

Invasion Dynamics in Spatially Heterogeneous Environments

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ABSTRACT: Biological invasions, including infectious disease outbreaks and biocontrol introductions, often involve small numbers of individuals arriving in spatially heterogeneous environments. Small numbers lead to demographic stochasticity, and spatial heterogeneity means that establishment success depends critically on the introduction sites and movement patterns of invaders. We present a general stochastic modeling framework to address how spatial heterogeneity and movement patterns determine establishment success, population growth, and rates of spatial spread. For dispersal-limited populations, our analysis reveals that spatial heterogeneity increases the expected population growth rate and that local reproductive numbers determine establishment success. Higher dispersal rates decrease the expected population growth rate but can enhance establishment success, particularly when movement patterns are positively correlated with local reproductive numbers. We also find that several small, randomly distributed propagules of invaders are more likely to succeed than a single large propagule. Even if invasions are ultimately successful, there may be substantial time lags before an invader reaches observable densities. These time lags are longer for invasions into patches where extinction risk is high and in landscapes where metapopulation-scale population growth rate is low, while the opposite holds true for rates of spatial spread. Sensitivity analysis of our models provides guidance for control efforts.

Keywords: spatial heterogeneity, biological invasion, infectious disease outbreaks, propagule pressure, multitype branching processes, metapopulation ecology.

Introduction

Understanding the fate of an invading organism is one of the most fundamental issues in ecology, evolution, and epidemiology. The mathematical theory of invasions has contributed greatly to our understanding of ecological processes (McArthur and Wilson 1967; Law and Morton 1996; Caswell 2001; Haccou and Vatunin 2003) and the epidemiology of infectious disease outbreaks (May et al. 2001; Lloyd-Smith et al. 2005). Invasions typically involve small

numbers of individuals, so demographic stochasticity plays a crucial role. This stochasticity makes the outcome of any particular invasion attempt unpredictable and greatly complicates the analysis of empirical data to estimate key quantities, such as the likelihood of establishment success, rates of population growth, and rates of spatial spread (Facon and David 2006). Since these likelihoods and rates depend on demographic rates that vary spatially, the initial distribution of an invading organism and its patterns of movement can influence the invasion process (Duncan et al. 2003; Pyšek and Hulme 2005). Here, we introduce and analyze a general stochastic model of invasion dynamics in a spatially heterogeneous environment with the aims of developing a conceptual framework to guide our interpretation of empirical patterns and aiding in the design of surveillance and control programs.

Demographic stochasticity, caused by chance events in individual survivorship and reproduction, produces random fluctuations in population sizes. Using branching process and diffusion approximations, theoreticians have examined the influence of demographic stochasticity on establishment success and population growth (McArthur and Wilson 1967; Gilpin and Soulé 1986; Mangel and Tier 1994; Haccou and Iwasa 1996; Fox 2005; Lloyd-Smith et al. 2005), and many of these studies have helped to guide and unify empirical research. The role of individual and temporal heterogeneity has been a particularly important theme in the past decade. For instance, variation of demographic rates among individuals can increase the chance of invasion success if the demographic rates of individuals are positively correlated with their parents (Fox 2005). Without these correlations, individual heterogeneity can reduce the chance of invasion success but result in more explosive invasions when establishment occurs (Lloyd-Smith et al. 2005). Alternatively, in temporally heterogeneous environments, temporal patterns of invasion attempts can dramatically influence the likelihood of invasion success. For example, sequential invasion attempts by few individuals are more likely to succeed than a single invasion attempt involving many individuals (Haccou and Iwasa 1996), although the presence of an Allee effect may

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reverse this trend (Hopper and Roush 1993; Grevstad 1999; Leung et al. 2004). These studies, however, do not examine the effects of spatial heterogeneity on establishment success, population growth, or spatial spread.

Biological invasions proceed in spatially heterogeneous environments. This spatial heterogeneity may be generated by variation in abiotic factors, such as temperature, precipitation, sunlight, and nutrient availability, or in biotic factors, such as densities of resources, competitors, and predators (Melbourne et al. 2007). The importance of this heterogeneity has been demonstrated in numerous experimental and observational studies (Lonsdale 1993; Schoener and Spiller 1995; Levine 2000; Jules et al. 2002; Miller et al. 2002; Davies et al. 2005; Pyšek and Hulme 2005). For example, Schoener and Spiller (1995) found that invasion success of spiders was greater on islands without lizard predators than on islands with lizards. Alternatively, manipulative field experiments by Levine (2000) demonstrated the importance of both spatial heterogeneity and propagule pressure for the invasion success of alien plants into riparian communities. Patch-level heterogeneity arising from varying degrees of community biodiversity resulted in a negative correlation between local diversity and the probability of invasive seed establishment. However, this pattern was reversed at large spatial scales as a result of correlations between propagule pressure and local diversity.

Despite this widespread empirical evidence and the clear need for a general conceptual framework of how spatial heterogeneity influences biological invasions, only a few studies have moved toward this aim (Hastings et al. 2005; Melbourne et al. 2007). A key theme in previous studies has been the influence of spatial heterogeneity on the rate of spatial spread. Low-quality habitats interspersed with higher-quality habitats can dramatically reduce rates of spatial spread (Shigesada et al. 1986, 1995) or lead to propagation failure when there are Allee effects (Keitt et al. 2001). Spatial heterogeneities also generate spatial correlations that alter invasion dynamics. Using deterministic models, Chesson (2000) showed that positive correlations between an organism's spatial distribution and within-patch fitness result in higher invasion rates. Similarly, Facon and David's (2006) analysis of stochastic patch occupancy models found that variation in patch sizes creates a positive correlation between colonization and emigration rates and that this correlation increases rates of spatial spread. Despite this progress, none of these studies account for demographic stochasticity in within-patch population growth, which is a key factor in the early stages of invasion.

The role of spatial heterogeneity has received more attention in the infectious disease literature, in part because geographic space and "social space" (i.e., contact patterns in a population) can be treated using the same theoretical

frameworks. A central concept in the analysis of disease invasions is the basic reproductive number, R_0 , which is defined as the expected number of individuals infected by a typical infectious individual in a susceptible population. R_0 acts as a threshold parameter for invasion success (Anderson and May 1991). A seminal study by Diekmann et al. (1990) presented a method to calculate R_0 for heterogeneous populations, and work by Adler (1992) showed that accounting for heterogeneity always increases R_0 or leaves it unchanged compared with average-based depictions of populations. These studies augmented an important body of deterministic models highlighting the crucial role of high-transmission "core groups" in fueling epidemics (Hethcote and Yorke 1984; May and Anderson 1987; Jacquez et al. 1988; Dushoff and Levin 1995). Once again, theoretical work on stochastic dynamics of outbreaks in spatially heterogeneous populations has been limited, although a number of studies have applied data-driven simulation models to particular outbreaks (Keeling et al. 2001; Smith et al. 2002; Riley et al. 2003; Haydon et al. 2006). These studies have consistently highlighted the importance of spatial heterogeneity for invasion dynamics.

Here, we introduce a general stochastic modeling framework to address how demographic stochasticity, spatial heterogeneity, and patterns of dispersal influence establishment success, population growth, and spatial spread. The framework is sufficiently flexible to account for large or small networks of patches, patch-specific demographic rates representing abiotic or biotic sources of heterogeneity, and complex patterns of dispersal. Our analysis is motivated by understanding four questions. Since invasive populations can invade only when their expected growth rate is positive, our analysis addresses how the expected growth rate of a population depends on its dispersal rate, its movement patterns, and spatial heterogeneity in its demographic rates. Surprisingly, we find that dispersal always decreases the expected rate of population growth. To reconcile this result with empirical observations that dispersal can enhance establishment success, we derive analytic results to understand how the likelihood of establishment depends on where the invaders arrive and how quickly they disperse. Motivated by empirical findings in the biological invasion and biocontrol literatures (Lockwood et al. 2005; Colautti et al. 2006), we also examine how two forms of propagule pressure—many individuals arriving in a few patches versus few individuals arriving in many patches—influence establishment. Finally, since understanding time lags and rates of spatial spread is critical for management efforts to control invaders (Keeling et al. 2001, 2003; Crooks 2005), our analysis concludes by providing a conceptual framework to understand how spa-

tial heterogeneities may accelerate spatial spread or reduce time lags.

