vol. 156, no. 5 the american naturalist november 2000

Extinction Thresholds and Metapopulation Persistence in Dynamic Landscapes

Juan E. Keymer,[1,*] Pablo A. Marquet,[2,†] Jorge X. Velasco-Hernández,[3,‡] and Simon A. Levin[1,§]

1. Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544-1003;
2. Departamento de Ecología, Pontificia Universidad Católica de Chile Casilla 114-D, Santiago, Chile;
3. Departamento de Matemáticas, Universidad Autonoma Metropolitana—Iztapalapa, Apartado Postal 55-534, Iztapalapa, Distrito Federal 09340, Mexico

Submitted November 12, 1999; Accepted June 6, 2000

abstract: Models of metapopulations have focused on the effects of extinction and colonization rate upon metapopulation persistence and dynamics, assuming static landscapes wherein patches are neither created nor go extinct. However, for species living in ephemeral (patchy) habitats, landscapes are highly dynamic rather than static. In this article, we develop a lattice metapopulation model, of the patch occupancy type, based on interacting particle systems that incorporate explicitly both metapopulation and patch dynamics. Under this scenario, we study the effects of different regimes of patch dynamics upon metapopulation persistence. We analyze the lattice behavior by numerical simulations and a mean field approximation (MF). We show that metapopulation persistence and extinction are strongly influenced by the rate at which the landscape changes, in addition to the amount of habitat destroyed. We derive MF analytical expressions for extinction thresholds related to landscape properties such as habitat suitability and patch average lifetime. Using numerical simulations, we also show how these thresholds are quantitatively overestimated by the MF equations, although the qualitative behavior of the spatial model is well explained by the MF when the array of habitat patches is dynamic or static but connected in space and time. The implications for conservation are also discussed.

Keywords: patch dynamics, metapopulation persistence, interacting particle systems, extinction thresholds, habitat fragmentation, environmental heterogeneity.

Since its introduction by Levins (1969, 1970), metapopulation theory has developed as a popular framework for analyzing the dynamics of species in patchy landscapes and for understanding the consequences of habitat loss and fragmentation upon species persistence (Levin 1974; Hastings 1980; Hanski and Simberloff 1997; Hanski 1999). Since the original papers, the subject has experienced diversification from simple patch occupancy–type models of single species metapopulations (Levins 1969, 1970; Hanski 1982, 1985, 1991; Gotelli 1991; Marquet and Velasco-Hernández 1997) to two species (Horn and MacArthur 1972; Levin 1974; Slatkin 1974; Hanski 1983; Nee and May 1992; Nee et al. 1997) to multispecies interactions (Levin 1974; Hastings 1980; Tilman 1994; Holt 1997). Of particular relevance here is the extension to their spatially explicit counterparts through the development of lattice models, such as coupled map lattices (Kaneko 1993), cellular automata (Caswell and Etter 1993; Molofsky 1994; Darwen and Green 1996; Keymer et al. 1998), and interacting particle systems (Durrett and Levin 1994*a*, 1994*b*).

Spatially explicit models of metapopulations have shown that landscape structure and patch dynamics can affect metapopulation dynamics and persistence (Bascompte and Solé 1996; Bevers and Flather 1999), the outcome of species interaction (Tilman et al. 1994, 1997*a*, 1997*b*; Dytham 1995; Huxel and Hastings 1998; Klausmeier 1998), and the behavior of territorial populations (Lande 1987).

Usually this effect is highly nonlinear, associated with the existence of critical thresholds determined by the structural properties of the landscape (environmental heterogeneity) and the demographic properties of the metapopulation (With and Crist 1995; Bascompte and Solé 1996). Landscape structure is used here in a general way to refer to factors shaping the distribution of the habitat (available patches) across space and time. In other words, by structure, we mean spatial and temporal heterogeneity.

In agreement with Fahrig (1992), we recognize two

---

[*] To whom correspondence should be addressed; e-mail: juank@eno.princeton.edu.

[†] E-mail: pmarquet@genes.bio.puc.cl.

[‡] E-mail: jxvh@xanum.uam.mx.

[§] E-mail: slevin@eno.princeton.edu.

Am. Nat. 2000. Vol. 156, pp. 478–494. © 2000 by The University of Chicago. 0003-0147/2000/15605-0002$03.00. All rights reserved.

broad categories of heterogeneity: spatial and temporal. Spatial heterogeneity (habitat patchiness) is determined by factors such as the number of available patches and their spatial pattern in determining the distribution of habitat. Temporal heterogeneity (habitat life span) is variability over time in the extent and/or quality of the habitat. By setting a random uncorrelated (spatial) pattern of habitat distribution, with no spatial contagion, and focusing on the effect of the amount of available habitat upon metapopulation persistence, several studies (Bascompte and Solé 1996; Boswell et al. 1998; Bevers and Flather 1999) have derived two major conclusions.

First, when dispersal is local, metapopulation extinction holds for smaller amounts of habitat destruction than predicted by mean field models because of the fact that local dispersal is less efficient than global dispersal in balancing the extinction rates of local populations. Second, landscape connectivity of this (uncorrelated) random pattern presents an abrupt transition as a function of the amount of available habitat, known as a "critical phase transition" in the percolation theory literature (see Stauffer and Aharony 1991 for an introduction to percolation theory). Basically, connectivity among patches falls into three distinct phases: disconnected/subcritical, critical, and connected/supercritical (see Green 1994 for role of landscape connectivity on ecological processes).

Spatial pattern in the distribution of habitat also has been shown to affect (meta-) population persistence. With and King (1999) and Hill and Caswell (1999) studied the effect of spatial pattern (spatial contagion), presenting a synthesis of metapopulation theory and percolation theory coupled with neutral landscape models. The main result of these studies is that the amount of habitat loss that a (meta-) population can tolerate depends upon the spatial pattern of suitable and unsuitable habitat. Fractal landscapes contain fewer and larger clusters of habitat patches than random landscapes and thus maintain connectivity for a greater amount of habitat loss (With and King 1999), thereby enhancing (meta-) population persistence.

The models discussed so far deal with species living in virtually permanent patchy environments, presenting different levels of landscape connectivity because of spatial pattern and/or habitat suitability. In such habitats, species persistence drastically depends upon the connectivity relationships dictated by dispersal capacity and distances between patches. Thus, such models have been applied to understand the effects of habitat destruction on populations living in stable habitats; these include many birds and mammals (see Andrén 1994) and woody plants (Bascompte and Solé 1998). However, for many systems, such as host-parasitoids, tidepool fishes, some agricultural systems, and infectious diseases with fast turnover, environments are highly dynamic.

Habitat life span is an important factor to consider in ephemeral or disturbed habitat; temporal components of the landscape, influencing habitat life span, interact with spatial components, such as habitat amount and/or spatial pattern, to determine metapopulation dynamics (for a review of dynamic landscape models and their applications, see Merriam et al. 1991).

By focusing on temporal components of landscape structure, Marquet and Velasco-Hernández (1997) and Brachet et al. (1999) studied the effects of landscape dynamics upon metapopulation persistence. These studies agree about the importance of dynamic properties of the landscape in determining metapopulation persistence. However, both studies are mean field models, thereby assuming global dispersal.

Very few fully spatially explicit models focus on the interaction between temporal and spatial components of landscape structure in determining population dynamics. Fahrig (1992; see also 1991, 1997) compared the relative effects of temporal scale (specifically rate of landscape change) and spatial scale (specifically measured distances among patches relative to species' dispersal range and patch sizes) upon metapopulation persistence of a single species. By using a lattice-based patch-dynamics model, she found that the effect of temporal scale far outweighed the effect of spatial scale on population persistence. Simulation models of this type have been extended to understand the dynamics of serpentine grasslands (Wu and Levin 1994; Moloney and Levin 1996) and the evolution of dispersal rate (Travis and Dytham 1999). Generally speaking, if habitat is very ephemeral, particulars about spatial parameters, such as dispersal distance and interpatch distance, may be ignored (Fahrig 1992). However, Fahrig (1992) varied distance among patches and patch sizes while keeping a constant amount of habitat. Thus, the combined effects upon population persistence of varying both the amount of available habitat and patch life span remain unknown.

Wu and Levin (1994) point out that the effect of disturbance on allowing species coexistence is spatiotemporal. Travis and Dytham (1999) show how higher dispersal rates evolve in ephemeral habitats in response to fluctuating habitat availability. The model of Wu and Levin (1994), as well as those of others (Fahrig 1992; Moloney and Levin 1996), rely upon a within-patch population dynamic submodel that depends upon many demographic parameters. As suggested by Wu and Levin (1994), we consider (in this article) a simpler landscape-metapopulation model in order to focus our attention upon how the thresholds of habitat loss and landscape connectivity are affected by considering landscape dynamics in the analysis. Particularly, we want to answer the following question: How does patch life span interact with habitat availability to determine landscape connectivity when there is dispersal limitation?

In this article, we introduce patch dynamics into a simple spatially explicit metapopulation patch-occupancy-type model, extending the static formalism previously used to a dynamical context in which generation and destruction of habitat patches take place. Thus, this article considers a spatially explicit version of the approaches of Levin and Paine (1974; see also Wu and Levin 1994; Marquet and Velasco-Hernández 1997; Hill and Caswell 1999).

We show that metapopulation persistence in dynamic landscapes depends on the interaction between three factors: the amount of habitat in the landscape, the rate of change of the amount of habitat, and the life history of the species living in the landscape. We suggest that including temporal considerations into landscape structure has two major implications. First, it shifts the problem of landscape connectivity from being a spatial problem of static patches to a spatiotemporal problem dealing with dynamic corridors connecting patches through space and time. Second, it changes the extinction threshold, the amount of habitat destruction a metapopulation can tolerate, by increasing local population extinction. In other words, it makes this threshold sensitive to the rates of destruction. Persistence is thus characterized by two interdependent thresholds: a threshold in habitat availability and a threshold in landscape dynamics.

