregate in harbors (McNeill et al., 1992; Floerl and Inglis, 2003), suggesting that the effects seen in our models likely occur in nature as well. Indeed, the importance of boundaries in our model may partially explain why regions like the Great Lakes of North America, with their many commercial harbors, are hotbeds of invasion (Ricciardi and MacIsaac, 2000; Vanderploeg et al., 2001). We emphasize, however, that similar effects may occur in terrestrial systems, in which many species are reluctant to cross habitat boundaries (Stamps et al., 1987; Haas, 1995; Ries and Debinski, 2001).

The strategy of reducing invasion risk by dispersing introductions relies on the assumption that Allee effects are important for invading species. Although undoubtedly there are many organisms for which Allee effects are of minor importance, the literature supports the notion that increased dispersion leads to reduced invasion risks. For example, some bird introductions in New Zealand failed despite numerous

introductions, at least partly because birds were introduced in widely dispersed locations (Veltman et al., 1996). If Allee effects are unimportant for a particular invader, however, our proposed strategy of increasing spatial dispersion might instead increase the area within which the invasion occurs (Moody and Mack, 1988; Fagan et al., 2002). Evaluating invasion risk under such circumstances would obviously require a different model.

Perhaps the most unexpected result from our analysis is the repeated appearance of saturating effects in our approximations and simulations. Eq. (9) revealed that as the combination $a\gamma$, the threshold level and the parameter affecting introduction sizes respectively, approaches 0, the expected time required to cross the threshold approaches the constant, $(1/\lambda)$. Because Eq. (9) assumes λ is small in the first place, this is reassuring, because it means that the expected time will be large, a very reasonable expectation for processes involving very small shocks. More generally, however, it is an instance of one element of the process being at an extreme and the system subsequently becoming insensitive to it. This general feature arose in two other contexts in our study. First, Fig. 6 a showed that as mean introduction size increases, the num-