Model and Methods

We consider a finite population living in a spatially heterogeneous landscape consisting of n patches. Our model is a continuous-time, spatially explicit stochastic model that can be analyzed using the theory of multitype branching processes (Harris [1963] 2002; Athreya and Ney [1972] 2004).

The Stochastic Modeling Framework

Let $N_i(t)$ denote the number of individuals in patch i at time t . The population dynamics within patch i are determined by patch-specific per capita birth rates b_i and per capita death rates d_i . When the model is applied to disease outbreaks, these parameters describe the population dynamics of infectious individuals; for example, b_i is the per capita transmission rate for infectious hosts in patch i (whereby new infectious hosts are “born”), and d_i is the rate at which hosts leave the infectious state by death or recovery. Movements between patches are determined by the per capita dispersal rates δ_{ij} from patch i to patch j . To examine how the mean dispersal rate influences invasion dynamics, we rewrite δ_{ij} as μm_{ij} , where $\mu = (1/n) \sum_{i \neq j} \delta_{ij}$ is the mean emigration rate and $m_{ij} = \delta_{ij}/\mu$ is the dispersal rate from patch i to patch j normalized by the mean emigration rate.

To account for demographic stochasticity, the population dynamics are modeled by a continuous-time branching process with the aforementioned transition rates (fig.

1a). Roughly, these transition rates assert that over a small time interval of length Δt , the probability of an individual in patch i giving birth is $b_i \Delta t$, dying is $d_i \Delta t$, and dispersing to patch j is $\mu m_{ij} \Delta t$. To simulate these branching processes (fig. 2c, 2d), we use Gillespie’s algorithm (Gillespie 1977; see app. A in the online edition of the *American Naturalist*).

Analysis of Population Growth and Extinction Risk

We analyze expected population growth and extinction probabilities using the theory of multitype branching processes (Harris [1963] 2002; Athreya and Ney [1972] 2004). Because this theory allows us to compute these quantities exactly, they exhibit smooth dependence on the parameter values despite the underlying stochasticity of the spatially structured model.

For determining the expected population growth rate, $N = (N_1, \dots, N_n)$ denotes the row vector of population abundances, and $\mu e_i = \mu \sum_{j=1}^n m_{ij}$ is the per capita emigration rate from patch i . The expected dynamics are given by

$$\frac{dN}{dt} = N(\mathbf{B} - \mathbf{D} - \mu \mathbf{E} + \mu \mathbf{M}),$$

where \mathbf{B} , \mathbf{D} , and \mathbf{E} are diagonal matrices with diagonal entries b_i , d_i , and e_i , respectively, and \mathbf{M} denotes the matrix whose entries are given by m_{ij} . The population is expected to grow asymptotically like $e^{\lambda t}$, where λ is the dominant eigenvalue of $\mathbf{B} - \mathbf{D} - \mu \mathbf{E} + \mu \mathbf{M}$. More precisely, the expected metapopulation size $E(N_1(t) + \dots + N_n(t)|N(0))$ grows like $e^{\lambda t}$ for sufficiently large t . Corresponding to this

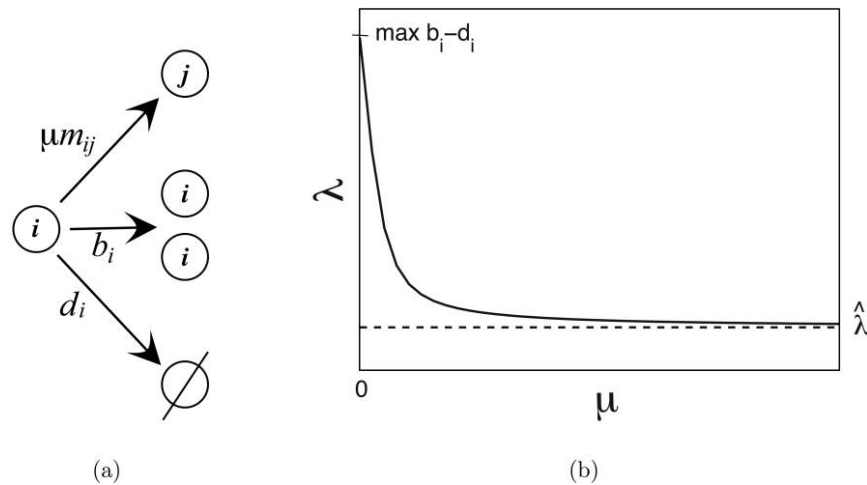


Figure 1: a, Transition rates for an individual in patch i . b, Asymptotic population growth rate (λ) as a function of the mean dispersal rate (μ).

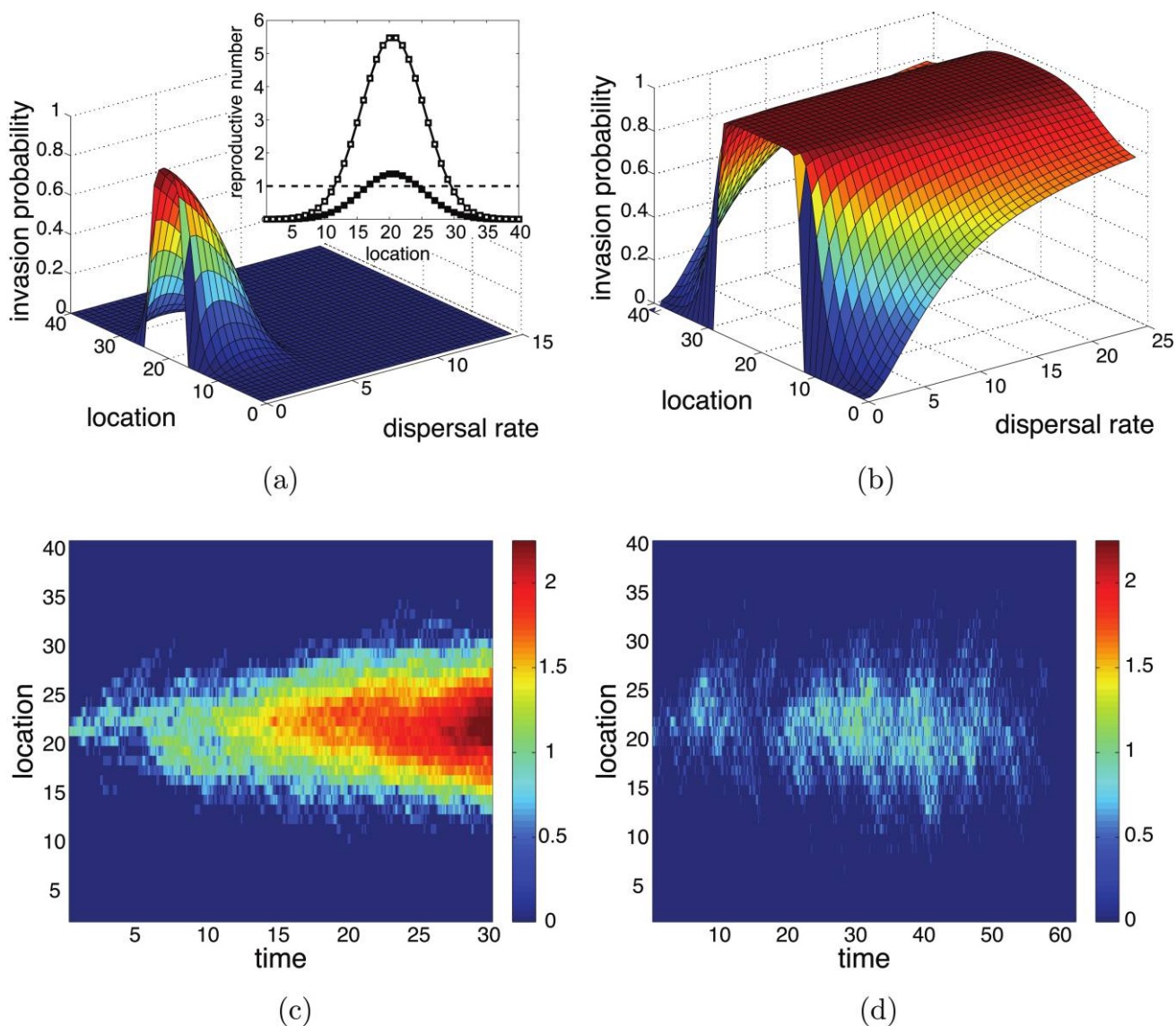


Figure 2: Invasions for populations dispersing diffusively on a one-dimensional environment. Inset in *a* shows how reproductive values vary along 40 patches in a more hostile environment (*solid squares*) with $\hat{R} = 0.42$ and a less hostile environment (*open squares*) with $\hat{R} = 1.68$. For an invading population of 20 individuals, the probabilities of invasion success in a more hostile environment (*a*) and a less hostile environment (*b*) are plotted as a function of where the invaders are released and the mean dispersal rate μ . *c, d*, A single realization of the spatial-temporal dynamics in the more hostile environment (*a*) is plotted. In each simulation, there were initially 20 individuals in location 20. *c, $\mu = 3$; d, $\mu = 10$* . Population densities are plotted on a \log_{10} scale, with warmer colors corresponding to higher densities.

