A spatially structured metapopulation model with patch dynamics

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Abstract

Metapopulation models that incorporate both spatial and temporal structure are studied in this paper. The existence and stability of equilibria are provided, and an extinction threshold condition is derived which depends on patch dynamics (patch destruction and creation) and metapopulation dynamics (patch colonization and extinction). These results refine threshold conditions given by previous metapopulation models. By comparing landscapes with different spatial heterogeneities with respect to weighted long-term patch occupancies, we conclude that the pattern of a landscape is of overwhelming importance in determining metapopulation persistence and patch occupancy. We show that the same conclusion holds when a rescue effect is considered. We also derive a stochastic differential equations (SDE) model of the Itô type based on our deterministic model. Our simulations reveal good agreement between the deterministic model and the SDE model.
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Keywords: Metapopulation models; Patch dynamics; Spatially realistic models; Fragmentation; Persistence

1. Introduction

When studying populations for which local interactions are relevant, the spatial components of the system are at least as important as average birth and death rates, competition, or predation (Hanski, 1998). Destruction and fragmentation of native habitats are widespread and viewed as the most important threats to biodiversity worldwide (Wilcox and Murphy, 1985). Agriculture, urban sprawl, deforestation, and other human activities change the composition and physiognomy of landscapes, often altering individual behavior (Sheperd and Swihart, 1995; Zollner, 2000), population dynamics (Hanski, 1998), genetic structure (Gaines and Lyons, 1997), and community composition (Wright et al., 1998) of organisms. Thus, the notion of spatially structured populations is increasingly relevant for many species, heightening the importance of spatial ecology in recent years.

From a conservation perspective, there is considerable interest in predicting the sensitivity of species to land-use change and habitat fragmentation as a function of a general suite of ecological (Ims et al., 1993) or behavioral (Laurance, 1995; Wolff, 1999) characteristics. The classic metapopulation model (Levins, 1969) emphasizes changes in patch occupancy as a function of rates of patch colonization and extinction processes. Hanski (1994) proposed using a generalized incidence function model to describe patch colonization and extinction dynamics as functions of patch area and isolation. Hanski and Ovaskainen (2000) and Frank and Wissel (1998, 2002) defined an index of metapopulation capacity for a landscape containing patches that varied in size and connectivity.

Real landscapes exhibit three characteristics not incorporated in most metapopulation models. First, real landscapes are not static; temporal changes in habitat patches occur (e.g. logging or vegetative succession can alter forest patches) and can have important effects on metapopulation persistence (Gu et al., 2002). Disturbance regimes, such as the distribution of anomalous weather events, often drive

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changes in the suitability of patches for occupancy. Second, the distribution and magnitude of disturbances in real landscapes have both a stochastic component (e.g. the timing of occurrence of a drought year) and a deterministic component (e.g. the predictable effects of drought on wetlands that vary in depth and size), both of which contribute to the legacy of a disturbance (sensu Turner and Dale, 1998) by altering the spatial structure of patches. Marquet and collaborators (see for example Marquet et al., 1997, 2003; Keymer et al., 1998, 2000) recognized the importance of patch dynamics and developed mean field and spatially explicit version models which provide estimates of metapopulation persistence as a function of the rate of habitat destruction. Third, real landscapes are structured spatially. The important role of spatial structure (i.e. heterogeneity) has been supported by many authors (Durrett and Levin, 1994; With and Crist, 1995; Moilanen and Hanski, 1995; Bascompte and Solé, 1996; Hanski, 1998; Bevers and Flather, 1999), who have concluded that spatial features such as connectivity of patches, patch size and dispersal are essential to understand the dynamics of a population. In addition to the spatial structure of the landscape, recent research has focused on the effects of temporal changes in landscape structure (Merriam et al., 1991; Fahrig, 1992; Brachet et al., 1999; Marquet et al., 1997, 2003; Keymer et al., 1998, 2000). The general consensus is that temporal components interact with the spatial components to determine metapopulation persistence (Keymer et al., 2000). Since complex landscapes are indeed dynamic in nature, the role of patch dynamics should not be neglected. We have developed a model (Feng and DeWoody, 2003; DeWoody et al., 2005) that combines the features of the spatially realistic Levins model (SRLM) (Moilanen and Hanski, 1995) with dynamic changes in patch quality (Marquet et al., 1997, 2003; Keymer et al., 2000).

In this article, we consider a more general model of which the model by DeWoody et al. (2005) is a special case. Our analytical results provide not only criteria for the persistence of metapopulation, uniqueness and global attractivity of the positive interior equilibrium, but also the global attractivity in the case of multiple positive interior equilibria, in which metapopulation size depends on the initial values. We compare the implications of these criteria with both the SRLM and the model of the Keymer et al. (2000). We have conducted numerical simulations of the models applied to landscapes with different spatial structures and compared the outcomes in terms of weighted long-term patch occupancies. In parallel to the analytical and numerical studies of the deterministic models, we also have derived corresponding stochastic differential equations (SDE) of the Itô type. Significantly, our results improve the metapopulation extinction thresholds provided by the SRLM and the model of Keymer et al. (2000). By highlighting differences between our model and previous models, we identify key factors that may change predictions derived by either the SRLM or the Keymer

et al. (2000) model. Our stochastic simulations agree nicely with the deterministic models, allowing extension of our model to include more realistic features that are difficult to analyse with deterministic models, and to examine the effects of the increased realism on metapopulation dynamics.