The Model: The Interacting Particle System

We assume that, at time *t*, each spatial location *r* in a two-dimensional regular lattice with periodic boundary conditions is in state $\xi_t(r)$ (see table 1), drawn from the following set of possible $S = \{0, 1, 2\}$. State 0 represents a nonhabitable site that cannot be colonized by any species; state 1 corresponds to an empty, habitable patch, and state 2, to an occupied patch.

Patches are not static. In particular, nonhabitable locations ($\xi_t(r) = 0$) can change to empty habitable patches at rate λ. When we say that an event occurs at rate λ, we mean that the times τ_i between successive occurrences have an exponential distribution with parameter λ; that is, $P(\tau_i \leq t) = 1 - \exp(-\lambda t)$. On the other hand, habitable patches (empty or occupied) can change to nonhabitable locations at rate *e*. These rates characterize patch creation and destruction processes acting simultaneously in the conformation of the landscape of habitat patches.

Metapopulation dynamics—that is, the dynamics of species within this patch dynamic framework—are restricted to spatial locations belonging to the landscape of habitable patches. Occupied patches ($\xi_t(r) = 2$) undergo local population extinction at rate δ and empty patches ($\xi_t(r) = 1$) are colonized at rate $\beta\rho(r, \xi)$. The parameter β is the propagule production rate of local populations, and $\rho(r, \xi)$ represents the proportion of occupied locations in the interaction neighborhood $\mathcal{N}_r$ surrounding a patch located at position *r*, when the process is in state ξ (see fig. 1*A*). In particular, we consider a neighborhood, of the (see fig. 1*B*) eight nearest cells (called "Moore").

In other words, we model metapopulation dynamics as a continuous-time stochastic process. This model is similar to the one used by Hill and Caswell (1999) to study the role of spatial pattern in persistence in static landscapes. In the mathematical literature, such models are technically known as "interacting particle systems" (Liggett 1985; Durrett and Levin 1994*b*). We incorporate dynamic properties in the structure of the landscape of habitable patches; by doing so, we are able to study the role of temporal as well as spatial features in the distribution of habitat upon metapopulation persistence and patch occupancy. Armed with this model, we want to investigate how thresholds of habitat loss are dependent upon the rate of habitat destruction and how the interaction between these two relates to landscape connectivity.

The model described above has four parameters: patch creation rate (λ), patch destruction rate (e), propagule production rate (β), and local population extinction rate (δ). This four-dimensional parameter space can be viewed as the Cartesian product of two planes—one representing the patch-dynamic parameter space and the other, the metapopulation-dynamics parameter space. The relationship between these two parameter spaces represents the relationships between landscape and demographic processes in determining metapopulation dynamics. In this article, we focus on the effects of different regimes of patch dynamics—patch creation and destruction rates—upon patch occupancy and metapopulation persistence of a given life history of patch colonization and local population extinction.

Results

Patch Dynamics and Landscape Structure

Habitat dynamics are driven by the conversion of nonhabitable locations into habitable patches and by the extinction of these, turning habitable patches back into nonhabitable locations. These transitions do not depend on particular spatial configurations. Thus habitat dynamics can be studied analytically as being the result of a random process across space.

In the degenerate case—when propagule production rate and local extinction rates are both equal to 0—the interacting particle system collapses into a set of independent (one for each location *r* in the lattice) continuous time Markov chains with two states representing habitable

Table 1: Definitions of frequently used symbols

Symbol	Definition
$\mathcal{N}_r$	Interaction neighborhood—centered at r—for the dispersal process
r	Position vector for sites in the lattice
r_0	Position vector of the origin of the lattice (0, 0)
$S = \{0, 1, 2\}$	Set of possible states a site can adopt: destroyed, empty, occupied
λ	Patch creation rate
e	Patch destruction rate
β	Propagule production rate of local populations
δ	Local population extinction rate
$\bar{\beta}$	Adjusted propagule production rate
$\tilde{\delta}$	Adjusted local population extinction rate
t	Index for time (continuous)
ξ_t	Configuration of the lattice at time t
$\xi_t(r)$	State of a focal site r at time t
ξ_0	Initial distribution for the process at time $t = 0$
ξ_0^i	Probability a site is set to i time $t = 0$
ξ_∞	Equilibrium distribution for the process
$\rho(r, \xi)$	Proportion of the neighborhood $\mathcal{N}_r$ with local populations
$\beta\rho(r, \xi)$	Colonization rate experienced by a site located at r
d_t	Stochastic process representing the amount of destroyed sites
$\bar{d}$	Long-term expected amount of "destroyed" sites in the spatial process
s_t	Stochastic process representing the amount of suitable habitat
$\ddot{s}(t)$	Expected amount of suitable habitat in the spatial process
$\bar{s}$	Long-term expected amount of suitable habitat in the spatial process
$\bar{\tau}$	Long-term expected life span of habitat patches in the spatial process
s_c	Minimum amount of habitat a mean field metapopulation can tolerate
τ_c	Minimum patch life span a mean field metapopulation can tolerate
p_t	Stochastic process representing patch occupancy
$\bar{p}$	Long-term expected patch occupancy in the spatial process
$\bar{p}_i$	Long-term expected proportion of sites in state i in the spatial process
$p_i(t)$	Mean field proportion of sites at state i at time t
$\hat{p}_i$	Mean field equilibrium proportion of sites at state i
$\hat{p}$	Mean field equilibrium proportion of occupied habitat
$\hat{p}^{\text{static}}$	Mean field equilibrium proportion of occupied habitat in the static landscapes
p_c	Critical value of habitat amount at which percolation occurs
R_0	Basic infective number; number of propagules produced per life span
R_0^*	Infective number adjusted for dynamic landscapes
γ	Balance between intrinsic and effective local population extinction rates

($\xi_t(r) = 0$) and nonhabitable locations ($\xi_t(r) \neq 0$). Each of these sites will have a long-term probability $\lambda/(\lambda + e)$ of being habitable and $e/(\lambda + e)$ of being nonhabitable (Feller 1968). Hence, we can treat the long-term proportion of habitable sites in the whole lattice as given by a binomial process with parameters N (the lattice size; we used 100×100 cells in most simulations, but larger lattices were also explored) and μ (average amount of suitable habitat). Therefore, the long-term expected proportion of habitable locations behaves in time as a binomial noise with expected value $\bar{s} = \lambda/(\lambda + e)$ and variance $N(\lambda e)/(\lambda + e)^2$ (see fig. 2). Here, the transient behavior of the expected value $\bar{s}(t)$ for the stochastic process s_t representing the amount of suitable habitat (or destroyed $d_t = 1 - s_t$) is

$$\bar{s}(t) = \bar{s} + [\bar{s}(0) - \bar{s}] \exp[-(\lambda + e)t]. \qquad (1)$$

For two-dimensional lattices with a Moore neighborhood, it is known that there exists a threshold percolation value of site occupancy probability $p_c \approx 0.4$ (Stauffer and Aharony 1991; Plotnick and Gardner 1993). In our model, at this threshold, the habitat percolates through the lattice, forming a large connected cluster of habitat patches. Below this threshold, the habitat is fragmented into many different unconnected clusters of patches. Thus, we can change the (long-term) average connectivity properties of the landscape by choosing λ and e in such a way as to make $\bar{s}$ above or below the critical threshold p_c.

Since, in our model, patches are created and go extinct

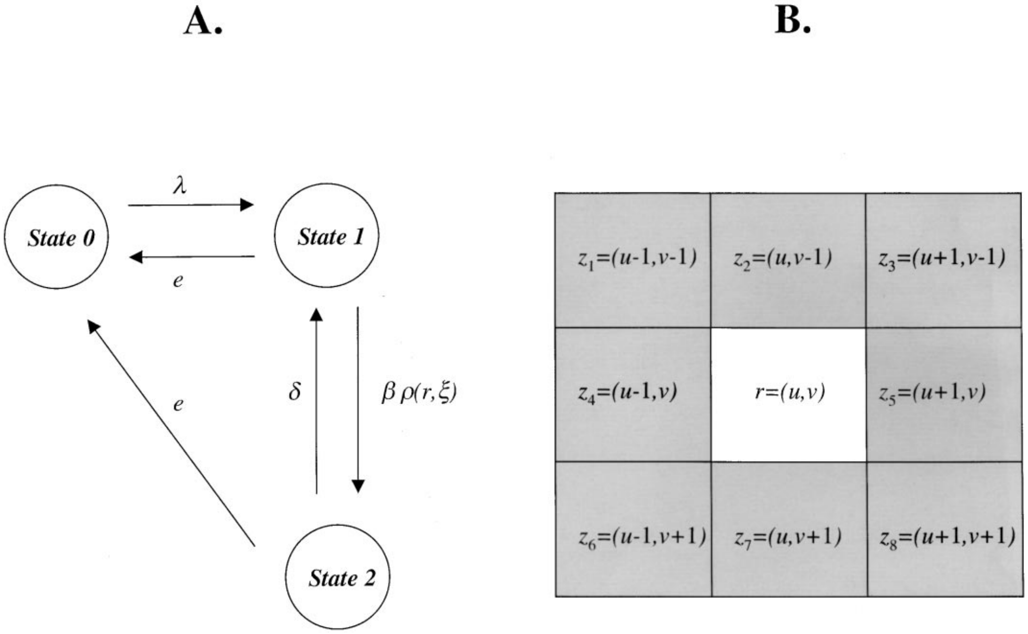

Figure 1: Structure of the model. *A*, Each site r in the lattice can adopt one of the states, $S = \{0, 1, 2\}$. These represent, respectively, nonhabitable sites, empty habitat patches, and occupied patches. The transitions between these states are given by the rates λ of patch creation, e of patch destruction, δ of population extinction, and $\beta\rho(r, \xi)$ of patch colonization, where β is the (local population) rate of propagule production and $\rho(r, \xi)$ represents the proportion of propagule sources in the neighborhood $\mathcal{N}_r$ of r when the process is in state ξ. *B*, Neighborhood $\mathcal{N}_r = \{z_1, z_2, \dots, z_8\}$ (*shaded cells*) of site $r = (u, v)$.

continuously, the landscape dictated by $\bar{s}$ will change over time, but its average connectivity properties will remain the same (since we fix $\bar{s}$ to a constant value). Since e is the rate of patch destruction, we have $\bar{\tau} = 1/e$ as the expected lifetime of a habitat patch. Thus, many different landscapes share the same expected topological properties (same $\bar{s}$) but change at different timescales (different $\bar{\tau}$), with smaller $\bar{\tau}$ being associated with higher patch turnover rates. Thus, in our model, habitat dynamics have both a spatial component ($\bar{s}$) and a temporal component ($\bar{\tau}$). In this article, we will explore how the dynamic aspects affect population persistence.