expectation, if $\lambda \leq 0$, then the population becomes extinct in finite time with probability 1 (i.e., invasion failure). Alternatively, when $\lambda > 0$, there is a positive probability of establishment success and a complementary probability of extinction.

A method for computing the probabilities of extinction and invasion success is presented in appendix A. To understand how local per capita birth rates and per capita

death rates contribute to invasion success, we examine how particular changes in these demographic rates alter the probability of extinction. These changes can be evaluated using either sensitivities or elasticities. Sensitivities describe the absolute changes in the extinction probability due to absolute changes in demographic parameters, while elasticities describe the relative changes. For example, if q_i is the probability of extinction when a single individual ar-

rives in patch i , then the sensitivity of q_i to b_i is $\partial q_i / \partial b_i$ and the elasticity is $(\partial q_i / \partial b_i)(b_i / q_i)$. In appendix F, we provide explicit expressions for the sensitivities and elasticities of the patch-specific extinction probabilities with respect to the demographic parameters.

Analysis of Time Lags and Spatial Spread

To understand how spatial heterogeneities influence time lags and rates of spatial spread, we ran 1,000 simulations using Gillespie's algorithm for six different scenarios corresponding to low, medium, and high dispersal rates ($\mu = 0.1, 1, 10$) and two forms of propagule pressure (five individuals released in one site and one individual released in each of five random sites). In these simulations, there were 10 patches. Between-patch dispersal rates μm_{ij} were chosen randomly from a uniform distribution on $[0, 1]$ and normalized to yield desired mean per capita emigration rates. Birth rates and death rates were chosen randomly from uniform distributions on $[0, 2.5]$ and $[0.1, 2.1]$, respectively. Each simulation ran until the population either reached 100 individuals or became extinct. For each simulation, we computed the probability of extinction q , the asymptotic growth rate λ , the time to reaching 100 individuals (when this occurred), and the fraction of the landscape covered when the population reached 100 individuals. Since extinction probabilities q and the asymptotic growth rate λ were significantly correlated, we performed a principal components analysis on the standardized extinction probabilities \hat{q} and growth rates $\hat{\lambda}$. This analysis revealed that for all scenarios, the first principal component (PC₁) was given by $(1/2^{1/2})(\hat{q} - \hat{\lambda})$. This principal component can be interpreted as a measure of the hostility of the environment encountered by the invaders, with positive values corresponding to invaders arriving in a patch with high extinction risk or in a landscape in which they have a low asymptotic growth rate. We conducted linear regressions of the time lags and rates of spatial spread against this principle component. Both time lags and spatial spread rates were log transformed before regression, in accordance with our expectation of exponential growth of populations that invade successfully.

Results

Effect of Mean Dispersal Rate on the Asymptotic Growth Rate

Provided there is heterogeneity in the per capita growth rates (i.e., there exist patches such that $b_i - d_i \neq b_j - d_j$) and dispersal eventually connects all habitats (i.e., $\mathbf{M} - \mathbf{E}$ is irreducible), the asymptotic growth rate λ is a decreasing function of the mean dispersal rate (fig. 1*b*; app.

B). The maximum asymptotic growth rate occurs for dispersal-limited populations (i.e., $\mu \approx 0$) and is given by the maximum of the per capita growth rates $\max_i (b_i - d_i)$. Whenever there is heterogeneity in the per capita growth rates, the maximal per capita growth rate is greater than the spatial average $E(b_i - d_i) = (1/n) \sum_{i=1}^n b_i - d_i$ of the per capita growth rates. Hence, for dispersal-limited populations, spatial heterogeneity increases the asymptotic growth rate.

The lowest asymptotic growth rate occurs for highly dispersive populations and depends on the stable patch distribution for the dispersal matrix \mathbf{M} . This distribution is given by the eigenvector $v = (v_1, \dots, v_n)$ satisfying $v(\mathbf{M} - \mathbf{E}) = 0$ and $\sum_{i=1}^n v_i = 1$. One can interpret v as the expected long-term spatial distribution of an ensemble of individuals following the movement rules determined by \mathbf{M} . The asymptotic growth rate for highly dispersive populations is given by the per capita growth rates averaged with respect to this distribution: $\lambda = \sum_{i=1}^n v_i (b_i - d_i) = v \times (b - d)$. This expression highlights an intuitive explanation for λ decreasing with μ : higher dispersal rates tend to average the per capita growth rates across patches, progressively diluting the influence of the patch with the maximum per capita growth rate.

The asymptotic growth rate for highly dispersive populations can be rewritten as

$$\hat{\lambda} = E(b_i - d_i) + \text{Cov}(b_i - d_i, mv_i), \quad (1)$$

where $\text{Cov}(b_i - d_i, mv_i)$ is the covariance between the per capita growth rates and the stable patch distribution. Equation (1) implies that positive correlations between movement patterns and per capita growth rates tend to increase the expected growth rate, while negative correlations tend to decrease the expected growth rate. In contrast to dispersal-limited populations, spatial heterogeneity enhances population growth only if there is a positive correlation between movement patterns and per capita growth rates.

Invasion Probabilities in Heterogeneous Environments

While the asymptotic growth rate varies in a consistent manner with the mean dispersal rate, the extinction probabilities are patch specific and, consequently, vary with the mean dispersal rate in a more subtle manner. Although it is not possible to write down a general solution for the extinction probabilities q_i as a function of μ , explicit expressions can be determined for dispersal-limited populations and highly dispersive populations. For dispersal-limited populations, the probability of extinction for a population initiated with a single individual in patch i is

given by $q_i = \min(1, 1/R_i)$, where $R_i = b_i/d_i$ is the reproductive number for an individual living in patch i (app. C). R_i represents the expected number of offspring produced in that individual's lifetime. Hence, the greater the reproductive number for an individual in a patch, the greater the likelihood of invasion success. When an invader arrives in a sink habitat (i.e., $R_i < 1$), invasion failure is highly likely, with a mean time to extinction of approximately $-\ln(1 - R_i)/b_i$ (app. D).

At sufficiently high dispersal rates, the probability of extinction is effectively patch independent, and the extinction probability for a population initiated with a single individual is given by $\hat{q} = \min\{1, 1/\hat{R}\}$ where $\hat{R} = \sum_{j=1}^n v_j b_j / \sum_{j=1}^n v_j d_j$ is an appropriately spatially averaged reproductive number (app. C). When $\hat{R} > 1$, the extinction probability \hat{q} is greater (respectively, lower) than the extinction probability for a dispersal-limited population initiated in the patch supporting the highest (respectively, lowest) reproductive number. Therefore, higher dispersal rates facilitate invasions starting in lower-quality patches and inhibit invasions starting in higher-quality patches. Alternatively, when $\hat{R} < 1$, extinction occurs with probability 1 no matter where an invader arrives, and the mean time to extinction is approximately $-\ln(1 - \hat{R})/(v \times b)$ (app. D).