This paper is organized as follows. In Section 2 we describe the SRLM, the model of Keymer et al. (2000), and our deterministic model. Analytical results and numerical studies of the deterministic model are given in Section 3. Simulations using an SDE model are presented in Section 4, and the simulation results are compared with those obtained from our deterministic model. In Section 5 we discuss our results and their implications.

2. Deterministic metapopulation models

The original single-species metapopulation model (Levins, 1969) has the form

$$\frac{\mathrm{d}p(t)}{\mathrm{d}t} = cp(t)(1 - p(t)) - ep(t),$$

where $p(t)$ denotes the proportion of the occupied patches at time t, c is the colonization rate of the empty patches, and e is the extinction rate of the occupied patches. This model assumes an infinite network of homogeneous patches and is spatially implicit. A classic result provided by this model is that metapopulation persistence is possible if and only if the colonization rate exceeds the critical threshold set by the extinction rate. Following Levins' framework, a large body of metapopulation theory has been developed in recent years (Moilanen and Hanski, 1995; Hanski and Gilpin, 1997; Bascompte and Solé, 1998; Hanski, 1999; Hanski and Ovaskainen, 2000, 2003; Dieckmann et al., 2000; Ovaskainen and Hanski, 2001). Developments have ranged from models of single species metapopulations (Levins, 1969, 1970; Hanski, 1985; Hanski and Gyllenberg, 1997; Keymer et al., 1998, 2000; Murrell and Law, 2000; Hanski and Ovaskainen, 2000, 2003; Ovaskainen and Hanski, 2001) to interactions of two species (Horn and MacArthur, 1972; Levin, 1974; Hanski, 1983; Nee and May, 1992; Nee et al., 1997) or multiple species (Levin, 1974; Hastings, 1980; Tilman, 1994; Holt, 1997).

The SRLM (Moilanen and Hanski, 1995; Hanski and Gyllenberg, 1997; Hanski and Ovaskainen, 2000; Ovaskainen and Hanski, 2001) incorporates the effects of the spatial characteristics of landscapes into the classical metapopulation dynamics of the Levins type. Assuming a finite number n of patches in a fragmented landscape, the model is an n-dimensional system, with one equation for each habitat patch giving the rate of change in the probability of that patch being occupied:

$$\frac{\mathrm{d}p_{i2}}{\mathrm{d}t} = c_i(\mathbf{p_2})(1 - p_{i2}) - e_i(\mathbf{p_2})p_{i2}, \tag{2.1}$$

where $c_i(\mathbf{p_2})$ is the colonization rate in patch i when it is empty, $e_i(\mathbf{p_2})$ gives the extinction rate in patch i when it is

occupied, and $\mathbf{p}_2$ is the n-dimensional vector of the occupancy probabilities (see Table 1). Under the assumption that the colonization rate of each patch is proportional to patch connectivity, which is dependent upon the patch areas, inter-patch distances, incidence of patches and a species' intrinsic dispersal ability (Adler and Nüernberger, 1994; Hanski, 1994, 1998, 1999), and that extinction rates decrease as a function of patch area, reflecting the belief that larger areas support larger populations and extinction risk should decrease as a population grows, the rates in (2.1) are quantified as

$$c_i(\mathbf{p}_2) = c \sum_{j \neq i} e^{-\alpha d_{ij}} A_j p_{j2}(t), \quad e_i(\mathbf{p}_2) = \frac{e}{A_i}, \qquad (2.2)$$

where A_i and d_{ij} are landscape parameters representing, respectively, the area of patch i and the distance between patches i and j. All other parameters are related to the life history characteristic of the focal species: α^{-1} is the average migration distance; c and e are the background species colonization and extinction rates, respectively. After a rigorous analysis of the model, Ovaskainen and Hanski (2001) concluded that a quantity ω_M, involving only the spatial landscape and the focal species, sets the condition for metapopulation persistence and can be used to rank