From the discussion above, we can express the patch-dynamics parameter space in the new coordinates defined by the following transformation:

$$\bar{s} = \frac{\lambda}{\lambda + e}, \tag{2}$$

$$\bar{\tau} = \frac{1}{e}. \tag{3}$$

Thus, henceforth, we note that any regime of patch dynamics, in terms of patch creation and extinction rates, represents a landscape with different combinations of habitat amount and patch life span. This provides us with different habitat templates to study metapopulation dynamics in heterogeneous and dynamic environments.

The Interaction between Metapopulation and Habitat Dynamics

The study of the full system, including both metapopulation and landscape dynamics, is analytically intractable but still amenable to numerical simulations and mean field approximations.

The Mean Field Approximation. Neglecting spatial correlations, we can approximate the lattice behavior by writing equations for the temporal evolution of the proportion $p_i(t)$ of particles (sites) in each state $i \in S$. Thus, we obtain the following system of mean field (MF) equations:

$$\frac{d}{dt}p_0 = e(p_1 + p_2) - \lambda p_0, \tag{4}$$

$$\frac{d}{dt}p_1 = \lambda p_0 - \beta p_1 p_2 + \delta p_2 - e p_1, \tag{5}$$

$$\frac{d}{dt}p_2 = \beta p_2 p_1 - (\delta + e) p_2, \tag{6}$$

which (see appendix) has the unique globally stable nontrivial equilibrium ($\hat{p}_2 \neq 0$):

$$\hat{p}_0 = \frac{e}{\lambda + e}, \tag{7}$$

$$\hat{p}_1 = \frac{\delta + e}{\beta}, \tag{8}$$

$$\hat{p}_2 = 1 - \frac{e}{\lambda + e} - \frac{\delta + e}{\beta}. \tag{9}$$

Notice that $1 - \hat{p}_0 = \lambda/(\lambda + e)$ corresponds to the long-term expected amount of suitable habitat $\bar{s} = \lim_{t\to\infty}\bar{s}(t)$, calculated for the spatial stochastic process (eqq. [1], [2]). So, we define $\hat{p} = \hat{p}_2/\bar{s}$ as the (long-term) proportion of suitable habitat occupied by a species. Thus,

$$\hat{p} = 1 - \frac{\delta + e}{\beta\bar{s}}. \tag{10}$$

Now defining $\tilde{\beta} \equiv \beta\bar{s}$, which represents the effective colonization rate corrected because of the loss of propagules arriving at nonhabitable locations, and $\tilde{\delta} \equiv \delta + e$, which is the effective rate of population extinction because of intrinsic extinction δ and habitat destruction e, we get

$$\hat{p} = 1 - \frac{\tilde{\delta}}{\tilde{\beta}}, \tag{11}$$

which corresponds to the classical equilibrium expression for metapopulation occupancy (Levins 1969, 1970).

Since $e = 1/\bar{\tau}$, we can rewrite equation (10) as a function of habitat amount $\bar{s}$ (or destruction $\bar{d} \equiv 1 - \bar{s}$) and expected patch lifetime $\bar{\tau}$. Thus,

$$\hat{p} = 1 - \frac{1}{\beta\bar{s}}\left(\delta + \frac{1}{\bar{\tau}}\right). \tag{12}$$

Figure 3 shows $\hat{p} \geq 0$ (from eq. [12]) as a surface over the (transformed) patch dynamics parameter space. Patch occupancy varies across different landscapes for two life histories, increasing as $\bar{\tau}$ and $\bar{s}$ increase. Figure 3*A* shows this surface for a species life history with parameters $\beta = 8$ and $\delta = 0.1$, while figure 3*B* is for parameters $\beta = 1$ and $\delta = 0.1$. Metapopulation persistence ($\hat{p} > 0$) depends on both habitat suitability $\bar{s}$ and patch lifetime $\bar{\tau}$.

In the slow limit ($\bar{\tau} \to \infty$), when the landscape is static, equation (12) collapses to

$$\hat{p}^{\text{static}} \equiv \lim_{\bar{\tau}\to\infty} \hat{p} = 1 - \frac{\delta}{\beta\bar{s}}, \tag{13}$$

which, under rescaling by $\bar{s} = 1 - \bar{d}$, becomes

$$\hat{p}_2^{\text{static}} \equiv \hat{p}^{\text{static}}\bar{s} = 1 - \bar{d} - \frac{\delta}{\beta}, \tag{14}$$

essentially the equation used by Bascompte and Solé (1996, 1998) to study static habitat loss. More generally,

$$\hat{p}_2 \equiv \hat{p}\bar{s} = 1 - \bar{d} - \frac{1}{\beta}\left(\delta + \frac{1}{\bar{\tau}}\right). \tag{15}$$

In figure 4, we can see however that different relationships between metapopulation occupancy (or persistence) and habitat destruction $\bar{d} = 1 - \bar{s}$ can be obtained, depending on the rate of landscape change $\bar{\tau}$ even with the same life history. In particular, if $e > 0.5$, species with low propagule production rates β are much more sensitive to $\bar{\tau}$ and are unable to persist even when the entire landscape is suitable (see fig. 3*B*).

An important quantity in metapopulation models (analogous to that in epidemiology) is the infective number $R_0 = \beta/\delta$ (Anderson and May 1992). The average number of propagules a local population produces during its life span (R_0) characterizes the "infective" properties of a particular life history, providing us with an invasion criterion that depends on the average colonization-extinction behavior of populations. If $R_0 > 1$, the (mean field) metapopulation persists, and if $R_0 \leq 1$, we have metapopulation extinction.

Note that, in our formulation, the condition for population persistence ($\hat{p}_2 > 0$) can be written as

$$R_0^* = \frac{\tilde{\beta}}{\tilde{\delta}} = \frac{\beta\bar{s}}{\delta + e} = \left(\frac{\beta}{\delta}\right)\bar{s}\left(\frac{\delta}{\delta + e}\right) > 1. \tag{16}$$

In this form, it becomes clear, at least in the mean field approximation, how the dynamic aspects of habitat loss, as represented by e, make persistence more difficult. The MF system (4)–(6) has a direct epidemiological analogue (Levin and Pimentel 1981; Anderson and May 1992; Nee 1994; Gyllenberg et al. 1997; Marquet and Velasco-Hernández 1997; Hernández-Suarez et al. 1999): p_0 represents the number of immune hosts in a population, p_1 the proportion of nonimmune susceptibles, and p_2 infected hosts; e is the natural death rate, λ the rate of loss of immunity, and δ the recovery rate. Births are balanced by deaths, and newborns are initially immune; otherwise, there is no immunity. Initial immunity (in this analogy) may be thought of as a result of behavioral factors. Under these assump-

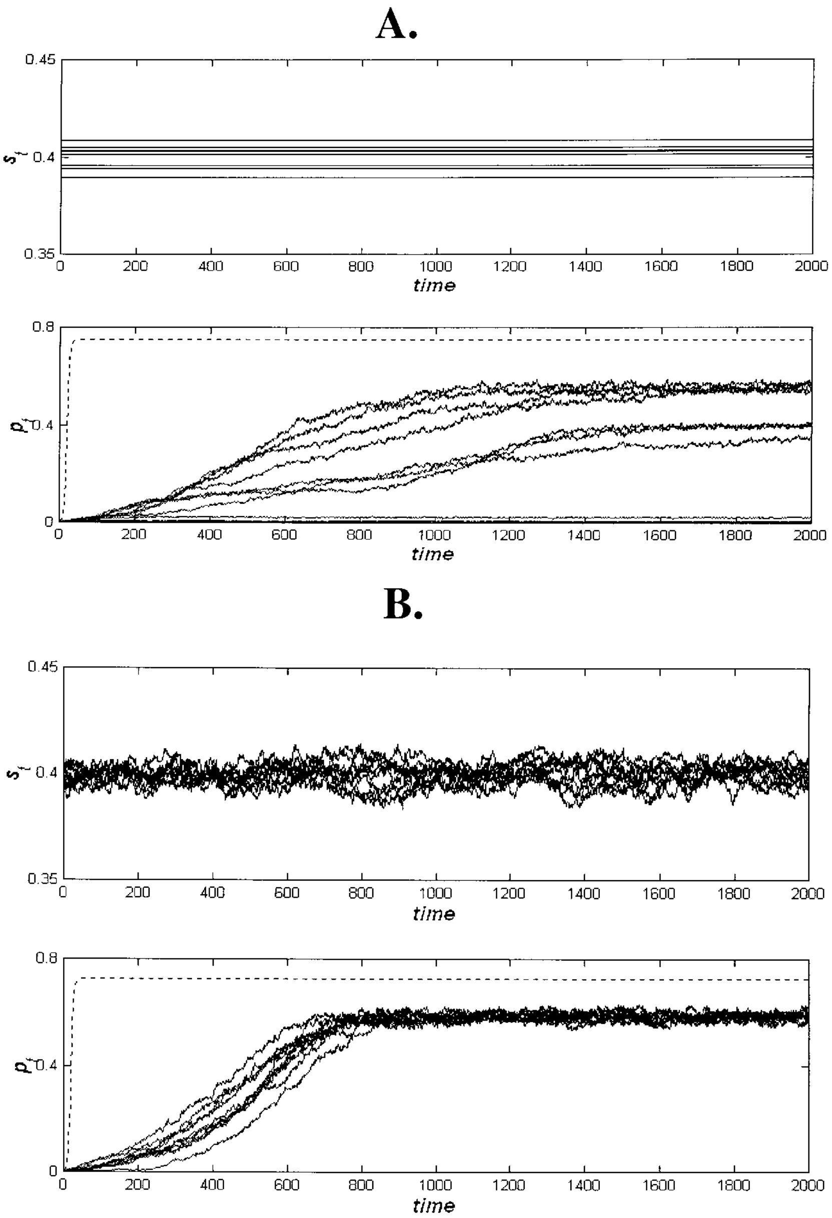

Figure 2: Long-term behavior of the system. Ten independent realizations of the process (IPS) for species ($\beta = 1$, $\delta = 0\ .1$) in (*A*), static ($\lambda = 0$, $e = 0$) and (*B*), dynamic ($\lambda = 0.006$, $e = 0.01$) landscapes. Amount of suitable patches (*top panels*) s or s_t (*A* or *B*) and patch occupancy p_t (*bottom panels*) are shown from $t = 0$ to $t = 2{,}000$, starting from the following initial conditions: we generate a (quasi-critical) percolation lattice representing the initial habitat distribution ($s = 1 - \xi_0 = 0.4$), and then we set the origin ($r_0 = (0, 0)$) and its neighborhood $\mathcal{N}_{r_0}$ to be completely occupied by local populations ($\xi_0(z) = 2$ for all $z \in \mathcal{N}_{r_0} \bigcup r_0$). The smooth (*dotted*) curves (*bottom panels*) are numerical integrations of the MF patch occupancy $p(t) = p_2(t)/(1 - p_0(t))$.