To illustrate some implications of these results, consider a population that disperses diffusively in a one-dimensional environmental gradient (fig. 2a, inset). For diffusive movement, the stable patch distribution places equal weight on all patches. Consequently, $\hat{R} = E(b_i)/E(d_i)$. If $\hat{R} < 1$ and $R_i > 1$ for some patch, then there is a dispersal threshold. Populations with dispersal rates below this threshold have a chance of invading, while populations with dispersal rates above this threshold cannot invade (fig. 2a, 2c, 2d). For populations initiated in patches with lower reproductive numbers, the probability of invasion success can be greatest at intermediate dispersal rates. If \hat{R} is sufficiently > 1 (fig. 2b), then invasion success increases sharply with dispersal for attempts initiated in patches with lower reproductive numbers and decreases marginally only for attempts initiated in patches with the largest reproductive numbers.

Effects of Correlations between Movement and Local Demographic Rates

The reproductive number for highly dispersive populations, \hat{R} , can be written as

$$\hat{R} = \frac{E(b_i) + \text{Cov}(b_i, nv_i)}{E(d_i) + \text{Cov}(d_i, nv_i)} \quad (2)$$

Hence, when movement patterns are positively correlated

with local reproductive rates or negatively correlated with local mortality rates, highly dispersive populations have a greater chance of invasion success. While diffusive patterns of movement (i.e., $m_{ij} = m_{ji}$ for all i, j) are uncorrelated to local demographic rates, movement patterns are often asymmetric because they are influenced by spatial structure of the landscape or other environmental cues (Colbert et al. 2001). To examine how nondiffusive movement can generate correlations, we consider landscapes with variable patch connectivity and movements driven by patch conditions.

Consider individuals that perform a random walk between patches in which individuals have a fixed emigration rate and that, on leaving a patch, are equally likely to go to any neighboring patch (Grimmett and Stirzaker 2001). If patch i has k_i neighbors, then the stable patch distribution is given by $v_i = k_i/(k_1 + \dots + k_n)$. In other words, the fraction of time individuals spend on a given patch is proportional to the number of neighboring patches (fig. 3a). Hence, if local demographic rates are higher in highly connected patches than in sparsely connected patches, then there can be a positive correlation between the stable patch distribution and the local demographic rates. Conversely, negative correlations arise when sparsely connected patches have higher demographic rates. For instance, if highly connected patches are sources and $\hat{R} < 1$, then intermediate levels of dispersal can enhance the likelihood of invasion success (fig. 3b). In contrast, if highly connected patches are sinks and $\hat{R} < 1$, then higher rates of dispersal always increase the risk of invasion failure.

Movement in response to environmental cues may result in adaptive or maladaptive behavior. Adaptive behavior occurs when individuals can use environmental cues to disperse to patches in which they have higher fitness (Stephens and Krebs 1987). On the other hand, if environmental cues in the new landscape differ significantly from the native landscape, then maladaptive behavior may arise. To understand the effects of maladaptive as well as adaptive behavior, let us return to a simple one-dimensional lattice of patches where individuals disperse to neighboring patches. As an illustrative model, we assume that the dispersal rate from patch i to patch j for $|i - j| = 1$ is proportional to $\exp[a(R_j - R_i)]$, where a measures the responsiveness of the individuals to fitness differences between patches. If $a > 0$, individuals tend to disperse adaptively by moving up the fitness gradient. If $a < 0$, individuals exhibit maladaptive behavior by preferentially moving down the fitness gradient. If $a = 0$, individuals disperse diffusively between neighboring patches. The stable patch distribution for these movement patterns is given by

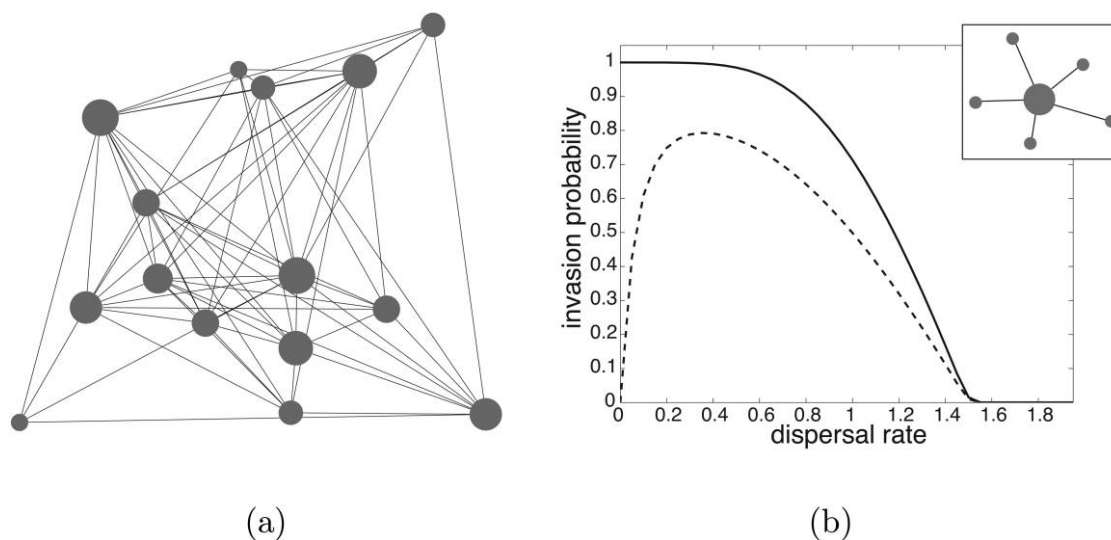


Figure 3: Stable patch distribution and invasion probabilities for a population performing a random walk between patches. *a*, Random collection of patches where connections are randomly determined by distances between patches. The size of each patch is proportional to its steady state patch occupancy, v_i . *b*, Inset shows a configuration of core and satellite patches. Invasion probabilities for a single individual arriving in a satellite patch are plotted. *Dashed line*, probabilities when satellite patches are sinks and core patch is a source. *Solid line*, probabilities when satellite patches are sources and core patch is a sink. Parameters are $b_i = 1$ in all patches, $d_i = 0.5$ in source patches, and $d_i = 1.5$ in sink patches. For both scenarios, $\hat{R} = 0.75 < 1$.

$$v_i = \frac{\exp [2a(R_i - R_i)]}{\sum_j \exp [2a(R_j - R_i)]}.$$

When $a = 0$, the stable patch distribution places equal weight on all habitats ($v_i = 1/n$ for all i). When $a > 0$, v_i is greater for patches where individuals have larger reproductive numbers. Hence, adaptive behavior promotes positive correlations between the stable patch distribution and the patch-specific reproductive numbers and thereby enhances chances for invasion success. Conversely, maladaptive dispersal behavior ($a < 0$) reduces chances for successful invasion.

For highly adaptive foragers ($a \gg 0$), the stable patch distribution is concentrated on the patch with the greatest reproductive number, in which case $\hat{R} \approx \max_i R_i$ (fig. 4*b*). Thus, for highly adaptive foragers, establishment occurs with positive probability at all dispersal rates, provided there is a source patch (fig. 4*c*). Surprisingly, local fitness peaks in the environment do not serve as “traps” when individuals are highly responsive to local fitness differences. In contrast, for highly maladaptive populations ($a \ll 0$), the stable patch distribution is concentrated on the patch with the lowest fitness (fig. 4*b*), in which case $\hat{R} \approx \min_i R_i$. Consequently, highly maladaptive foragers cannot establish at high dispersal rates if there are sink patches in the environment (fig. 4*d*).

Propagule Pressure and Invasion Success

Propagule pressure is the product of the number of invasion events (propagule number) and the average number of individuals arriving per invasion event (propagule size). To see how different forms of propagule pressure affect invasion success, we examine two scenarios: a single propagule with k individuals (the single release scenario) versus k propagules with one individual each (the multiple release scenario). Appendix E shows whether there is spatial heterogeneity in the extinction likelihoods ($q_i \neq q_j$ for some i and j), then $k \geq 2$ independent invasion attempts by single individuals are more likely to result in invasion success than a single invasion attempt by k individuals arriving in one patch.

Figure 5 illustrates this result for less hostile ($\hat{R} > 1$) and more hostile ($\hat{R} < 1$) environments. For less hostile environments, the probability of invasion success increases with the total number of individuals released and the mean dispersal rate. For more hostile environments, invasion success is most likely at intermediate dispersal rates. In both environments, multiple releases exhibit a significantly higher probability of invasion success at low dispersal rates and higher propagule pressure. Higher dispersal rates tend to homogenize the extinction probabilities and thereby reduce the difference between invasion success in the single-release and multiple-release scenarios.