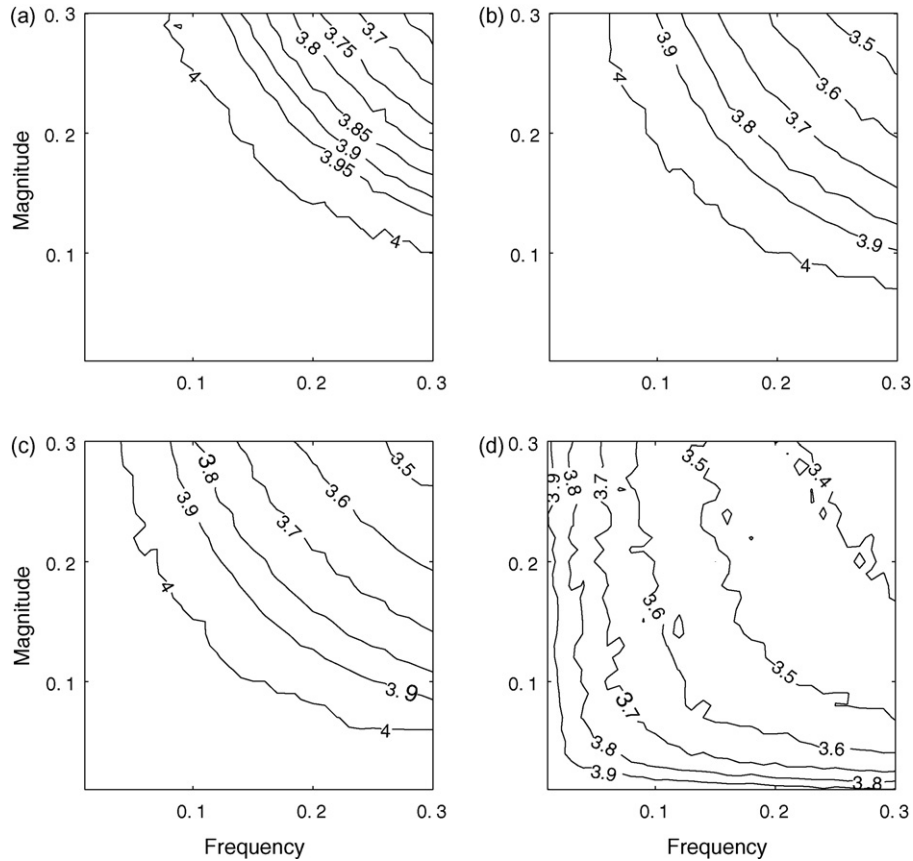


Fig. 9 – \log_{10} isobars of average time to invasion with $\sigma^2 = 0.5$ except where noted otherwise. (a) Central release, (b) central release with variance $\sigma^2 = 0.05$, (c) edge release and (d) corner release. Comparing (a) and (b) reveals that decreasing the dispersion of a release scenario decreases the mean time to invasion $E(\mathcal{T})$ so that (b) is quite similar to (c). This means that decreasing dispersion around a center release yields contours similar to an edge release with higher dispersion. (d) shows the pronounced decrease in $E(\mathcal{T})$ when releases occur near a corner.

ber of introductions required before the population exceeded the threshold decreased at a decreasing rate. The maximum mean introduction size we explored was (1/2) the threshold and so it is easy to see why in this case the expected number of introductions should approach 1, because on average, the first introduction will already exceed the threshold. Saturating effects appeared in our results again in the fully spatial process, and again they appeared at extreme values of the parameters governing the process. Specifically, when introductions are on average very infrequent, but large, increasing the mean size of the introductions has little effect on the ultimate time to invade. Conversely, when introductions are instead extremely small, but quite frequent, increasing the rate of introductions has little effect (see Fig. 9d). This suggests that if one component of the process can be maintained at a low level, then there may be latitude in the level of the others. Thus, the recommendations that emerge from our analysis inform us about how to reduce risk, but also reveal that attempting to reduce risk is a realistic goal because strict control of a single element of the process, such as local frequency, may be sufficient.

In conclusion, although invasion processes and management strategies are generally more complex than can be described easily by any single model (Smith et al., 1999;

Endresen, et al.; Marchetti et al., 2004), our model nevertheless represents an important first step towards understanding the effects of repeated introductions in a spatial context. Indeed, this model can be built upon to also consider the effects of evolution in the invader’s original community (Reid and Orlova, 2002), niche opportunities in the new community (Shea and Chesson, 2002), release from native enemy complexes (Williamson and Fitter, 1996; Clay, 2003)(but see Maron and Vilà, 2001), and other species interactions (Mitchell and Power, 2003). There is also good evidence that repeated introduction failures may finally become successful once adaptation to the new environment occurs (Lee and Remfert, 2003). In such cases, repeated introductions may instead reduce invasion risks, by reducing fitness in the new environment through gene flow. Also, in addition to diffusion, physical processes may lead to directional flow or “advection” (but see Lewis and Kareiva, 1993). Here we have forsaken some of these details to focus on features that may be controlled by managers, or tested in natural invasion processes. Nevertheless, it seems likely that the qualitative effects of frequency, magnitude, and location of immigration events in our model would not change by very much if we incorporated additional details. Our model may therefore serve as a useful guide for management decisions. Moreover, including additional details does