tions, the disease will be maintained if equation (16) is satisfied, where $1/(\delta + e)$ is the mean infectious period.

Defining $\gamma \equiv (\delta/\tilde{\delta}) = \delta/(\delta + e)$ as the ratio between the intrinsic and the effective population extinction rates, we can rewrite equation (16) as

$$R_0^* = R_0 \bar{s} \gamma. \qquad (17)$$

In other words, (mean field) metapopulation persistence in dynamic landscapes ($R_0^* > 1$) is determined by three different factors: the life history of the species living in the landscape (R_0), the amount of habitat ($\bar{s}$), the ratio (γ) between the intrinsic population extinction rate δ and the effective population extinction rate $\tilde{\delta}$ because of the scale of landscape change ($\bar{\tau}$).

We can determine the values for two different kinds of (interdependent) extinction thresholds affecting species of different life histories living in dynamic landscapes. First, there is a threshold corresponding to the minimum amount of suitable habitat $s_{\min}$ that a (dynamic) landscape needs in order to support a species for a life history, given that $R_0 > 1$ (figs. 3, 4). Equivalently, the critical condition may be expressed in terms of a threshold that relates to the minimum expected lifetime $\tau_{\min}$ of patches in the landscape (figs. 3, 4). From equation (16), we obtain these thresholds as

$$s_{\min} = \frac{1}{\beta}\left(\delta + \frac{1}{\bar{\tau}}\right), \tag{18}$$

$$\tau_{\min} = (\beta\bar{s} - \delta)^{-1}. \tag{19}$$

Notice however, that these thresholds are functions of each other, so they define a curve ($\beta\bar{s} = \delta + e$) in the patch-dynamics parameter space where the $\hat{p}$ surface (eq. [12]) intersects the plane $\hat{p} \equiv 0$ (see fig. 3). The region $\mathcal{P}$ composed of landscapes above the curve (i.e., $\beta\bar{s} > \delta + e$) represents the set of landscapes where persistence is possible ($\hat{p} > 0$) for a given life history. Notice that the size of this region decreases as R_0 decreases (cf. fig. 3*A*, 3*B*).

Thus, in MF scenarios, for the population to achieve (mean field) metapopulation persistence, the following three equivalent conditions must be satisfied: $R_0^* > 1$, $\bar{s} > s_{\min}$, $\bar{\tau} > \tau_{\min}$.

Numerical Simulations of the Particle System. Setting $\lambda = e = 0$, we produce a static landscape ($\bar{\tau} = \infty$) representing heterogeneity in the (uncorrelated) spatial distribution of the (static) habitat. In this case, the MF system (eqq. [4], [6]) collapses into Levins's (1969) classic model (without any term representing habitat loss) describing metapopulation dynamics but restricted to the subset of sites representing habitable patches. This array of patches can have any desired amount of habitat and connectivity, as specified by the initial distribution $\xi_0 = (\xi_0^0, \xi_0^1, \xi_0^2)$ (where ξ_0^i represents the probability that a site is assigned to state i at $t = 0$) of the interacting particle system (IPS). In particular, if we set $\xi_0^0 = 0$ (i.e., all sites are habitable patches), and rescale $\beta' = 8\beta$, we obtain the model studied by Durrett and Levin (1994*b*) known as the "basic contact process"; so by the complete convergence theorem (Durrett and Levin 1994*b*, p. 335) we know the IPS will converge to a nontrivial equilibrium distribution ξ_∞. We conjecture (supported by numerical simulations; fig. 2; see below) that this result remains valid if the array of patches is dynamic or static but totally connected (i.e., all patches in the landscape are accessible by dispersal from every patch). The distribution ξ_∞ describes the long-term average proportion of sites in each particular state ($\bar{p}_0, \bar{p}_1, \bar{p}_2$). We define $\bar{p} = \bar{p}_2/(1 - \bar{p}_0)$ to be the long-term expected value for the stochastic process p_t corresponding to patch occupancy in the IPS.

If the array of patches is not totally connected, the system experiences anomalies because of the loss of habitat connectivity and no longer has a unique equilibrium distribution ξ_∞ (see fig. 2*A*). Instead, it has multiple equilibrium distributions depending on the initial conditions. However, three main classes of behavior can be characterized by percolation theory: supercritical, critical, and subcritical (Green 1994). If the landscape is subcritical ($\bar{s} < p_c$), then most of the landscape is broken into many isolated habitat patches and small clusters of patches. If it is a critical landscape ($\bar{s} = p_c$), a single large region—the spanning cluster—connects much of the landscape and patches are clumped into clusters of all sizes. In supercritical landscapes ($\bar{s} > p_c$), almost the entire landscape is connected, with few isolated patches remaining.

In our formulation, we produce a random (uncorrelated) static landscape by a percolation map characterized by ξ_0^0; thus, sites are defined as available with probability $(1 - \xi_0^0)$ and unavailable with probability ξ_0^0. This random landscape will have (on average) a constant proportion $s = 1 - \xi_0^0$ of sites available for colonization. We start with the origin ($r_0 = (0, 0)$) and its neighborhood completely occupied by local populations at time $t = 0$ (i.e., $\xi_0(z) = 2$ for the origin and all z in the neighborhood), and we focus on the spread of these "founder populations" through the landscape of habitat patches. This phenomenon has been studied in analogous problems of diffusion in disordered media (Orbach 1986; Stauffer and Aharony 1991).

Above the critical (spatial) percolation threshold ($\bar{s} > p_c$), metapopulation dynamics will be (statistically) similar to the case of homogeneous landscapes since the behavior on the spanning cluster will dominate over many realizations. Thus, in this class of "supercritical (static) landscapes," metapopulation dynamics are statistically well described by the case of homogeneous landscapes. This means that, independent of the initial conditions (where the initial populations invade the array of patches), species will (mostly) spread to the whole landscape. At the critical value ($\bar{s} = p_c$), the landscape is self-similar, having clusters of all sizes (between one and the lattice size). Thus, different (but not equally probable) occupancies can be reached, depending on the initial conditions. Figure 2*A* shows 10 realizations of the process for a critical static

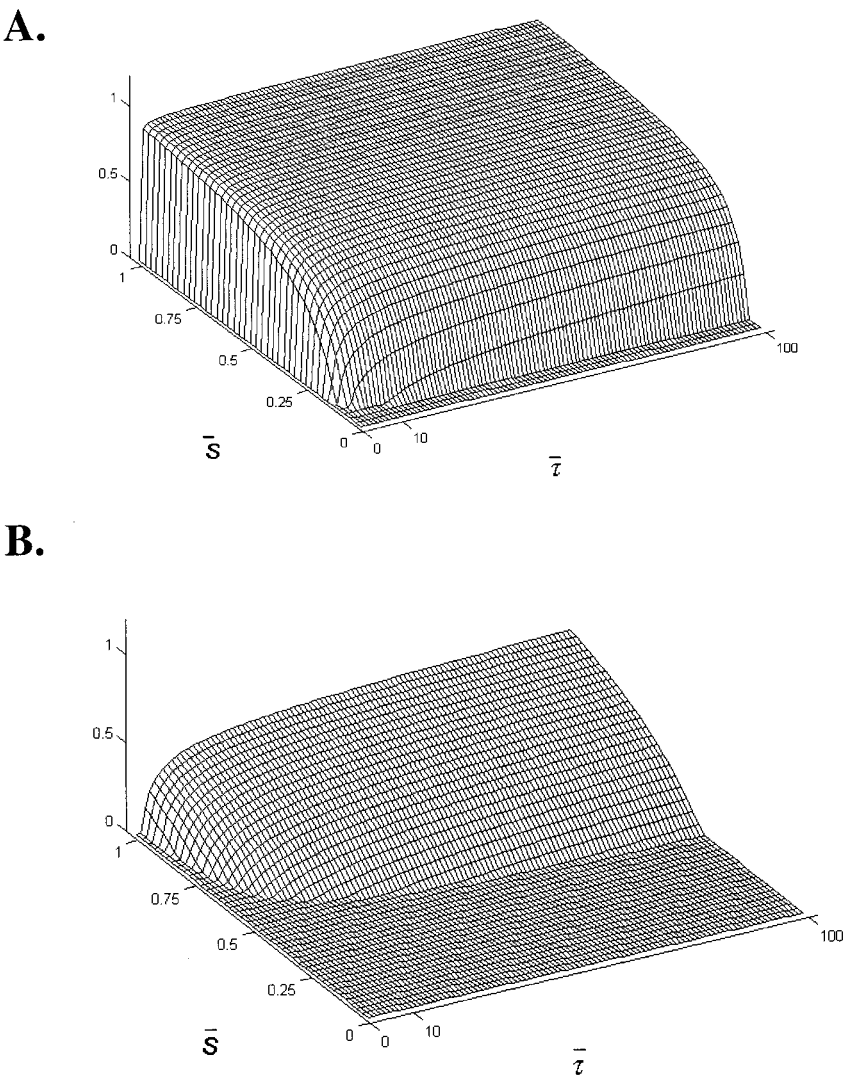

Figure 3: Positive equilibrium occupancy in the mean field model ($\hat{p} \geq 0$). The quantity $(1/2)(|\hat{p}| + \hat{p})$ derived from equation (12) is plotted as a function of habitat suitability $\bar{s}$ and patch mean lifetime $\bar{\tau}$. *A*, $\beta = 8$ and $\delta = 0.1$. *B*, $\beta = 1$ and $\delta = 0.1$. Notice that the $\bar{\tau}$-axis is in log-scale.

landscape, starting from the initial conditions described above. Notice how, after a long transient that is a function of the lattice size (we used 100 × 100 cells), the process converges to different proportions of patch occupancy. Below the critical value ($\bar{s} < p_c$), habitat is fragmented into a set of disconnected clusters of characteristic sizes (dependent on the $\bar{s}$ value) embedded in an ocean of nonhabitable locations (matrix sites). In this case, patch occupancy is seriously depressed, since habitat fragmentation prevents species from propagating through the landscape (see figs. 5*A*, 6*A*) keeping occupancy restricted to small (in relation to the whole lattice) clusters.