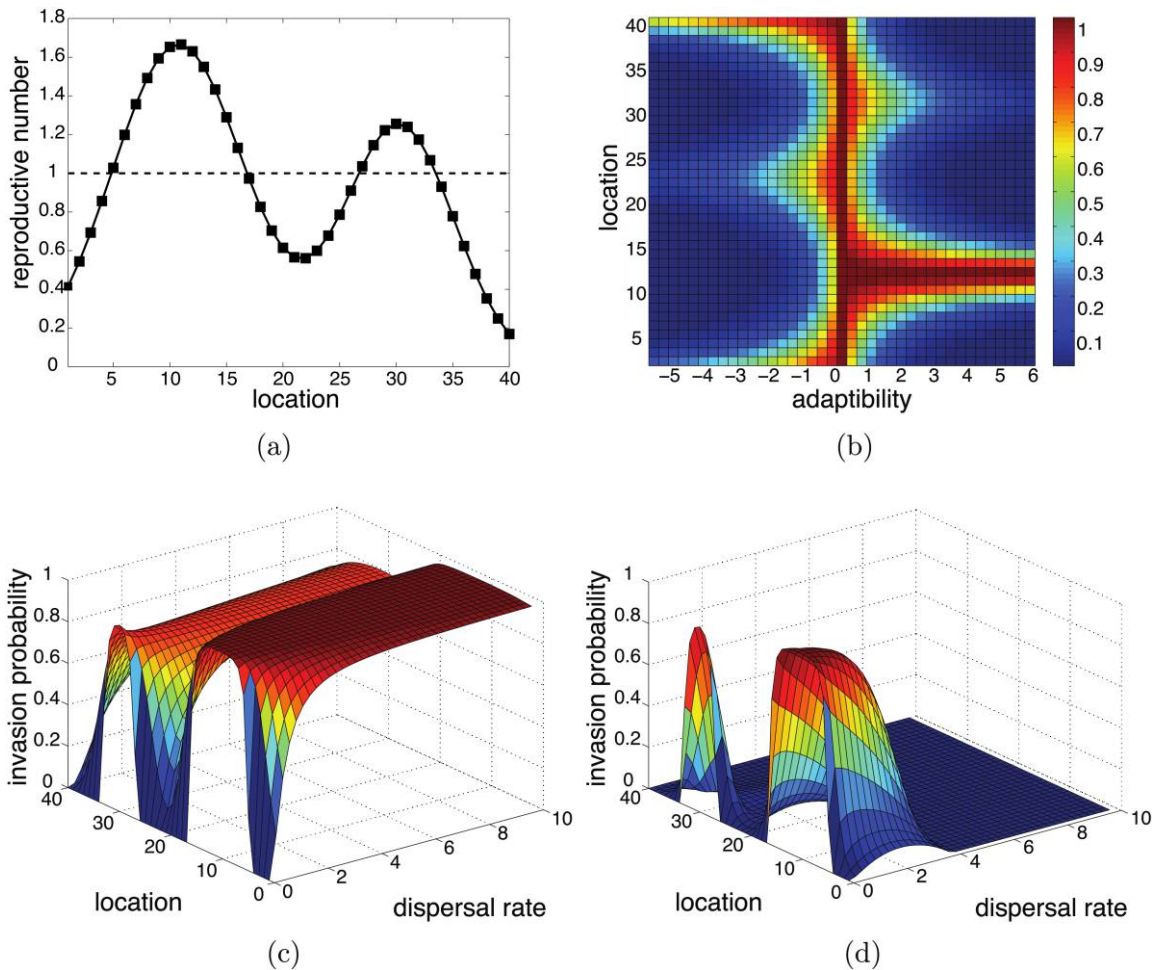


Figure 4: Adaptive foraging and population viability. Individuals move along a one-dimensional landscape where per capita birth rates vary to yield reproductive numbers (a). Dispersal rates from patch i to j with $|i - j| = 1$ are proportional to $\exp[a(R_j - R_i)]$, where a measures the adaptiveness of movement. b, Renormalization $v_i / \max_j v_j$ of the stable patch distribution is plotted as a function of the patch location and a . c, d, Probability of invasion success for adaptive ($a = 6$) and maladaptive ($a = -2$) dispersal is plotted for populations of initially 20 individuals as a function of their mean dispersal rate μ and the location where they were released.

Sensitivities and Elasticities

To understand how local per capita birth rates and per capita death rates contribute to invasion success, appendix F presents analytical expressions for the sensitivities and elasticities of extinction probabilities to demographic parameters. To illustrate these results, we discuss how dispersal and spatial heterogeneity interact to determine the influence of local birth rates on global invasion probabilities. For dispersal-limited populations, the probability of extinction in habitat i is $q_i = d_i/b_i$. Therefore, the elasticity of q_i with respect to the per capita birth rate in habitat i is -1 . Hence, for dispersal-limited populations, the larger elasticity values are concentrated around the diagonal of the elasticity matrix $E_{ij} = (\partial q_i / \partial b_j)(b_j / q_i)$ (fig. 6a). In con-

trast, for highly dispersive populations, the extinction probabilities $q_i \approx 1/\hat{R}$ are patch independent. The elasticity of this extinction probability to the per capita birth rate in patch i is given by $-v_i b_i / \sum_j v_j b_j$. Hence, at high dispersal rates, the extinction probability is most sensitive to changes of reproduction in patches where, on average, individuals produce more progeny either because the local reproductive number is higher or because the patch has higher levels of occupancy (fig. 6d). For example, for random walks on a network of patches of similar quality, the extinction probabilities are most sensitive to changes in the most connected patches (i.e., patches with largest v_i). At intermediate dispersal rates, particularly for invasions that begin in patches close to higher-quality patches, extinction