Table 1
Definitions of frequently used symbols

Symbol	Definition
c_i	The colonization rate of patch i when empty
c^*	The colonization rate of patches in the mean field model (Keymer et al., 2000)
e_i	The extinction rate of patch i
e^*	The extinction rate of patches in the mean field model (Keymer et al., 2000)
β_i	The destruction rate of patch i
β^*	The destruction rate of patches in the mean field model (Keymer et al., 2000)
E_i	A general extinction or destruction function of patch i
A_i	The area of patch i
$1/\alpha$	The average migration distance
d	The long-term habitat loss
$\mathbf{B}$	The vector of the long-term habitat loss, $(B_1, B_2, \ldots, B_n)$, $B_i = \beta_i/(\lambda_i + \beta_i)$
$\lambda_{H_1 D_1}$	The leading eigenvalue of matrix $H_1 D_1^{-1}$
ω_M	The leading eigenvalue of matrix M
p_{i2}	The probability of the ith patch occupied by a focal species
$\mathbf{p}_2$	The n-dimensional vector of patch occupancies p_{i2}
$\mathbf{p}_2^m, \mathbf{p}_2^M$	The minimal and maximal equilibria (componentwise)
$\mathbf{p}_2^*$	Denoting the unique positive equilibrium
p_ω	The average of patch occupancies weighted by patches' relative values U_i^R
$\hat{p}$	The average of patch occupancies weighted by patches' absolute values V_i^R
p_A	The average of patch occupancies weighted by patches' areas A_i
$\bar{p}$	$\hat{p}/(1 - d)$, the long-term proportion of occupied suitable habitat
Ω	n-cube $\{\mathbf{x} = (x_i) \in \mathbb{R}^n : 0 \leqslant x_i \leqslant 1, \forall i\}$
Σ	Occupancy space $\{\mathbf{x} = (x_i) \in \mathbb{R}^n : 0 \leqslant x_i \leqslant 1 - B_i, \forall i\}$

landscapes and examine the relative roles of habitat loss and fragmentation on metapopulation persistence. They termed ω_M the metapopulation capacity of a landscape.

Model (2.1) provides an essential framework for understanding responses of species to habitat fragmentation. Nonetheless, Ovaskainen and Hanski (2001) assumed that landscapes are static, despite the fact that complex landscapes often are dynamic. Keymer et al. (2000) recognized the importance of patch dynamics and developed a mean field model with which they estimated metapopulation persistence as a function of the rate of habitat destruction. However, the model of Keymer et al. (2000) ignored spatial structure.

Combining the features of both the SRLM and the Keymer et al. model, we developed the following model:

$$\frac{dp_{i0}}{dt} = \beta_i(p_{i1} + p_{i2}) - \lambda_i p_{i0},$$
$$\frac{dp_{i1}}{dt} = \lambda_i p_{i0} - c_i(\mathbf{p}_2)p_{i1} + e_i(\mathbf{p}_2)p_{i2} - \beta_i p_{i1},$$
$$\frac{dp_{i2}}{dt} = c_i(\mathbf{p}_2)p_{i1} - (e_i(\mathbf{p}_2) + \beta_i)p_{i2}. \qquad (2.3)$$

This model considers a landscape of n patches, each of which may be at one of the three stages $i = 0, 1, 2$ (uninhabitable, habitable yet empty, and occupied). $p_{i0}(t), p_{i1}(t), p_{i2}(t)$ denote the probabilities of patch i being in three states at time t. β_i and λ_i give the destruction and creation rates of patch i, respectively. For the case when $c_i(\mathbf{p}_2)$ and $e_i(\mathbf{p}_2)$ have the same forms as given in (2.2) with $\mathbf{p}_2$ representing the vector of n occupancy probabilities, DeWoody et al. (2005) discussed some of the properties of the model (2.3) without detailed proofs. We provide these proofs and allow $c_i(\mathbf{p}_2)$ and $e_i(\mathbf{p}_2)$ to have more general forms. Denote by $E_i(\mathbf{p}_2)$ a general extinction rate of patch i. Then, for the model (2.3), $E_i(\mathbf{p}_2) = e_i(\mathbf{p}_2) + \beta_i$. In the next section, Theorem 3.1 can be applied to the model (2.1) by replacing $1 - B_i$ by 1 and E_i by e_i in system (3.3) while Theorem 3.2 aims at the model (2.3). Suppose that c_i and E_i are smooth functions, and that:

(H1) $c_i(0) = 0, c_i(\mathbf{p}_2) > 0$ in $\Omega \backslash \{0\}$, and $c_{ij}(\mathbf{p}_2) := \frac{\partial c_i(\mathbf{p}_2)}{\partial p_{j2}} \geqslant 0$ in Σ if $i \neq j$. In biological terms, there is no immigration from external sources, there are no completely isolated patches, and the occupied patches in the network make either a positive or zero contribution to the colonization rate of an empty patch.

(H2) $E_i(\mathbf{p}_2) > 0$ in Ω, $E_{ij}(\mathbf{p}_2) := \frac{\partial E_i(\mathbf{p}_2)}{\partial p_{j2}} \leqslant 0$ in Σ for $i \neq j$. In biological terms, it is assumed that each local population has a positive rate to go extinct, the extinction rate of an extant local population is independent of or reduced by the presence of other local populations.

Here, $\Omega = \{\mathbf{p}_2 = (p_{i2}) \in \mathbb{R}^n : 0 \leqslant p_{i2} \leqslant 1, \forall i\}$, and $\Sigma = \{\mathbf{p}_2 = (p_{i2}) \in \mathbb{R}^n : 0 \leqslant p_{i2} \leqslant 1 - B_i, \forall i\}$, and $B_i = \frac{\beta_i}{\beta_i + \lambda_i}$ represents the long-term destruction probability of patch i. In assumption (H2), if $E_{ij}(\mathbf{p}_2) < 0$ for some $i \neq j$, the biological

rational is that the populations in the neighborhood of a given local population may send migrants which enter the focal patch and thus elevate its local population size such that the extinction rate of the given population is reduced. This has been termed a rescue effect. Assumption (H2) has no requirements on $E_{ii}(\mathbf{p}_2)$. Actually, we may have $E_{ii}(\mathbf{p}_2) < 0$ because the extinction rate of a local population decreases with increasing population size. We also call this phenomena a rescue effect. Usually, rescue effects will lead to multiple positive equilibria for models. Later, we will provide an example.