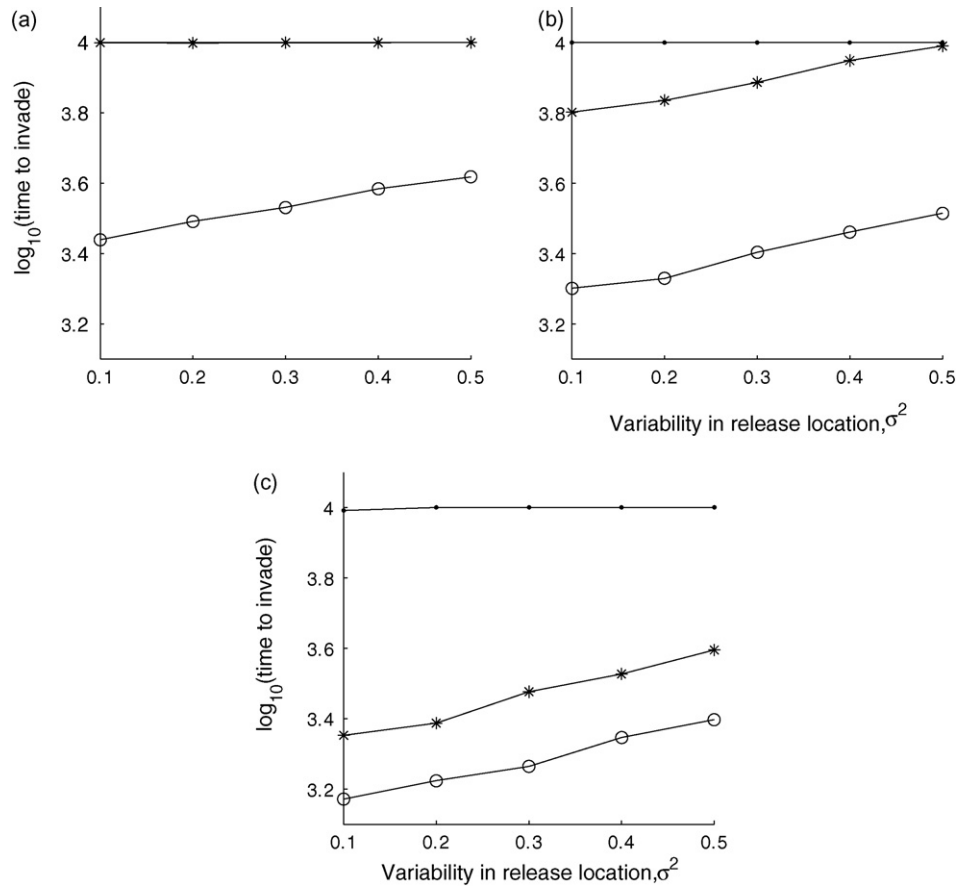


Fig. 10 – $E(T_1)$ vs. variance σ^2 around mean release location (\bar{x}, \bar{y}) . Low frequency-magnitude combinations (0.01–0.01, solid circles) intermediate combinations (0.15–0.15, asterisks) and high combinations (0.3–0.3, open circles). Releases were in (a) center, (b) at edge, or (c) in corner.

not always produce a more useful model. For example, we have assumed that the environment is homogeneous, even though boundaries in aquatic habitats often differ from habitat centers in temperature and insolation and in having wave action and periodic desiccation, any of which could alter population growth rates and thus invasion times (Connell, 1961; Hunt and Scheibling, 2001). Rouget and Richardson (2003) and Parker (2000), however, have suggested that propagule pressure tends to be reduced by such effects, whereas Frenot et al. (2001)'s results, and several references in Mack et al. (2000), suggest exactly the opposite. Adding the effects of physical variability at the boundaries to our model would thus be premature.

Complete elimination of accidental species introductions is impossible, but reducing the chance that such introductions will lead to successful invasions is surely worthwhile, and according to our results, does not require unrealistic levels of control on multiple facets of the process. Instead, avoiding high risk scenarios, such as concentrating releases in corners, and manipulating either local frequency through introduction dispersion, or magnitude, can dramatically reduce risk. Indeed, the early stages of introductions present the best opportunity for reducing the impact of invasions (Mack et al., 2000; Marchetti et al., 2004), and for that reason most management efforts have focused on controlling rather than preventing invasions (Ashton et al., 1989). Ships will thus

continue to arrive in harbors of the North American Great Lakes from the Ponto-Caspian region in Europe (Grigorovich et al., 2002), and they will continue to accidentally carry nonnative species (Smith et al., 1999; MacIsaac et al., 2002), despite the risks (Mack et al., 2000). Given that ships arrive on predictable schedules (Endresen, et al.), and at known locations, however, our model should be useful for devising protocols that minimize invasion risks, through the manipulation of the frequency, magnitude and dispersion of introductions. Additionally, because of the generality of our approach, straight-forward modifications to, and extensions of, this framework can yield useful predictions in other systems.

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