In the case of dynamic landscapes ($\lambda + e > 0$), since the only source for spatial correlations is due to local dispersal, the MF equations accurately predict the temporal behavior of the average amount of habitat $\bar{s}(t)$. Notice that, setting $\beta = \delta = p_2(t) \equiv 0$ and integrating equation (6), we get equation (1). Figure 2*B* shows numerical simulations in support of our conjecture that, in the case of dynamic landscapes, the system converges to the equilibrium distribution ξ_∞. Figure 4 shows that $\bar{p}$ behaves qualitatively similarly to $\hat{p}$ (derived from the MF) as a function of different amounts of suitable habitat ($\bar{s}$) and patch life span $\bar{\tau}$. However, $\hat{p}$ overestimates the expected patch occupancy

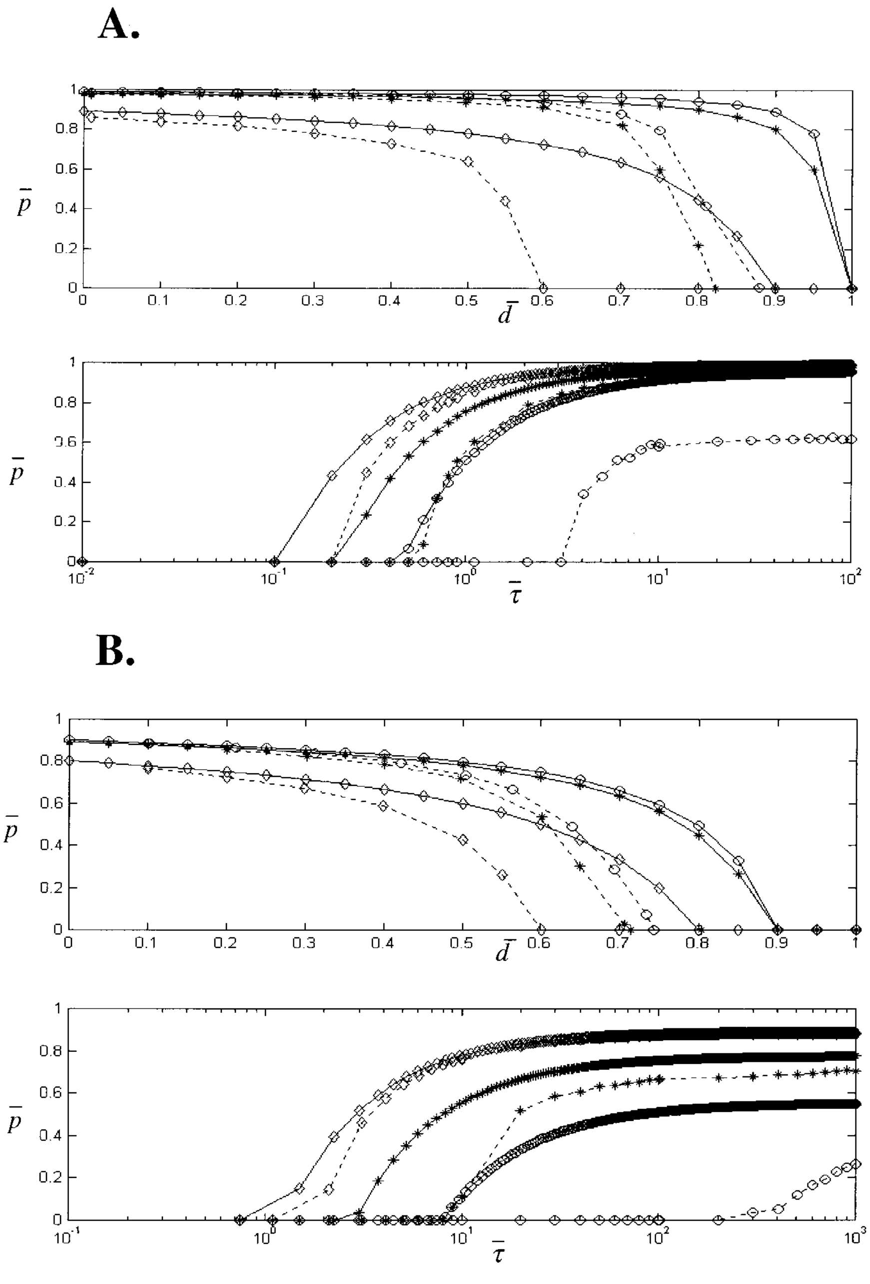

Figure 4: Expected occupancy in the spatial model. Numerical estimates of expected patch occupancy $\bar{p}$ of the spatial model are plotted as functions of expected destroyed habitat $\bar{d} = 1 - \bar{s}$ (*top panels*) and mean patch lifetime $\bar{\tau}$ (*bottom panels*). Solid line represents the mean field prediction; and the dotted lines, the numerical simulations of the IPS. *A*, $\beta = 8$ and $\delta = 0.1$. In the upper panel: (*diamonds*) $\bar{\tau} = 1$, (*stars*) $\bar{\tau} = 10$, and (*circles*) $\bar{\tau} = 100$. In the bottom panel: (*diamonds*) $\bar{s} = 0.90$, (*stars*) $\bar{s} = 0.45$, and (*circles*) $e = 0.225$. *B*, $\beta = 1$ and $\delta = 0.1$. In the upper panel: (*diamonds*) $\bar{\tau} = 10$, (*stars*) $\bar{\tau} = 100$, and (*circles*) $\bar{\tau} = 1{,}000$. In the bottom panel: (*diamonds*) $\bar{s} = 0.90$, (*stars*) $\bar{s} = 0.45$, and (*circles*) $\bar{s} = 0.225$.

of the spatial model $\bar{p}$, as well as the extinction thresholds ($s_{\min}$ and $\tau_{\min}$), since it neglects spatial correlations because of local dispersal. This means that the three persistence conditions described above have to be corrected by an error term, the result of neglecting the spatial structure. Thus, (spatial) metapopulation persistence depends on the achievement of the following conditions: $R_0^* > 1 + \epsilon_{R_0}$, $\bar{s} > s_{\min} + \epsilon_s$, $\bar{\tau} > \tau_{\min} + \epsilon_\tau$, where ϵ_{R_0}, ϵ_s, and ϵ_τ account for the approximation errors in the MF equations (see fig. 4). In almost static (very large $\bar{\tau}$) and highly connected