In the following sections we will focus on system (2.3). We show that species persistence is determined by a threshold condition which generalizes the threshold conditions provided by either the SRLM or the model of Keymer et al. (2000).

3. Model analysis

Note that for model (2.3), $p_{i0} + p_{i1} + p_{i2} = 1$. Therefore, instead of model (2.3), we can study the following equivalent system:

$$\frac{dp_{i0}}{dt} = \beta_i(1 - p_{i0}) - \lambda_i p_{i0}, \tag{3.1}$$

$$\frac{dp_{i2}}{dt} = c_i(\mathbf{p}_2)(1 - p_{i0} - p_{i2}(t)) - E_i(\mathbf{p}_2)p_{i2},$$
$$i = 1, 2, \ldots, n, \tag{3.2}$$

with a general extinction function E_i satisfying assumption (H2).

3.1. General theorems

Under assumptions (H1) and (H2) system (3.1)–(3.2) admits a trivial equilibrium

$$O = (\mathbf{B}, \mathbf{0}) := (B_1, B_2, \ldots, B_n, 0, \ldots, 0),$$

where $p_{i0} = B_i$, $p_{i2} = 0$, $i = 1, 2, \ldots, n$. The stability of the equilibrium O is determined by the eigenvalues of the matrix $H_1 - D_1$, where $D_1 = diag(E_i(0) - (1 - B_i)c_{ii}(0))$, and

$$H_1 = \begin{pmatrix} 0 & (1-B_1)c_{12}(0) & \cdots & (1-B_1)c_{1n}(0) \\ (1-B_2)c_{21}(0) & 0 & \cdots & (1-B_2)c_{2n}(0) \\ \cdots & \cdots & \cdots & \cdots \\ (1-B_n)c_{n1}(0) & (1-B_n)c_{n2}(0) & \cdots & 0 \end{pmatrix}.$$

As proven by Diekmann et al. (1990), $H_1 - D_1$ has at least one eigenvalue with positive real part if and only if

$\lambda_{H_1 D_1}$ = the leading eigenvalue of $H_1 D_1^{-1} > 1$.

Note that Eq. (3.1) can be decoupled, and the solution $p_{i0}(t)$ always converges to B_i as t goes to infinity. Therefore, we first consider the limiting system

$$\frac{dy_i}{dt} = c_i(\mathbf{y})(1 - B_i - y_i) - E_i(\mathbf{y})y_i := f_i(\mathbf{y}), \tag{3.3}$$

where $\mathbf{y} = (y_i)_{i=1}^n \in \Omega$. This is actually an extension of model (2.1). Let $\mathbf{f}(\mathbf{y}) = (f_i(\mathbf{y}))_{i=1}^n$. For any $\mathbf{x}, \mathbf{y} \in \mathbb{R}^n$, we write $\mathbf{x} \leqslant \mathbf{y}$ if the components satisfy $x_i \leqslant y_i$, $\mathbf{x} < \mathbf{y}$ if $x_i \leqslant y_i$ and $\mathbf{x} \neq \mathbf{y}$, $\mathbf{x} \ll \mathbf{y}$ if $x_i < y_i$. Then we have:

Theorem 3.1. *For any* $\mathbf{y} \in \Omega$, *let* $\tilde{\Phi}(t)\mathbf{y}$ *denote the solution of system* (3.3) *with* $\tilde{\Phi}(0)\mathbf{y} = \mathbf{y}$. *The following statements hold.*

(i) *There exists a maximal equilibrium* $\mathbf{p}_2^M \in \Sigma$ *such that for any* $\mathbf{y} \in \Omega$, $\omega(\mathbf{y}) \subset [0, \mathbf{p}_2^M]$, *where* $\omega(\mathbf{y})$ *is the omega limit set of the orbit* $\gamma^+ = \{\tilde{\Phi}(t)\mathbf{y} : t \geqslant 0\}$, *and* $[0, \mathbf{p}_2^M] = \{\mathbf{p}_2 \in \mathbb{R}^n : 0 \leqslant \mathbf{p}_2 \leqslant \mathbf{p}_2^M\}$. *Moreover, for each* $\mathbf{y} \in \Sigma$ *with* $\mathbf{y} \geqslant \mathbf{p}_2^M$, $\lim_{t \to \infty} \tilde{\Phi}(t)\mathbf{y} = \mathbf{p}_2^M$.

