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Spatial dynamics of invasion: the geometry of introduced species

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Abstract

Many exotic species combine low probability of establishment at each introduction with rapid population growth once introduction does succeed. To analyse this phenomenon, we note that invaders often cluster spatially when rare, and consequently an introduced exotic's population dynamics should depend on locally structured interactions. Ecological theory for spatially structured invasion relies on deterministic approximations, and determinism does not address the observed uncertainty of the exotic-introduction process. We take a new approach to the population dynamics of invasion and, by extension, to the general question of invasibility in any spatial ecology. We apply the physical theory for nucleation of spatial systems to a lattice-based model of competition between plant species, a resident and an invader, and the analysis reaches conclusions that differ qualitatively from the standard ecological theories. Nucleation theory distinguishes between dynamics of single- and multi-cluster invasion. Low introduction rates and small system size produce single-cluster dynamics, where success or failure of introduction is inherently stochastic. Single-cluster invasion occurs only if the cluster reaches a critical size, typically preceded by a number of failed attempts. For this case, we identify the functional form of the probability distribution of time elapsing until invasion succeeds. Although multi-cluster invasion for sufficiently large systems exhibits spatial averaging and almost-deterministic dynamics of the global densities, an analytical approximation from nucleation theory, known as Avrami's law, describes our simulation results far better than standard ecological approximations.
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1. Introduction

The breakdown of biogeographic barriers allows some introduced species to reshape communities (Drake et al., 1989; Hengeveld, 1989; Rosenzweig, 2001) and threaten local biodiversity (Kolar and Lodge, 2002; Pimm, 1987), especially in nature reserves (Usher et al., 1988). Most introductions fail to initiate invasion (Lonsdale, 1999; Simberloff, 2000). However, an exotic's abundance often increases rapidly once introduction does succeed (Christian and Wilson, 1999; Sax and Brown, 2000; Shigesada and Kawasaki, 1997), particu-

larly when an established exotic has an ecological advantage promoting its growth (Callaway and Aschehoug, 2000; Mack et al., 2000; Pimentel et al., 2000).

Veltman et al. (1996) analyse 496 documented, intentional introductions of 79 bird species to New Zealand. The strongest predictor of establishment is repeated introduction. Most species introduced four or fewer times never became established. Despite multiple introduction attempts for most species, only 20% of the birds ever became established (Veltman et al., 1996). Repeated failure of introduction, followed by ecological success once established, appears characteristic of both natural dispersal and human-mediated introduction (Sax and Brown, 2000). The seeming inconsistency between repeated failure of the introduction process and an invader's rapid growth once established motivates our study.

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Despite the observed uncertainty of introduction, spatial models for invasion processes typically yield deterministic criteria for growth when rare (Andow et al., 1990; Caraco et al., 2002; Chesson, 2000; Kot et al., 1996; cf. Lewis and Pacala, 2000). An invader's growth or decline will ordinarily depend on locally structured interactions (Ellner et al., 1998; Wilson, 1998), so that chance mechanisms should often govern the population dynamics of rarity (Durrett and Levin, 1994a). Our results show how introduction rates and the size of the environment can generate random variation in an invader's success or failure, through effects on the invader's spatial clustering.

Our analysis specifically distinguishes single-cluster growth from multi-cluster growth of a rare exotic competing with a resident plant species through clonal propagation (Harada and Iwasa, 1994; Inghe, 1989). Simulating the model reveals interesting variation in the waiting time for successful introduction and subsequent spread of the exotic. To characterize our particular results and, more importantly, to offer a new perspective on the population dynamics of invasion, we invoke the physical theory for homogeneous nucleation of spatial systems (Avrami, 1940; Johnson and Mehl, 1939; Kolmogorov, 1937). Originally formulated to model processes such as crystallization, nucleation theory readily addresses ecological clustering generated by local propagation in viscous populations (Gandhi et al., 1999). We emphasize that under multi-cluster growth of the exotic species, the dynamics of competition for space, specifically the time-dependent decay of the resident's density, follows a powerful analytic approximation referred to as Avrami's law (Duiker and Beale, 1990; Ishibashi and Takagi, 1971; Ramos et al., 1999; Rikvold et al., 1994).

2. Spatial model for invader-resident competition

Individual plants typically interact more with nearby than with distant individuals (Rees et al., 1996; Tilman et al., 1997). Consequently, an introduction's success or failure can depend on effects regulated by neighborhood, rather than global, densities (Higgins et al., 1996; Wilson, 1998). We model two clonal species, a resident and an invader, competing for space in a lattice environment. Each of the L^2 lattice sites is either empty or occupied by a single plant; a site represents the minimal space an individual (ramet) requires. Competition for space is preemptive; a site already occupied cannot be colonized by either species until the occupant's mortality opens the site. Table 1 defines the model's symbols.

The elementary state of any site x belongs to the set $\sigma = \{0, i, r\}$. The states indicate, respectively, an empty

Table 1
List of model symbols, definitions (numerical value or range used in the simulations, where appropriate)

Symbol	Definition
L	Lattice length/width ($32 \leqslant L \leqslant 512$)
σ	Set of lattice site's elementary states (empty, invader, resident)
β_i	Invader's introduction rate ($10^{-8} \leqslant \beta_i \leqslant 10^{-2}$)
β_r	Resident's introduction rate ($\beta_r = \beta_i = \beta$)
δ	Neighborhood size for clonal growth (4)
α_i	Invader's clonal propagation rate (0.8)
α_r	Resident's clonal propagation rate (0.7)
$\eta_i(x, t)$	Number of invader neighbors around site x at time t
$\eta_r(x, t)$	Number of resident-species neighbors around site x at time t
μ_i	Invader's mortality rate (0.1)
μ_r	Resident's mortality rate ($\mu_i = \mu_r = \mu = 0.1$)
ρ_i	Invader's global density
ρ_r	Resident's global density
r_{ms}	Resident's "metastable" global density
$\langle \tau \rangle$	Resident's metastable lifetime
t_i	Waiting time for invader's nucleation
t_g	Time for successful invader to grow to competitive dominance
$I(\beta)$	Nucleation rate per unit area
V	Velocity at which cluster radius grows
$S(t, t')$	Volume of cluster at time t formed at time $t' < t$
r_c	Initial radius of nucleating cluster
C_d	Dimension-dependent multiplier
d	Dimension of volume within which nucleation occurs

site, occupation by an individual invader, and occupation by an individual of the resident species.

First, we describe $(0 \rightarrow i)$ and $(0 \rightarrow r)$ transitions. An empty site may become occupied as a result of introduction from outside the environment, or through local clonal propagation (Cook, 1983; Iwasa, 2000). The invader occupies each empty site via dispersal at constant probabilistic introduction rate β_i. The introduction rate for the resident species is β_r. The introduction process does not depend on an open site's local neighborhood; introduction corresponds to a spatially uniform, typically weak, background process, modeling long-distance propagule dispersal.

Local clonal propagation depends on neighborhood composition. A plant occupying a site x may propagate locally if at least one of the δ sites neighboring x is open. An invader at site x attempts to colonize neighboring sites at total probabilistic rate α_i; the propagation rate per neighboring site is α_i/δ. The resident's total propagation rate is α_r, so the rate per site is α_r/δ. The chance of successful clonal growth declines with local density. $\eta_i(x, t)$ counts invaders neighboring an open site x at time t. $\eta_r(x, t)$ counts individuals of the resident species on the same neighborhood; $\eta_i(x, t) + \eta_r(x, t) \leqslant \delta$.

We assume density-independent mortality. If a site is occupied by an invader, that site becomes open at