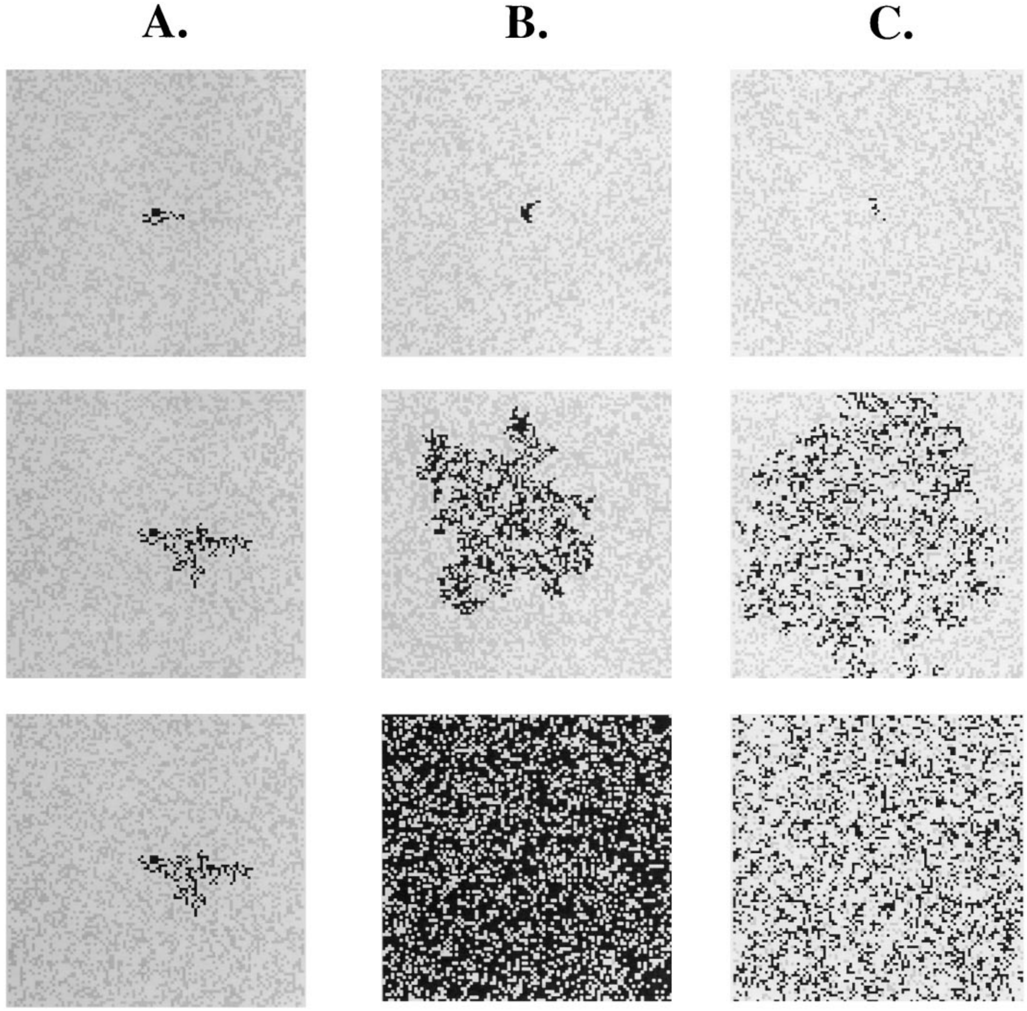

Figure 5: Spatial pattern of the model. Spatial snapshots for species $\beta = 8$ and $\delta = 0.1$, living in three landscapes that differ only in their temporal component $\bar{\tau}$. All landscapes are (spatially) disconnected, with $\bar{s} = 0.35 < p_c$. *A*, *B*, and *C* correspond, respectively, to $\bar{\tau} = \infty$ (a static landscape), $\bar{\tau} = 100$ (slightly changing), and $\bar{\tau} = 5$ (fast landscape). From top to bottom, $t = 10$, $t = 100$, and $t = 250$. The shading represents nonhabitable locations (*white*), habitable empty patches (*gray*), and occupied patches (*black*).

($\bar{s} \rightarrow 1$) landscapes, the disagreement between the MF and the IPS is a decreasing function of R_0. Thus, highly infective ($R_0 \rightarrow \infty$) species are well predicted by MF equations, while in the case of weakly infective ($R_0 \rightarrow 1$) species the MF prediction is poor.

In slow (large $\bar{\tau}$ and positive λ) landscapes, clusters of patches change dynamically, connecting to each other through spatiotemporal corridors that transport propagules among clusters (fig. 6*B*). Thus, independently of the expected properties of spatial connectivity (characterized by $\bar{s}$), populations always spread through the whole landscape in the long term (fig. 5*B*). As the landscape changes faster (figs. 5*C*, 6*C*), $\bar{\tau}$ gets smaller (cf. the landscape component of fig. 6*B* and 6*C*), so the conductivity of these corridors gets higher since more contacts occur per unit of time (cf. the spread of occupancy between fig. 6*B* and 6*C* and between fig. 5*B* and 5*C*), but patch occupancy gets lower because of the additive effect of the destruction rate *e* upon the effective population extinction $\tilde{\delta} = \delta + e$. If the landscape changes even faster, metapopulation extinction holds when we cross the threshold $\tau_{\min} + \epsilon_{\tau}$ (see fig. 4*A*, 4*B*, *lower panel*). This reflects a connectivity problem in the space-time of landscape dynamics known in physics as "direct percolation" (Kinzel 1983; see Stauffer and Ahar-

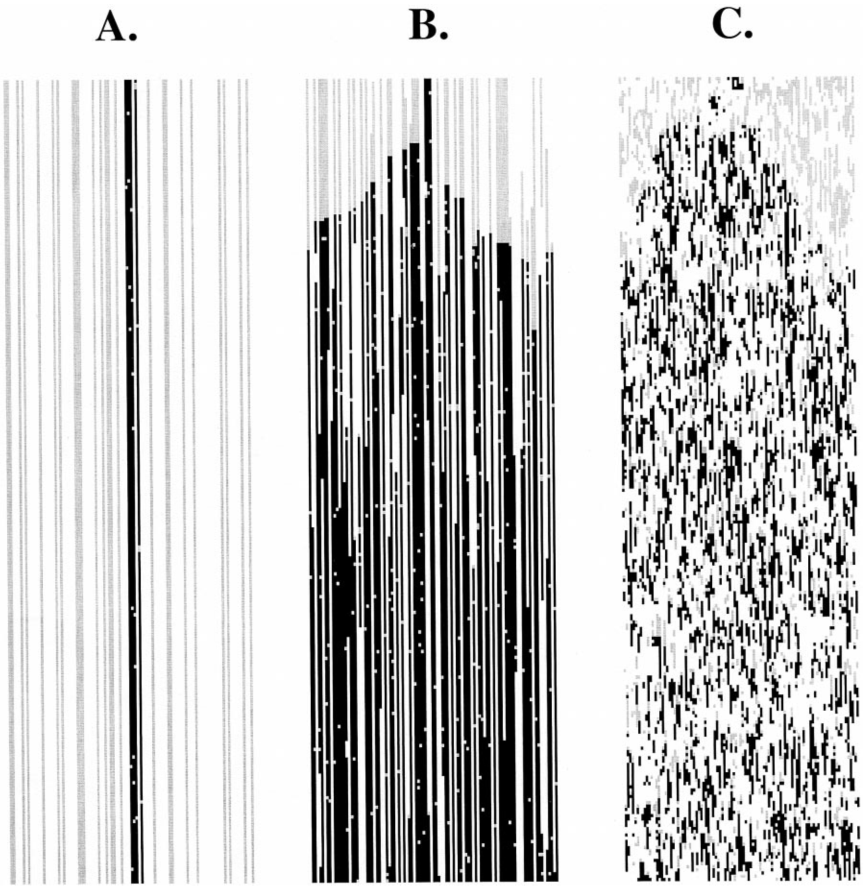

Figure 6: Spatiotemporal pattern of the model. Slides through the space-time of figure 5 simulations are taken by following the temporal evolution of a one-dimensional transect through the middle of the lattice. *A–C* correspond, respectively, to $\bar{\tau} = \infty$ (static landscape), $\bar{\tau} = 100$ (slightly changing), and $\bar{\tau} = 5$ (fast landscape); $\bar{s} = 0.35 < p_c$, $\beta = 8$, and $\delta = 0.1$. The shading represents nonhabitable locations (*white*), habitable empty patches (*gray*), and occupied patches (*black*). Time t goes from $t = 0$ at the top to $t = 250$ at the bottom.

ony 1991). Analogous to the spatial counterpart, there exists a critical value for $\bar{s}$ and $\bar{\tau}$ (critical curve) at which landscape dynamics percolate (in a directed sense) through the space-time of the IPS (Kinzel 1983), allowing species to propagate through the whole array of patches even though the spatial component of the landscape is disconnected (notice that $\bar{s}$ in figs. 5, 6 is below p_c). Determining the values at which this phase transition occurs is a fascinating area of current statistical physics, and clearly goes beyond the scope of this article.

In the case of landscapes with parameters $\lambda = 0$ and $e > 0$, of course the process will converge to a lattice with only destroyed sites ($\bar{s} = 0$). But it is important not to forget that it will do it as a function $\bar{s}(t) = (1 - \xi_0^0)\exp(-et)$ of the rate e of patch destruction (see eq. [1]). This underscores the fact that the minimum amount of habitat required for population persistence is a function of the rate $e = 1/\bar{\tau}$ of patch destruction (see eq. [18]). Respectively, if $\lambda > 0$ and $e = 0$ after the landscape transient governed by $\bar{s}(t) = (1 - \xi_0^0)\exp(\lambda t)$, the system will converge to Durrett and Levin's (1994*b*) contact process in a homogeneous lattice.

Discussion

Previous studies of habitat fragmentation on static landscapes generally have concluded that habitat loss and spatial pattern can deeply affect the long-term persistence of metapopulations (Lande 1987; Nee and May 1992; Tilman et al. 1994, 1997*a*, 1997*b*; Bascompte and Solé 1996, 1998; With and King 1997; Boswell et al. 1998; Klausmeier 1998; Bevers and Flather 1999; Hill and Caswell 1999); our model is no exception. We agree with these studies with respect to the existence of thresholds of habitat destruction above which extinction is attained. We also agree in the inaccuracy of the MF approximation in the (quantitative) prediction of these thresholds and the behavior of their spatial counterparts. However, we find that these thresholds are not independent of the rate of habitat destruction. In ephemeral environments, metapopulation persistence and patch occupancy can be very sensitive to further increases in habitat destruction rates, regardless of the amount of habitat available.

By saying "while slowly increasing the number of sites destroyed" (Tilman et al. 1997*b*, p. 12) or "we increase the number of destroyed sites" (Bascompte and Solé 1996, p. 470), one implicitly assumes a specific rate of destruction (even though small). However this hidden assumption is not explicitly represented in the equations governing the spatial models used in those studies (Bascompte and Solé 1996; Tilman et al. 1997*b*). Thus, the mean field thresholds (habitat destruction) reported there do not include the factor e/β because of the additive effect of the rate of destruction upon local population extinction (eq. [18]). Therefore, the inaccuracy of the MF equations used in those studies to understand the spatial models is not exclusively due to spatial correlations (as in our model) but is confounded by the effects of both neglecting spatial correlations and not considering the rate of destruction. We also found that this inaccuracy is a decreasing function of the life-history invasion criterion $R_0 > 1$.

Regarding this model, our most important result is that long-term metapopulation persistence depends on the relationship between the scale of metapopulation dynamics (given by the life-history parameters) and landscape dynamics (γ in eq. [17]). We found that for a given species with a particular life history (in terms of propagule production rate and extinction proneness), there exists a critical value τ_c for habitat life span above which metapopulation persistence is ensured. Below this critical value, the landscape changes too fast in relation to the scale of colonization-extinction process, so metapopulation extinction holds. Landscapes with dynamics close to this critical value—ephemeral habitats—are of particular interest for environmental management, since arbitrary alterations of the scale of landscape change—patch life span—can lead to deep consequences for patch occupancy and metapopulation persistence (see fig. 3). Life-history strategies of species living in dynamic landscapes can be deeply affected by policies of landscape management that consist of simultaneously destroying and restoring particular habitats. In other words, restoration ecology is not enough; we also need to decrease the current rates of habitat destruction and to ensure habitat conservation and restoration (Dobson et al. 1997).