(ii) *If* H_1 *is irreducible and* $\lambda_{H_1 D_1} > 1$, *then there exists an equilibrium* $\mathbf{p}_2^m$ *with* $0 \ll \mathbf{p}_2^m \leqslant \mathbf{p}_2^M$ *such that for any* $\mathbf{y} \in \Omega \backslash \{0\}$, $\omega(\mathbf{y}) \in [\mathbf{p}_2^m, \mathbf{p}_2^M]$. *Moreover,* $\lim_{t \to \infty} \tilde{\Phi}(t)\mathbf{y} = \mathbf{p}_2^m$ *for each* $0 < \mathbf{y} \leqslant \mathbf{p}_2^m$. *In particular, if* $\mathbf{p}_2^m = \mathbf{p}_2^M$, *then* $\mathbf{p}_2^m$ *is globally attractive with respect to* $\Omega \backslash \{0\}$.

(iii) *Suppose that the Jacobian matrix* $D\mathbf{f}(\mathbf{y})$ *is irreducible for every* $\mathbf{y} \in \Sigma$, *and*

    (1) $\mathbf{f}$ *is sublinear, i.e.* $\mathbf{f}(\varepsilon \mathbf{y}) \geqslant \varepsilon \mathbf{f}(\mathbf{y})$, $\forall \varepsilon \in [0, 1]$, $\mathbf{y} \geqslant 0$, *then for any two equilibria* $\mathbf{p}_2^*, \mathbf{p}_2^{**} \in \Sigma$ *with* $\mathbf{p}_2^*, \mathbf{p}_2^{**} \gg 0$ (*if existing*), *there is* $\xi > 0$ *such that* $\mathbf{p}_2^* = \xi \mathbf{p}_2^{**}$. *Moreover, every solution* $\tilde{\Phi}(t)y$ $(t \geqslant 0)$ *will converge to an equilibrium.*

    (2) $\mathbf{f}$ *is strictly sublinear, i.e.* $\mathbf{f}(\varepsilon \mathbf{y}) > \varepsilon \mathbf{f}(\mathbf{y})$, $\forall \varepsilon \in (0, 1)$, $\mathbf{y} \geqslant 0$, *then if* $\lambda_{H_1 D_1} \leqslant 1$, *zero is globally asymptotically stable, while if* $\lambda_{H_1 D_1} > 1$, *system* (3.3) *admits a unique positive equilibrium* $\mathbf{p}_2^* \gg 0$ *and* $\mathbf{p}_2^*$ *is globally asymptotically stable.*

Proof. It is easy to check that Σ is a positive invariant set for the solution semiflow $\tilde{\Phi}(t)$, and for any $\mathbf{y} \in \Omega \backslash \Sigma$, $\tilde{\Phi}(t)\mathbf{y} \in \Sigma$ for all sufficiently large t. Therefore, in order to know the behavior of $\tilde{\Phi}(t)\mathbf{y}$ in Ω, we only need to study the semiflow $\tilde{\Phi}(t) : \Sigma \to \Sigma$.

Assumptions (H1) and (H2) imply that system (3.3) is a cooperative system on Σ. By Proposition 3.1.1 of Smith (1995), $\tilde{\Phi}(t)$ is monotone, i.e. $\tilde{\Phi}(t)\mathbf{x} \leqslant \tilde{\Phi}(t)\mathbf{y}$, $\forall t \geqslant 0$ if $\mathbf{x} \leqslant \mathbf{y}$. Moreover, if $D\mathbf{f}(\mathbf{y})$ is irreducible on Σ, $\tilde{\Phi}(t)$ is strongly monotone, i.e. $\tilde{\Phi}(t)\mathbf{x} \ll \tilde{\Phi}(t)\mathbf{y}$, $\forall t > 0$ if $\mathbf{x} < \mathbf{y}$ (see Theorem 4.1.1 of Smith (1995)).

(i) The result is a direct consequence of the continuous version of Theorem 2.1.1 of Zhao (2003).

(ii) By Corollary 3.1 of Zhao and Jing (1996), there exists an equilibrium $\mathbf{p}_2^m \gg 0$ such that $\lim_{t \to \infty} \tilde{\Phi}(t)\mathbf{y} = \mathbf{p}_2^m$ for each $0 < \mathbf{y} \leqslant \mathbf{p}_2^m$, and for any $\mathbf{y} \in \Sigma \backslash \{0\}$, $\liminf_{t \to \infty} \tilde{\Phi}(t)\mathbf{y} \geqslant \mathbf{p}_2^m$. Combining these results with (i), we obtain (ii) immediately.

(iii) For any fixed $t > 0$, consider the map $\tilde{\Phi}(t)$. Then the equilibria of system (3.3) are fixed points of map $\tilde{\Phi}(t)$. Therefore, Lemma 2.3.1 of Zhao (2003) gives conclusion (1). Conclusion (2) is a direct result of Corollary 3.2 of Zhao and Jing (1996) and Theorem 2.1 of Wang and Zhao (2003). $\square$

Remark 3.1. The irreducibility condition of the theorem actually means that there are no completely isolated patches. Thus, under our assumptions, the conditions are always satisfied.

