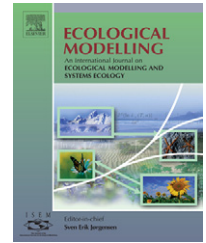


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# Immigration events dispersed in space and time: Factors affecting invasion success

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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  $\nabla^2$  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,  $R_{\text{crit}}$ , 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-

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