Also notice that, in competitive-hierarchy scenarios, inferior competitors rely on the space left empty by the superior competitor as their limiting resource. Therefore, changes in the spatiotemporal distributions of superior competitors result in changes in the distribution of the available habitat for inferior species. In these cases, management of the superior competitor's distribution is equivalent to managing the landscape of available sites for inferior species. A similar situation holds with other "habitat structuring species," such as in the case of gopher-driven disturbance in grasslands (Wu and Levin 1994; Moloney and Levin 1996) or communities associated with islands of *Mytilus edulis* (Tsuchiya and Nishira 1986). In these communities, the rates of clearance and recruitment of certain species—keystone habitat architects—are crucial in determining community organization; their population dynamics determines other species' (effective) habitat distribution. If these rates (clearance and recruitment) are associated with environmental gradients of productivity (Menge et al. 1997*a*, 1997*b*), different community structures are expected to self-organize across the gradient. Currently, we are applying this rationale to study the organization of algal assemblages along the coast of Oregon, where such a gradient and patterns have been reported (Menge et al. 1997*b*).

Traditionally, landscape management tactics based on metapopulation principles have emphasized the importance of landscape spatial pattern as affecting persistence (McCullough 1996). However, our results and those of Fahrig (1992) clearly show that landscape dynamics, and in particular rates of landscape change, should be taken into account, especially under current global change scenarios (Vitousek 1994) where, in addition to changes in climate, human encroachment of natural areas is fragmenting landscapes at an accelerated rate (Melillo et al. 1985; Skole and Tucker 1993). Our model predicts that metapopulation extinction in dynamic landscapes will occur more often than expected by considering only the effects of reductions in area, increase in isolation and loss of connectivity. The rates at which the processes take place also matter. When destroying habitat, we are not only diminishing the amount of habitat available for colonization but also decreasing the life span of local populations. In this respect, we also agree with Fahrig (1992) regarding the question of the best design of nature reserves; for particular species, perhaps the size of the reserves is less important than their persistence over time. This is particularly true for endangered species inhabiting ephemeral habitats. However, Fahrig (1992) studied landscape pattern and not habitat amount. After reviewing the effects of habitat fragmentation in birds and mammals, Andrén (1994, p. 362) concluded, "in most landscapes the total area of suitable habitat will be of greater importance than its spatial arrangement"; therefore, we studied the effects of habitat amount.

In this vein, the results presented in this work provide the following new insights into the behavior of species living in highly dynamic patchy environments (ephemeral habitat). First, in agreement with Fahrig (1992), our model shows that species living in ephemeral environments are more sensitive to changes in temporal rather than spatial components of the landscape. By looking at figure 3 or by deriving equation (12) with respect to $\bar{s}$ and $\bar{\tau}$, we notice that for ephemeral landscapes (small $\bar{\tau}$) the effect of changing habitat life span is bigger than changing its amount (i.e., $|\partial\hat{p}/\partial\bar{\tau}| \gg |\partial\hat{p}/\partial\bar{s}|$ when $\bar{\tau}$ is very small). On the other hand, in virtually permanent environments (large $\bar{\tau}$) the effect of changing habitat amount is greater than changing its life span (i.e., $|\partial\hat{p}/\partial\bar{\tau}| \ll |\partial\hat{p}/\partial\bar{s}|$ when $\bar{\tau}$ is very large).

Second, in ephemeral environments, habitat dynamics as reflected in patch life span also overwhelm the importance of spatial components, such as habitat amount, in determining landscape connectivity properties and long-term population occupancy. Patches that are spatially isolated can became connected through space-time, allowing populations to spread among patches (see figs. 5, 6). Thus, if a species manages to survive in ephemeral environments, it will spread to the whole landscape. Moreover, the faster the landscape (the smaller the patch life span), the faster that populations will spread through the whole array of suitable habitat (patches) provided that the rate of increase of landscape change has not been increased beyond the threshold that engenders population collapse. Further research on spatially correlated patch dynamics is strongly needed. The study of co-varying habitat spatial pattern, amount, and life span is the obvious next step toward the understanding of the spatiotemporal interaction between metapopulation and habitat dynamics.

Acknowledgments

We acknowledge the financial support of a grant to J.E.K. by the Program in Latin American Studies at Princeton University; Mellon, Sloan, and Packard grants to S.A.L.; Mellon and Presidential Chair in Science grants to F. Jaksic; Consejo Nacional de Ciencia y Tecnología grant to J.X.V.-H.; and a Fondo Nacional de Ciencia y Tecnología (FONDECYT 7990051) grant to P.A.M. We also thank B. Bolker, L. Buttel, J. Chave, R. Durrett, J. Dushoff, M. Lima, S. Pacala, and L. Worden for helpful comments that improved both the manuscript and the research. We are particularly thankful to two anonymous reviewers for help in improving the manuscript.

APPENDIX

Stability Analysis of the Mean Field Equilibrium

Since $p_0 + p_1 + p_2 = 1$, we know that the system described above is actually two-dimensional. Thus, it can be written as

$$\frac{d}{dt}p_1 = \lambda(1 - p_1 - p_2) - \beta p_2 p_1 + \delta p_2 - e p_1, \tag{A1}$$

$$\frac{d}{dt}p_2 = [\beta p_1 - (\delta + e)]p_2. \tag{A2}$$

This system has $\vec{p}_*^{(-)} = [1/(\lambda + e)](\lambda, 0)$ and $\vec{p}_*^{(+)} = \{(\delta + e)/\beta, 1 - [e/(\lambda + e)] - [(\delta + e)/\beta]\}$ as fixed points and the following Jacobian matrix:

$$\vec{\mathbf{Df}} = \begin{bmatrix} -(\lambda + \beta p_2 + e) & -(\lambda + \beta p_1) + \delta \\ \beta p_2 & \beta p_1 - (\delta + e) \end{bmatrix}. \tag{A3}$$

The local stability of the fixed points $\vec{p}_*^{(-)}$ and $\vec{p}_*^{(+)}$ depends on the sign of the dominant eigenvalue of $\vec{Df}$ at those points. For two-dimensional systems, we know (May 1973) that the nessesary and sufficient conditions that both eigenvalues are negative (if real) or have negative real parts (if complex) is that, first, $\det\{\vec{Df}[\vec{p}_*]\} > 0$ and, second, $\mathrm{trace}\{\vec{Df}[\vec{p}_*]\} < 0$.

Case 1: $\vec{p}_*^{(-)}$

The first condition is satisfied if

$$\det\{\vec{Df}[\vec{p}_*^{(-)}]\} = -\{[\beta p_1 - (\delta + e)](\lambda + e)\}. \tag{A4}$$

Since $(\lambda + e) > 0$, the first condition is satisfied if and only if

$$\beta p_1 - (\delta + e) < 0 \Longleftrightarrow \beta < (\delta + e)/p_1 = (\delta + e)/\bar{s}. \tag{A5}$$

From equation (16), this holds if and only if $R_0^* \leq 1$; however, considering metapopulation persistence ($R_0^* > 1$), we find that $\vec{p}_*^{(-)}$ is not locally stable if $R_0^* > 1$.

Case 2: $\vec{p}_*^{(+)}$

Since $\beta\hat{p}_2^{(+)} > 0$, we find that

$$\det\{\vec{Df}[\vec{p}_*^{(+)}]\} = -[-(\lambda + \beta p_1 - \delta)\beta p_2] > 0 \tag{A6}$$

is satisfied if and only if $\lambda + \beta\hat{p}_1^{(+)} - \delta > 0$. Since $\hat{p}_2^{(+)} =$

$(\delta + e)/\beta$, the first condition holds when $\lambda + e > 0$ (all the interesting cases). So now we have to prove that the second condition also holds. Thus,

$$\mathrm{trace}\{\vec{Df}[\vec{p}_*^{(+)}]\} = -(\lambda + \beta p_2 + e) < 0, \qquad \text{(A7)}$$

which of course holds because $\lambda + \beta p_2 + e > 0$ since at least $\beta \hat{p}_2^{(+)} \neq 0$. So we get that $\vec{p}_*^{(+)}$ is locally stable.

Since $1 = p_0 + p_1 + p_2$, we know that all trajectories live within the simply connected region $\Omega \in \Re^2$ defined by $p_1 + p_2 \leq 1$. Using Bendixson's criterion (Guckenheimer and Holmes 1983), we obtain the result that no closed orbits exist within Ω if the quantity $(\partial f_1/\partial p_1) + (\partial f_2/\partial p_2)$: the first condition is not identically 0, and the second condition does not change sign. From equation (A3), we have

$$\frac{\partial f_1}{\partial p_1} + \frac{\partial f_2}{\partial p_2} = -[(\lambda + 2e + \delta) + \beta(p_1 + p_2)]. \qquad \text{(A8)}$$

If at least one of the parameters λ, e, δ, or β is not 0, we have $(\lambda + 2e + \delta) > 0$ and $\beta(p_1 + p_2)$, so $-[(\lambda + 2e + \delta) + \beta(p_1 + p_2)] < 0$, which means that $(\partial f_1/\partial p_1) + (\partial f_2/\partial p_2)$ is not identically 0 and does not change sign in Ω. Thus, if $R_0^* > 1$ then $\vec{p}_*^{(+)}$ is globally stable.

Literature Cited

Anderson, R. A., and R. M. May. 1992. Infectious diseases of humans: dynamics and control. Oxford University Press, Oxford.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat. Oikos 71:355–366.

Bascompte, J., and R. Solé. 1996. Habitat fragmentation and extinction thresholds in explicit models. Journal of Animal Ecology 65:465–473.

———. 1998. Models of habitat fragmentation. Pages 127–150 *in* Modeling spatiotemporal dynamics in ecology. Springer, Berlin.

Bevers, M., and C. Flather. 1999. Numerically exploring habitat fragmentation effects on populations using cell-based coupled map lattices. Theoretical Population Biology 65:465–473.