Remark 3.2. Let $F_i(\mathbf{y}) = \frac{(1-B_i)c_i(\mathbf{y})}{c_i(\mathbf{y})+E_i(\mathbf{y})}$, $\mathbf{F}(\mathbf{y}) = (F_i(\mathbf{y}))_{i=1}^n$. Consider the iteration equation

$$\mathbf{y}^{n+1} = \mathbf{F}(\mathbf{y}^n). \tag{3.4}$$

Then the equilibria of system (3.3) are fixed points of $\mathbf{F}$. Moreover, the iteration orbits have the same dynamical behavior about $\mathbf{p}_2^M$ as implied in Theorem 3.1. Thus, to obtain $\mathbf{p}_2^M$, one just needs to iterate (3.4) from $\mathbf{B}$. If the Jacobian matrix $D\mathbf{F}(\mathbf{0})$ is strongly positive and $\mathbf{F}$ satisfies certain monotonicity and sublinearity conditions, we can obtain the same conclusion about the discrete dynamical system (3.4) as in Theorem 3.1(ii) and (iii). Therefore, we can compute $\mathbf{p}_2^m$ by iterating (3.4) from any point in a small neighborhood of zero. Note that if a point $\mathbf{p}_2$ is an equilibrium of (3.3), then $(\mathbf{B}, \mathbf{p}_2)$ is an equilibrium of system (3.1)–(3.2). Therefore, by the iteration, we actually obtain the corresponding equilibrium of (3.1)–(3.2).

Theorem 3.2. Let $\Omega_2 = \{(p_{i0}, p_{i2}) \in \mathbb{R}_+^{2n} : p_{i0} + p_{i2} \leqslant 1, \forall 1 \leqslant i \leqslant n\}$. For any $\mathbf{p} \in \Omega_2$ denote by $\Phi(t)\mathbf{p} = (\Phi_0(t)\mathbf{p}, \Phi_2(t)\mathbf{p})$ the solution of system (3.1)–(3.2) with $\Phi(0)\mathbf{p} = \mathbf{p}$. Then we have the following statements.

(i) For any $\mathbf{p} \in \Omega_2$, $\omega(\mathbf{p}) \subset \mathbf{B} \times [0, \mathbf{p}_2^M]$, where $\omega(\mathbf{p})$ is the omega limit set of the orbit $\gamma^+ = \{\Phi(t)\mathbf{p} : t \geqslant 0\}$;
(ii) If H_1 is irreducible and $\lambda_{H_1 D_1} > 1$, then $\omega(\mathbf{p}) \subset \mathbf{B} \times [\mathbf{p}_2^m, \mathbf{p}_2^M]$ for each $\mathbf{p} \in \Omega_2 \backslash \{0\}$. In particular, if $\mathbf{p}_2^m = \mathbf{p}_2^M$, then $(\mathbf{B}, \mathbf{p}_2^m)$ is globally attractive with respect to $\Omega_2 \backslash \{0\}$;
(iii) Suppose that $D\mathbf{f}(\mathbf{y})$ is irreducible for every $\mathbf{y} \in \Sigma$, and $\mathbf{f}$ is strictly sublinear. If $\lambda_{H_1 D_1} \leqslant 1$, the trivial equilibrium $(\mathbf{B}, \mathbf{0})$ is globally attractive, while if $\lambda_{H_1 D_1} > 1$, the unique positive equilibrium $(\mathbf{B}, \mathbf{p}_2^*)$ is globally attractive with respect to $\Omega_2 \backslash \{0\}$;

where $\mathbf{p}_2^m, \mathbf{p}_2^M$ and $\mathbf{p}_2^*$ are defined in Theorem 3.1.

Proof. Here, we only give the proof of (ii). (i) and (iii) can be proved using the same arguments.

Note that Ω_2 is a positive invariant set for the solution semiflow $\Phi(t)$. For any $\mathbf{p} \in \Omega_2 \backslash \{0\}$, since $\Phi(t)\mathbf{p}$ is bounded, $\omega(\mathbf{p})$ is a compact, invariant, internally chain transitive and nonempty set for semiflow $\Phi(t)$. Since $\lim_{t \to \infty} \Phi_0(t)\mathbf{p} = \mathbf{B}$, we can set $\omega(\mathbf{p}) = \mathbf{B} \times \Gamma$. Then there holds

$$\Phi(t)\mathbf{x} = (\mathbf{B}, \tilde{\Phi}(t)\mathbf{y}), \quad \forall \mathbf{x} = (\mathbf{B}, \mathbf{y}) \in \omega(\mathbf{p}).$$

It follows that Γ is a compact, invariant and internally chain transitive set for $\tilde{\Phi}(t)$. Since $\tilde{\Phi}(t)$ has a global attractor in $[\mathbf{p}_2^m, \mathbf{p}_2^M]$ with respect to $\Omega \backslash \{0\}$, by Lemma 1.2.8 of Zhao (2003) and the fact $\Gamma \subset \Omega$ (more precisely, $\Gamma \subset \Sigma$),

we have $\Gamma \subset [\mathbf{p}_2^m, \mathbf{p}_2^M]$ or $\Gamma = \{0\}$. We need to exclude the second case.