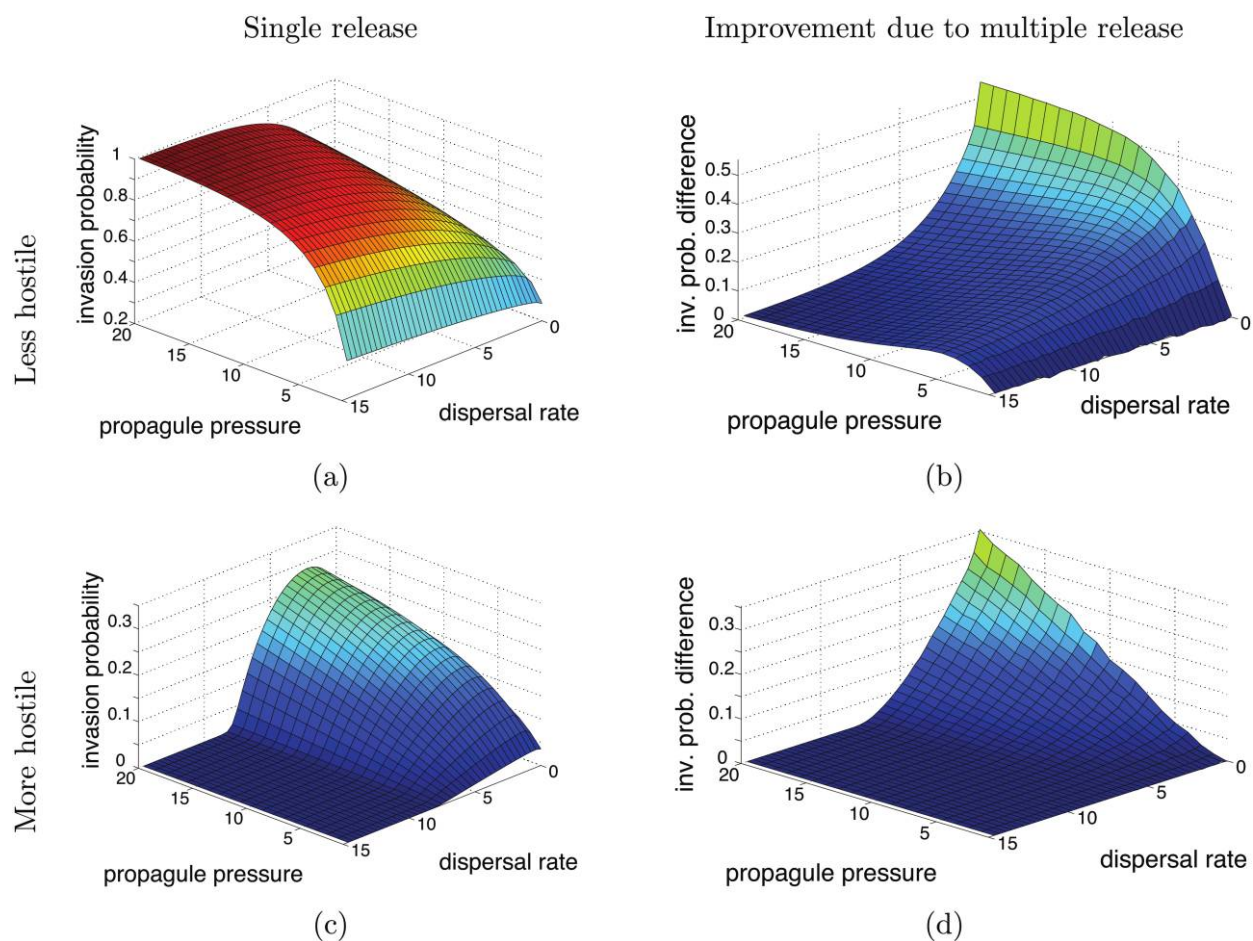


Figure 5: Invasion success with variable propagule pressure for populations living on a one-dimensional landscape with 40 patches. Reproductive values are as in figure 2. *a, c*, Probability of invasion success for a single release of invaders is plotted as a function of propagule pressure and mean dispersal rate. *b, d*, Probability of successful invasion for a multiple release minus the probability of success for a single release is plotted as a function of propagule pressure and mean dispersal rate.

probabilities can be more sensitive to changes in demographic rates in the neighboring high-quality patches than in the patch where introduction occurred (fig. 6c).

Time Lags and Spatial Spread

To understand how spatial heterogeneities influence time lags and rates of spatial spread, we built on our earlier analyses and examined how these quantities correlate with the patch-specific extinction probabilities and the asymptotic growth rates. Table 1 reports the results of a log-linear regression of time lags and rates of spatial spread against the principal component PC_1 (see “Model and Methods”), which measures the “hostility” of the landscape. In all scenarios, the time lags were positively correlated with PC_1 (fig. G1a in the online edition of the

American Naturalist). In other words, low asymptotic growth rates or arriving in patches with higher extinction risk results in longer time lags. Invasions that succeed despite arriving in patches with high extinction risk may experience longer time lags because populations arriving in low-quality patches tend to “sputter” along until individuals ultimately disperse to higher-quality patches, at which point the population growth is much more rapid. Also, we showed previously that higher dispersal rates lead to lower λ . Given the positive correlation of time lags with PC_1 , this result implies that higher dispersal rates should lengthen time lags. This expectation is confirmed by our simulations, since intercepts and slopes of the regression lines increase with dispersal rates (table 1). Similarly, because multiple releases of small propagules (i.e., five individuals in five different patches) are less likely to lead

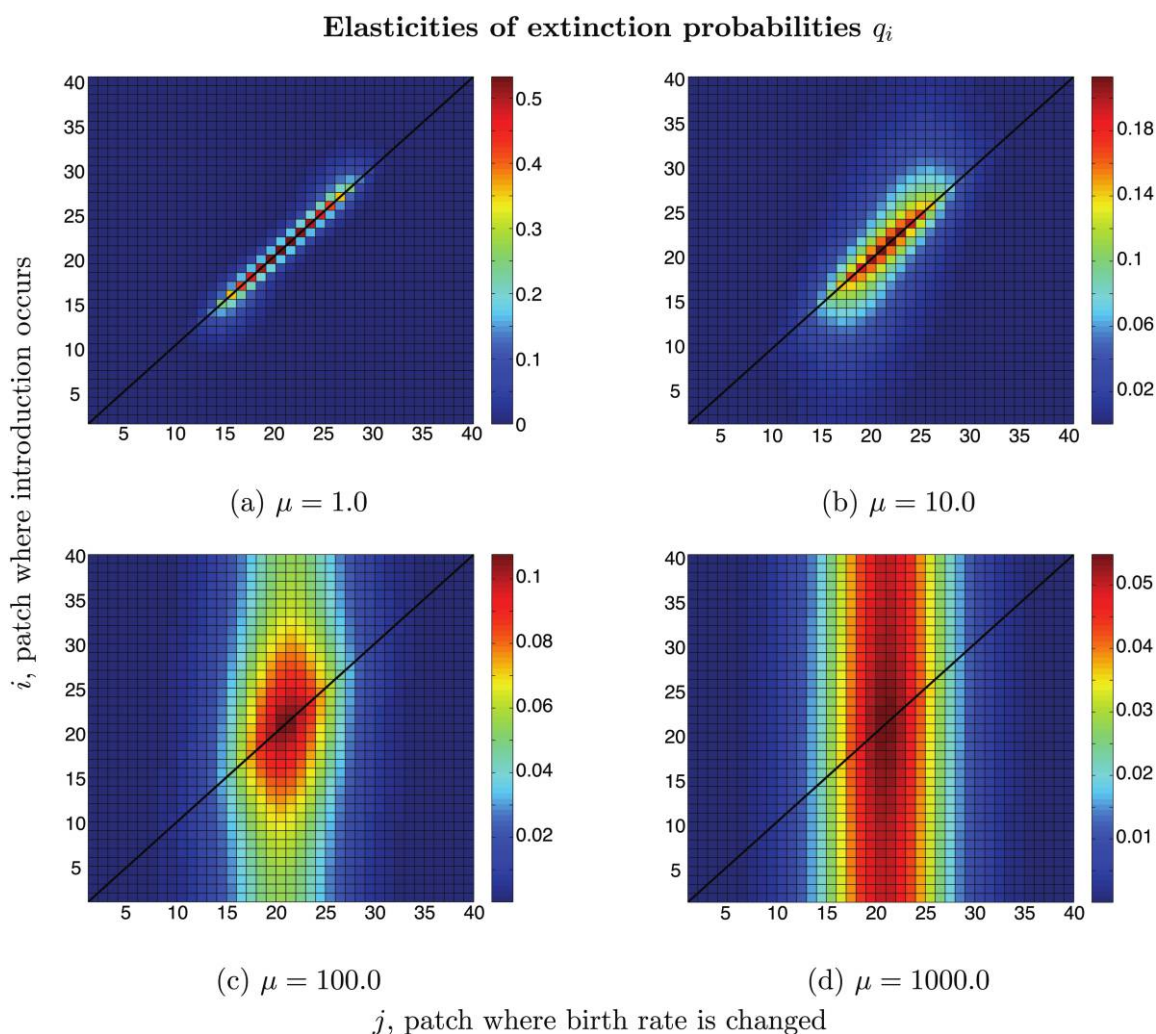


Figure 6: Elasticities of extinction probabilities with respect to patch-specific per capita birth rates. Reproductive values are as in figure 2a for the less hostile environment. Individuals move diffusively on a one-dimensional landscape. The color of each cell shows the absolute value of the elasticity of the patch-specific extinction probabilities q_i (i.e., for an introduction occurring on patch i) with respect to the patch-specific birth rates b_j . Mean dispersal rates are indicated.

to extinction than a single release of a large propagule (i.e., five individuals in a single patch), we would expect more diffuse propagule pressure to result in shorter time lags, and this expectation is confirmed by our simulations (i.e., intercepts and slopes for the regression lines are lower for the multiple releases).

In contrast to time lags, the rates of spatial spread are always negatively correlated with PC_1 (fig. G1b). Lower asymptotic growth rates or arriving in locations with higher extinction risk (given that the invasion is successful) results in slower spatial spread. Multiple releases of small propagules tended to result in higher rates of spatial spread than single large releases (table 1), as intuition and our

earlier results would predict. The effect of dispersal rates on the rate of spatial spread is more complex, since dispersal has two competing effects on invasion dynamics: higher dispersal rates facilitate faster spatial spread for populations of similar size but also slow down population growth, which can impede spatial spread.