Boswell, G. P., N. F. Britton, and N. R. Franks. 1998. Habitat fragmentation, percolation theory and the conservation of keystone species. Proceedings of the Royal Society of London B, Biological Sciences 1409: 1921–1925.

Brachet, S., I. Olivieri, B. Godelle, E. Klein, N. Frascaria-Lacoste, and P. Gouyon. 1999. Dispersal and metapopulation viability in a heterogeneous landscape. Journal of Theoretical Biology 198:479–495.

Caswell, H., and R. Etter. 1993. Ecological interactions in patchy environments: from patch-occupancy models to cellular automata. Lecture Notes in Biomathematics 96: 93–109.

Darwen, P. J., and D. Green. 1996. Viability of populations in a landscape. Ecological Modelling 85:165–171.

Dobson, A. P., A. D. Bradshaw, and A. J. M. Baker. 1997. Hopes for the future: restoration ecology and conservation biology. Science (Washington, D.C.) 277:515–522.

Durrett, R., and S. A. Levin. 1994*a*. The importance of being discrete (and spatial). Theoretical Population Biology 46:363-394.

———. 1994*b*. Stochastic spatial models: a user's guide for ecological applications. Philosophical Transactions of the Royal Society of London B, Biological Sciences 343:329–350.

Dytham, C. 1995. The effect of habitat destruction pattern on species persistence: a cellular model. Oikos 74: 340–344.

Fahrig, L. 1991. Simulation methods for developing general landscape-level hypotheses of single-species dynamics. Pages 417–442 *in* M. G. Turner and R. H. Gardner, eds. Quantitative methods in landscape ecology. Springer, New York.

———. 1992. Relative importance of spatial and temporal scales in a patchy environment. Theoretical Population Biology 41:300–314.

———. 1997. Relative effects of habitat loss and fragmentation on population extinction. Journal of Wildlife Management 61:603–610.

Feller, W. 1968. An introduction to probability theory and its applications. Vol. 2. 3d ed. Wiley, New York.

Gotelli, N. J. 1991. Metapopulation models: the rescue effect, propagule rain, and the core-satellite hypothesis. American Naturalist 138:768–776.

Green, D. G. 1994. Simulation studies of connectivity and complexity in landscapes and ecosystems. Pacific Conservation Biologist 3:194–200 (available online at http://life.csu.edu.au/dgreen/papers/esa93.html).

Guckenheimer, J., and P. Holmes. 1983. Nonlinear oscillations, dynamical systems, and bifurcations of vector field. Vol. 42. Applied mathematical sciences. Springer, New York.

Gyllenberg, M., I. Hanski, and A. Hastings. 1997. Structured metapopulations models. Pages 93–122 *in* I. Hanski and M. Gilpin, eds. Metapopulation biology: ecology, genetics, and evolution. Academic Press, New York.

Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. Oikos 38:210–221.

———. 1983. Coexistence of competitors in a patchy environment. Ecology 64:493–500.

———. 1985. Single species spatial dynamics may contribute to long term rarity and commoness. Ecology 66: 335–343.

———. 1991. Single species metapopulation dynamics: concepts, models and observation. Journal of the Linnean Society 42:17–38.

———. 1999. Metapopulation ecology. Oxford Series in Ecology and Evolution. Oxford University Press, Oxford.

Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation biology. Pages 5–27 *in* I. Hanski and M. Gilpin, eds. Metapopulation biology: ecology, genetics, and evolution. Academic Press, New York.

Hastings, A. 1980. Disturbance, coexistence, history, and competition for space. Theoretical Population Biology 18:363–373.

Hernández-Suarez, C. M., P. A. Marquet, and J. Velasco-Hernández. 1999. Threshold parameters and metapopulation persistence. Bulletin of Mathematical Biology 61: 341–353.

Hill, M. F., and H. Caswell. 1999. Habitat fragmentation and extinction thresholds on fractal landscapes. Ecology Letters 2:121–127.

Holt, R. D. 1997. From metapopulation dynamics to community structure: some consequences of spatial heterogeneity. Pages 149–165 *in* I. Hanski and M. Gilpin, eds. Metapopulation biology: ecology, genetics and evolution. Academic Press, New York.

Horn, H. S., and R. MacArthur. 1972. Competition among fugitive species in a harlequin environment. Ecology 53: 749–752.

Huxel, G. A., and A. Hastings. 1998. Population size dependence, competitive coexistence and habitat destruction. Journal of Animal Ecology 67:446–453.

Kaneko, K. 1993. Theory and applications of coupled map lattices. Wiley, New York.

Keymer, J. E., P. Marquet, and A. Johnson. 1998. Pattern formation in a patch occupancy metapopulation model: a cellular automata approach. Journal of Theoretical Biology 194:79–90.

Kinzel, W. 1983. Directed percolation. Pages 425–446 *in* R. Weil, ed. Percolation structures and processes. Vol. 5. Annuals of the Israeli Physical Society.

Klausmeier, C. A. 1998. Extinction in multispecies and spatially explicit models of habitat destruction. American Naturalist 152:303–310.

Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. American Naturalist 130:624–635.

Levin, S. A. 1974. Dispersion and population interactions. American Naturalist 108:207–225.

Levin, S. A., and R. B. Paine. 1974. Disturbance, patch formation, and community structure. Proceedings of the National Academy of Sciences of the USA 71:2744–2747.

Levin, S. A., and D. Pimentel. 1981. Selection of intermediate rates of increase in parasite-host systems. American Naturalist 117:308–315

Levins, R. 1969. Some demographic and genetic consequences of environmental hetereogeneity for biological control. Bulletin of the EntomologicaI Society of America 15:237–240.

———. 1970. Extinction. Pages 77–107 *in* Some mathematical problems in biology. Mathematical Society of America, Providence, R.I.

Liggett, T. M. 1985. Interacting particle systems. Springer, Berlin.

Marquet, P. A., and J. X. Velasco-Hernández. 1997. A source-sink patch occupancy metapopulation model. Revista Chilena de Historia Natural 70:371–380.

May, R. 1973. Stability and complexity in model ecosystem. Monographs in Population Biology. Princeton University Press, Princeton, N.J.

McCullough, P. M. 1996. Metapopulations and wildlife conservation. Island, Washington, D.C.

Melillo, J. M., C. A. Palm, R. A. Houghton, G. M. Woodwell, and N. Myers. 1985. A comparison of two recent estimates of disturbance in tropical forests. Environmental Conservation 12:37–40.

Menge, B. A., B. A. Daley, P. A. Wheeler, P. Dahlhoff, E. Sanford, and P. T. Strub. 1997*a*. Benthic-pelagic links and rocky intertidal communities: bottom-up effects on top-down control? Proceedings of the National Academy of Sciences of the USA 94:14530–14535.

Menge, B. A., B. A. Daley, P. A. Wheeler, and P. T. Strub. 1997*b*. Rocky intertidal oceanography: an association between community structure and nearshore phytoplankton concentration. Limnology and Oceanography 42:57–66.

Merriam, G., K. Henein, and K. Stuart-Smith. 1991. Landscape dynamics models. Pages 399–416 *in* M. G. Turner and R. H. Gardner, eds. Quantitave methods in landscape ecology. Springer, New York.

Molofsky, J. 1994. Population dynamics and pattern formation in theoretical populations. Ecology 75:30–39.

Moloney, K. A., and S. A. Levin. 1996. The effects of disturbance architecture on landscape-level population dynamics. Ecology 77:375–394.

Nee, S. 1994. How populations persist. Nature (London) 367:123–124.

Nee, S., and R. May. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. Journal of Animal Ecology 61:37–40.

Nee, S., R. May, and M. Hassell. 1997. Two-species metapopulation models. Pages 123–147 *in* I. Hanski and M. Gilpin, eds. Metapopulation biology: ecology, genetics and evolution. Academic Press, New York.

Orbach, R. 1986. Dynamics of fractal networks. Science (Washington, D.C.) 231:814–819.

Plotnick, R., and R. Gardner. 1993. Lattices and landscapes. Lectures on Mathematics in the Life Sciences 23:129–156.

Skole, D., and C. Tucker. 1993. Tropical deforestation and habitat fragmentation in the amazon: satellite data from 1978 to 1988. Science (Washington, D.C.) 260: 1905–1910.

Slatkin, M. 1974. Competition and regional coexistence. Ecology 55:128–143.

Stauffer, D., and A. Aharony. 1991. Introduction to percolation theory. Taylor & Francis, London.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75:2–16.

Tilman, D., R. May, C. Lehman, and M. Nowak. 1994. Habitat destruction and the extinction debt. Nature (London) 371:65–66.

Tilman, D., D. Lehman, and C. Yin. 1997*a*. Habitat destruction, dispersal, and deterministic extinction in competitive communities. American Naturalist 149: 407–435.

Tilman, D., D. Lehman, and P. Kareiva. 1997*b*. Population dynamics in spatial habitats. Pages 3–20 *in* D. Tilman and P. Kareiva, eds. Spatial ecology: the role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton, N.J.

Travis, J. M., and C. Dytham. 1999. Habitat persistence, habitat availability and the evolution of dispersal. Proceedings of the Royal Society of London B, Biological Sciences 266:723–728.

Tsuchiya, M., and M. Nishihira. 1986. Islands of *Mytilus edulis* as a habitat for small intertidal animals: effect of *Mytilus* age structure on the species composition of the associated fauna and community organization. Marine Ecology Progress Series 31:171–178.

Vitousek, P. M. 1994. Beyond global warming: ecology and global change. Ecology 75:1861–1876.

With, K. A., and T. Crist. 1995. Critical thresholds in species' responses to landscape structure. Ecology 76:2446–2459.

With, K. A., and A. W. King. 1999. Extinction thresholds for species in fractal landscapes. Conservation Biology 13:314–326.

Wu, J., and S. A. Levin. 1994. A spatial dynamic modeling approach to pattern and process in an annual grassland. Ecological Monographs 64:447–464.

Associate Editor: Lenore Fahrig