Suppose, by contradiction, that there exists a point $\mathbf{p} \in \Omega_2 \backslash \{0\}$ such that $\Gamma = \{0\}$. Then, for any $\varepsilon > 0$, there exists a $t_1 > 0$ such that $\|\Phi_2(t)\mathbf{p}\| < \varepsilon$ for all $t \geqslant t_1$. Set $\bar{\mathbf{y}}(t) = (\bar{y}_i(t))_{i=1}^n = \Phi_2(t)\mathbf{p}$. Consider the following system:

$$\frac{dy_i}{dt} = c_i(\mathbf{y})(1 - B_i - \varepsilon - y_i) - E_i(\mathbf{y})y_i,$$
$$\mathbf{y} = (y_i)_{i=1}^n \in \Omega. \tag{3.5}$$

By the continuous dependence of solutions on parameters and Theorem 3.1, for sufficiently small $\varepsilon > 0$, the solutions of (3.5) with positive initial values are greater than $\mathbf{p}_2^m/2$ for all large t. Let us fix such an ε. Without loss of generality, we may choose $\varepsilon < \|\mathbf{p}_2^m\|/2$. Then there exists a $t_0 = t_0(\varepsilon) > 0$ such that $\Phi_0(t)\mathbf{p} \leqslant \mathbf{B} + \varepsilon I, \|\bar{\mathbf{y}}(t)\| < \varepsilon, \forall t \geqslant t_0$, where $I = \{1, 1, \ldots, 1\} \in \mathbb{R}^n$. Therefore,

$$\frac{d\bar{y}_i(t)}{dt} \geqslant c_i(\bar{\mathbf{y}}(t))(1 - B_i - \varepsilon - \bar{y}_i(t)) - E_i(\bar{\mathbf{y}}(t))\bar{y}_i(t),$$
$$\forall t \geqslant t_0. \tag{3.6}$$

Note that $\bar{y}_i(t) > 0$ for all $t > 0$. By the comparison theorem and the monotonicity of system (3.5), $\bar{\mathbf{y}}(t) \geqslant \mathbf{y}_\varepsilon(t) > \mathbf{p}_2^m/2$ for all $t \geqslant t_0$, where $\mathbf{y}_\varepsilon(t)$ is the solution of (3.5) with $\mathbf{y}_\varepsilon(t_0) = \bar{\mathbf{y}}(t_0)$, a contradiction. Therefore, we established (ii). $\square$

3.2. Effect of patch dynamics

The theorems imply that the focal species goes extinct if $\lambda_{H_1 D_1} < 1$ and the species persists if $\lambda_{H_1 D_1} > 1$. In the special case when there is no patch destruction, this threshold condition has been derived in Hanski and Ovaskainen (2000) and Ovaskainen and Hanski (2001). Clearly, our threshold condition allows for an assessment of the impact of patch dynamics on species persistence as the matrix H_1 involves parameters β_i and λ_i, which represent patch destruction and creation, respectively.

3.2.1. Threshold for metapopulation persistence

To illustrate the effects of patch dynamics, we now consider specific forms of colonization and extinction rates c_i, e_i as used by Hanski and Ovaskainen (2000), Ovaskainen and Hanski (2001). That is, for system (3.1)–(3.2),

$$E_i = e_i + \beta_i = e/A_i + \beta_i,$$
$$c_i(\mathbf{p}_2) = c \sum_{j \neq i} e^{-\alpha d_{ij}} A_j p_{j2}(t). \tag{3.7}$$

Similarly we assume that patch creation and destruction also depend on patch areas:

$$\lambda_i = \frac{\lambda}{A_i}, \quad \beta_i = \frac{\beta}{A_i}, \quad i = 1, 2, \ldots, n,$$

where λ and β are the corresponding background rates. In this case $B_i = \frac{\beta}{\beta + \lambda}$ for all i. Straightforward calculations

show that $H_1 D_1^{-1} = \frac{\lambda}{\beta+\lambda} \frac{c}{e+\beta} M$, where

$$M = \begin{pmatrix} 0 & e^{-\alpha d_{12}} A_2^2 & \cdots & e^{-\alpha d_{1n}} A_n^2 \\ e^{-\alpha d_{12}} A_1^2 & 0 & \cdots & e^{-\alpha d_{2n}} A_n^2 \\ \cdots & \cdots & \cdots & \cdots \\ e^{-\alpha d_{1n}} A_1^2 & e^{-\alpha d_{2n}} A_2^2 & \cdots & 0 \end{pmatrix}.$$

Let ω_M denote the leading eigenvalue of M. Then, according to our theorems, the trivial equilibrium $(\mathbf{B}, \mathbf{0})$ of the system (3.1)–(3.2) is globally attractive if $\omega_M < \frac{e+\beta}{c} \frac{\lambda+\beta}{\lambda}$. In this case, species extinction will occur. Noticing that for the functional forms given in (3.7) the right hand side of system (3.1)–(3.2) is strictly sublinear, from our theorems we know that system (3.1)–(3.2) admits a unique positive equilibrium $(\mathbf{B}, \mathbf{p}_2^*)$ and it is globally attractive if

$$\omega_M > \bar{\omega} = \left(\frac{e+\beta}{c}\right)\left(\frac{\lambda+\beta}{\lambda}\right). \tag{3.8}$$

In this case species persistence is expected. In the special case of a static landscape ($\beta = 0$), the threshold condition (3.8) reduces to that obtained by Ovaskainen and Hanski (2001).