Discussion

Effects of Spatial Heterogeneity and Dispersal on Invasion Dynamics

To become invasive following an introduction, a species must become established, increase in abundance, and

Table 1: Time lags and spatial spread

μ	Intercept	Slope	R^2
One propagule of five individuals:			
Logarithm of mean lag time:			
.01	1.666 \pm .012	.330 \pm .011	.465
1	1.754 \pm .006	.370 \pm .005	.853
10	2.702 \pm .007	.572 \pm .006	.916
Logarithm of mean spread rate:			
.01	-2.361 \pm .010	-.291 \pm .009	.495
1	-1.787 \pm .006	-.363 \pm .005	.851
10	-2.702 \pm .007	-.572 \pm .006	.916
Five propagules of one individual:			
Logarithm of mean lag time:			
.01	1.506 \pm .008	.293 \pm .007	.670
1	1.753 \pm .004	.364 \pm .003	.918
10	2.682 \pm .007	.567 \pm .006	.925
Logarithm of mean spread rate:			
.01	-2.158 \pm .007	-.279 \pm .006	.680
1	-1.788 \pm .004	-.357 \pm .003	.916
10	-2.683 \pm .007	-.567 \pm .006	.925

Note: Using the simulated data described in "Model and Methods," a linear regression was performed on the logarithm of mean time lag (i.e., time to reach 100 individuals) and the logarithm of mean rate of spatial spread (i.e., average change in fraction of landscape covered per unit time) versus the principal component PC_1 of the standardized $q - \lambda$ values. μ is the mean dispersal rate.

spread spatially. Spatial heterogeneity in environmental conditions and movement patterns of the invader in this heterogeneous landscape can influence each of these phases of the invasion process as well as the time lags between these phases. In the establishment phase, our analysis shows that the mobility of the invader plays an important role. For dispersal-limited invaders, the likelihood of establishment failure is inversely proportional to the local reproductive number R_i of the invaded patch, namely, the mean number of offspring produced during the lifetime of an individual in the invaded patch. The importance of reproductive numbers in determining establishment success has been demonstrated in earlier theoretical work (McArthur and Wilson 1967; Anderson and May 1991; Metz and Gyllenberg 2001), in field experiments on the colonization of islands by mice and voles (Crowell 1973; Ebenhard 1989), and in a meta-analysis of invasion success for 36 species of exotic introduced birds in New Zealand (Veltman et al. 1996). Since spatial heterogeneity can generate variation in local reproductive numbers, invasion success for dispersal-limited populations can be highly contingent on where an organism arrives. For example, Schoener and Spiller (1995) found that colonization success of spiders was greater in islands without lizard predators than with lizards. This is consistent with the widespread finding that "habitat matching" is a key determinant of invasion success (Duncan et al. 2003; Hayes and Barry 2008).

The effect of dispersal rates on establishment success is subtle and depends on an appropriately spatially averaged reproductive number, \hat{R} . For populations with very rapid dispersal (i.e., dispersal events much more frequent than demographic events), \hat{R} is a threshold parameter so that invasion cannot succeed if $\hat{R} < 1$. For populations with intermediate dispersal rates, this threshold behavior is weakened, but \hat{R} still provides crucial insight into how spatial heterogeneity influences invasion success. Because \hat{R} lies between the extremes of the local reproductive numbers, the effect of dispersal rates on establishment depends on where an invader initially arrives. For invaders arriving in patches with $R_i > \hat{R}$, dispersal tends to decrease the likelihood of invasion success, since individuals are likely to move into patches associated with lower reproductive numbers. For invaders arriving in patches with $R_i < \hat{R}$, the effect of dispersal depends on the value of \hat{R} . If $\hat{R} > 1$, then higher dispersal rates always increase the likelihood of invasion success. However, if $\hat{R} < 1$, then the probability of invasion success is greatest at intermediate dispersal rates. These results suggest that dispersal can enhance the chance for invasion success and thereby serve as a bet-hedging strategy for invading organisms arriving in a novel environment. These results also suggest the possibility that invasions into heterogeneous environments may result in selection for higher dispersal rates. Given the universality of spatial heterogeneity in invaded landscapes, we believe

that these hypotheses may provide fruitful avenues for empirical study.

For more dispersive populations, our analysis also shows that correlations between local reproductive numbers and movement patterns influence the likelihood of establishment. Positive correlations tend to increase this likelihood, while negative correlations inhibit establishment. These correlations can arise in a diversity of ways. For organisms moving randomly on a network of patches, positive correlations between patch connectivities and local reproductive numbers enhance the likelihood of establishment, since individuals are more likely to disperse to patches with high connectivity (fig. 3). The importance of correlations between local reproductive numbers and connectivity was demonstrated by Jules et al. (2002) for the invasion of a nonnative root pathogen *Phytophthora lateralis* across a heterogeneous landscape populated with its host, Port Orford cedar. Establishment success within a creek (a “patch” for this system) was greater for creeks with higher host densities (i.e., higher local reproductive numbers for the invading pathogen). Connectivity between creeks was determined primarily by roads that serve as routes for dispersal vectors (vehicles). Positive correlations between host abundance and proximity to roads were found to enhance establishment success, consistent with our model prediction. Alternatively, correlations can arise from organisms moving in response to environmental cues. If these environmental cues are accurate indicators of local reproductive numbers, then dispersal can greatly enhance the probability of invasion success by moving individuals from patches with lower reproductive numbers to patches with higher reproductive numbers (fig. 4). When the response to local differences in reproductive numbers is sufficiently strong, highly dispersive individuals (at least in one-dimensional environments) eventually spend most of their time in the patch that maximizes their establishment likelihood.

Following successful establishment, an invading population will grow in abundance and spread across space. Since the population growth rate can be calculated trivially for a given patch, we focus on the growth rate for the entire metapopulation that integrates characteristics of the heterogeneous landscape and dispersal patterns. Extending earlier theoretical work (Hastings 1983; Adler 1992; Dockery et al. 1998), our analysis implies that spatial heterogeneity increases the expected growth rate of dispersal-limited populations as a result of the influence of favorable patches but that this effect is diluted progressively as dispersal rates increase. The invasion of a woody weed *Mimosa pigra* into the wetlands of tropical Australia illustrates this dilution. A relatively fast disperser, this weed had a population doubling time of 1.2 years on favorable patches but exhibited much slower growth at the regional scale

(doubling time of 6.7 years) as a result of separation of suitable wetland habitats by eucalypt savannas that *M. pigra* can colonize less readily (Lonsdale 1993). While the earlier theoretical work considered only diffusive movement, we find that negative correlations between movement patterns and the patch-specific per capita growth rates (as opposed to the patch-specific reproductive numbers) result in spatial heterogeneity lowering population growth rates for highly dispersive populations, while positive correlations can mitigate the dilutionary effect of dispersal. These correlations may be particularly important for spatial spread, since we found that invasions spread more rapidly in landscapes supporting higher metapopulation growth rates. This finding complements results from the metapopulation literature (Day and Possingham 1995; Facon and David 2006). For example, using stochastic patch occupancy models to analyze the spread of the introduced snail *Tarebia granifera* on the island of Martinique, Facon and David (2006) found that heterogeneity in patch sizes leads to positive correlations between immigration rates (larger patches attract more immigrants) and colonization rates (larger patches send out more propagules), and these positive correlations result in faster rates of spatial spread.

A feature of many invasions is a time lag between establishment and the onset of rapid population growth (Sakai et al. 2001; Crooks 2005; Facon et al. 2006). While time lags are expected for invading populations exhibiting exponential growth, stochasticity (Facon and David 2006) or Allee effects (Taylor et al. 2004) can prolong these time lags. Our analysis implies that spatial heterogeneity is another potent source of prolonged time lags. In particular, we found that time lags are longer for successful invasions initiated in patches with high extinction risk or in landscapes supporting a lower metapopulation growth rate. Consequently, longer time lags can occur when an invader’s movement patterns are negatively correlated with habitat quality, for example, when there is an initial mismatch between environmental cues in the new environment and the invader’s native environment. Alternatively, invaders arriving in low-quality patches may persist at low levels for extended periods of time before successfully dispersing to higher-quality patches. Hence, spatial heterogeneity can amplify time lags due to demographic stochasticity. These ecological time lags are analogous to the time lags generated by evolutionary adaptation to a new environment (Sakai et al. 2001; Crooks 2005; Facon et al. 2006). However, instead of waiting for the evolution of an adapted genotype, there is the delay in finding a suitable habitat.

Propagule Pressure

Propagule pressure is a composite measure of the number of individuals released into a novel environment (Lockwood et al. 2005). Propagule pressure has been shown to be positively correlated with invasion success in many systems (Rejmanek and Richardson 1996; Cassey et al. 2004; Holle and Simberloff 2005; Memmott et al. 2005; Sax et al. 2005; Moyle and Marchetti 2006). Since propagule pressure entails both the number of release events (propagule number) and the number of individuals in a given release event (propagule size), the same pressure can be realized in a diversity of ways. If releases occur randomly across the landscape, our analysis implies that several small releases are more likely to result in invasion success than a single large release. This prediction is consistent with meta-analyses of introductions of exotic birds in New Zealand (Veltman et al. 1996) and Australia (Duncan et al. 2003) and exotic ungulates in New Zealand (Forsyth and Duncan 2001), all of which found that establishment success increased with the number of releases. While this conclusion follows mathematically from Muirhead's inequality (app. E), its intuitive underpinning is clear: several small releases increase the likelihood of some individuals landing in patches with a higher reproductive number and thereby increase the chance of invasion success. The argument presented here for spatially heterogeneous environments extends to other forms of heterogeneity. For instance, it can be used to generalize earlier findings that in a temporally heterogeneous environment a sequence of n releases of a single individual is more likely to lead to invasion success than releasing n individuals at once (e.g., Haccou and Iwasa 1996). In addition to having a positive impact on establishment success, we found that multiple small releases distributed across space result in shorter time lags and, quite intuitively, enhance rates of spatial spread.

Extensions and Challenges

While not addressed specifically by this analysis, it is interesting to speculate how our results relate to recent work on genetic and evolutionary aspects of invasibility (Facon et al. 2006). Fundamentally, our work is focused on the importance of habitat matching, that is, of invading individuals finding environments where their fitness is relatively high. By studying the influence of dispersal rates on invasion success, our analysis incorporates the possibility that individuals may change their fitness by moving to better (or worse) environments. There is a direct analogy to genetically heterogeneous invaders in a constant environment, where the matching pertains to having the right genotype for the given environment, and the possibility of changing fitness arises through evolution rather

than movement. Our predictions for spatial heterogeneity can then be generalized to the genetic context. For instance, if there is genetic variation in the invading species, then releasing small numbers of many genotypes is more likely to lead to invasion success than releasing large numbers of a few genotypes. Indeed, this prediction is supported by experimental work by Ahlroth et al. (2003), who translocated mated female water striders into streams and found that colonization success was highest for propagules that originated from two different, genetically distinct source populations. Kolbe et al. (2004) studied invasive *Anolis* lizards in various locations worldwide and argued that occurrence of multiple introductions from genetically distinct source populations was a key driver of invasion success. They also identified two instances where the extended lag phases before expansion of the invasive populations were best explained by the late arrival of better-adapted genotypes in separate introduction events. Facon et al. (2008) went further in a study of the invasive snail *Melanoides tuberculata* in Martinique, demonstrating surprisingly high adaptive potential in these recently established populations by linking genetic variation to phenotypic variation in five key life-history traits. Taking advantage of the mixed sexual/asexual reproductive strategy of the organism, they partitioned the causes of phenotypic variance between multiple introductions (the major component) and subsequent creation of novel variants by interbreeding. This natural system thus exhibits the interplay between fitness of the founding propagules and subsequent changes to that fitness, that is, just what we have analyzed in the current study but with populations structured by genotype rather than space. In future work, we will modify our framework to explicitly consider the problem of evolutionary adaptation of invading populations.

Our model assumes independence among individuals in their reproduction and survival, and it is important to note that density dependence could lead to different outcomes. The existence of an Allee effect certainly could alter the conclusions regarding propagule pressure. A series of modeling studies in the biocontrol literature have shown that larger release sizes have a better chance of establishing in the presence of a strong Allee effect (Hopper and Roush 1993; Grevstad 1999; Shea and Possingham 2000; Jonsen et al. 2007). Grevstad (1999) further explored how Allee effects interact with temporal variability in the environment and found that small, intermediate, or large release sizes could be optimal, depending on the relative strength of the two effects. Empirical analyses of insect introductions have found that larger releases have higher establishment probabilities, but this effect did not carry over to influence population growth in subsequent years (Hopper and Roush 1993; Memmott et al. 2005). Negative den-

sity dependence can also arise during invasions, for instance, owing to resource competition among the invaders if patches are sufficiently small. This issue has received particular attention for disease outbreaks, where local depletion of the susceptible population can cause extinction if mixing rates among groups (or replenishment of the susceptible pool) are not rapid enough (Cross et al. 2005; Cross et al. 2007). Human efforts to control undesirable invasions—and, indeed, any predator responses—may also increase with invader density. In contrast to Allee effects, any such negative density dependence will further increase the benefit of many small releases.

Our analysis and modeling framework allow for arbitrary complexity in spatial heterogeneity in demographic (or epidemiological) rates and patch connectivity, but we have illustrated our results for landscapes with relatively simple spatial structures. We expect that our qualitative conclusions will be robust to differences in spatial structure, but figure 3 demonstrates that spatial heterogeneity may interact with complex movement patterns in non-trivial ways. We leave these interactions as a topic for future study and refer the reader to the comparatively well-developed literature on the effects of complex metapopulation structure on invasion dynamics (e.g., Watts et al. 2005; Colizza and Vespignani 2007; Vazquez 2007).

Implications for Conservation and Control

Our sensitivity and elasticity analyses yield insights for effective control of invasions in heterogeneous landscapes, including the nonintuitive result that it is often more effective to focus control efforts on high-quality patches even when the invasion begins elsewhere. In contrast, for slow-dispersing invaders, efforts should be focused on surveillance for rapid detection and response at the site of introduction. In the invasive species context, measures to reduce birth rate include contraception or releasing egg predators, and measures to increase death rate include culling or trapping. In the disease context, reductions in birth rate correspond to transmission-reducing interventions (such as vaccination, hand washing, or social distancing), while increased “death rate” of infectious individuals corresponds to treatment, case finding and isolation, or culling. Our findings echo the classic “cities and villages” result of Anderson and May (1991), who show that the optimal vaccination pattern to achieve deterministic eradication of an endemic disease will focus greater effort on larger cities, where transmission is assumed to be more intense. Our results also provide a theoretical underpinning for earlier findings on outbreak control derived from simulation models, such as analyses of spatial vaccination strategies for rabies or foot-and-mouth disease, which take account of patch-specific values of

R_0 and dispersal patterns across the landscape (Keeling et al. 2003; Haydon et al. 2006; Real and Biek 2007).

Since degradation of patches with high connectivity decreases the correlation between connectivity and habitat quality more than degradation of patches with low connectivity, our results reinforce the importance of protecting or restoring highly connected patches to reduce extinction risk or increase reestablishment success of a valued species (Wahlberg et al. 1996; Lipcius et al. 2008). More generally, understanding correlations between species movement patterns and habitat quality and how these correlations might change in the face of climate change is likely to play an important role in conservation.

Our results show that while spatial heterogeneity can increase the likelihood of establishment of invasive species, it can also increase the time lags before new invaders are detected or exhibit exponential growth. Paradoxically, these periods of low detectability can provide significant windows of opportunity for control, but seizing these opportunities will require the deployment of early detection and rapid response systems (Crooks 2005). These time lags also emphasize the need for a precautionary principle: consistent behavior of an invasive species in one part of the landscape may be a poor predictor of what will happen if the species reaches another part of the landscape.

In conclusion, while we have mostly focused on idealized scenarios to reach broad conceptual conclusions, our spatially explicit stochastic framework and analytical results can be easily adapted to specific situations (i.e., specific landscapes or forms of demographic heterogeneity) in order to understand their invasive dynamics and to evaluate and guide control measures.

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