To assess how dynamic landscapes may affect the persistence threshold we introduce the notation $d = \frac{\beta}{\beta+\lambda}$, which represents the expected fraction of destroyed habitat. Then $1 - d = \frac{\lambda}{\beta+\lambda}$ represents the expected fraction of suitable habitat. Rewrite the threshold expression $\bar{\omega}$ as

$$\bar{\omega} = \left(\frac{e+\beta}{c}\right)\left(\frac{1}{1-d}\right). \tag{3.9}$$

This provides an explicit description of the threshold value as a function of d, and therefore the dependence of extinction risk of the metapopulation on the expected fraction of destroyed habitat. Furthermore, noticing that $\bar{\omega} = \frac{e+\beta}{c}(1 + d + O(d^2))$ for small d, we see that the dependence of $\bar{\omega}$ on d is almost linear with the slope dependent on the patch destruction rate β when d is small. We remark that for fixed β, the value of d is determined by the patch creation rate λ.

We next discuss how dynamic landscapes may change the earlier conclusion (Hanski and Ovaskainen, 2000; Ovaskainen and Hanski, 2001) about the influence of the structure of a landscape on metapopulation growth and size at equilibrium. The metapopulation size at the equilibrium $(\mathbf{B}, \mathbf{p}_2^*)$ can be defined by a weighted average of $\mathbf{p}_2^*$. There are various ways to weight the contribution of each individual patch to the long-term metapopulation persistence. Following Hanski and Ovaskainen (2001) we adopt the concept of "relative value of a patch" to measure the contribution of a patch. Let Q be a landscape with a patch $q \in Q$. Define the relative value of patch q by

$$U_q^R = \frac{\omega_M(Q) - \omega_M(Q\backslash\{q\})}{\omega_M(Q)}.$$

Thus, U_q^R describes the relative decrease in $\omega_M(Q)$ due to removal of patch q from the landscape. Define the absolute

value of patch q by $V_q^R = U_q^R \omega_M(Q)$. According to Proposition 5.3 of Ovaskainen and Hanski (2001), we can easily obtain that the total fraction (or probability) of occupied patches weighted by relative values at the equilibrium is

$$p_\omega = \sum_i U_i^R p_{i2}^* \approx 1 - \left(\frac{e+\beta}{c}\right)\left(\frac{1}{(1-d)\omega_M}\right), \tag{3.10}$$

where $\mathbf{p}_2^* = (p_{i2}^*)$. Again, in the case of static landscapes ($\beta = 0$), estimate (3.10) reduces to that of Hanski and Ovaskainen (2000), i.e.

$$p_\omega \approx 1 - \left(\frac{e}{c}\right)\left(\frac{1}{\omega_M}\right). \tag{3.11}$$

We observe from (3.10) and (3.11) that, in comparison with the Levins model which gives an estimate for the metapopulation persistence at the equilibrium to be $p^* = 1 - e/c$, the SRLM provides an improved estimate (see (3.11)) by incorporating the role of landscape capacity (ω_M). Our model provides a further improved estimate (see (3.10)) by accounting for both the landscape capacity (ω_M) and the expected suitable habitat ($1 - d$).

In Keymer et al. (2000), the condition for metapopulation persistence ($\mathbf{p}_2 > 0$) is also expressed in terms of the reproduction number $\mathscr{R}_0^*$. If we denote the colonization, extinction and patch destruction rates by c^*, e^*, β^*, respectively, then $\mathscr{R}_0^*$ can be expressed as

$$\mathscr{R}_0^* = \frac{c^*(1-d)}{e^* + \beta^*}, \tag{3.12}$$

which gives the average number of propagules a local population produces during its life span (analogous to the *basic reproduction number* in epidemiology). The (mean field) metapopulation persists if $\mathscr{R}_0^* > 1$, and metapopulation extinction is expected if $\mathscr{R}_0^* < 1$. We also can derive a formula for the reproduction number $\mathscr{R}_0$ for our model. Using the expression in (3.9) we can rewrite our threshold condition for metapopulation persistence as $\mathscr{R}_0 > 1$, where

$$\mathscr{R}_0 = \frac{c(1-d)\omega_M}{e + \beta}. \tag{3.13}$$

Similar conclusions hold, i.e. metapopulation persists if $\mathscr{R}_0 > 1$, and we have metapopulation extinction if $\mathscr{R}_0 < 1$. Note that in the case of homogeneous landscape ($\alpha = 0, A_i = A, i = 1, \ldots, n$),

$$cnA = c^*, \quad \beta_i = \beta/A = \beta^*,$$
$$e_i = e/A = e^* \quad \text{and} \quad \omega_M = (n-1)A^2 \tag{3.14}$$

(see DeWoody et al., 2005). We have $\mathscr{R}_0 = \mathscr{R}_0^*(n-1)/n$, and hence our reproduction number $\mathscr{R}_0$ approaches $\mathscr{R}_0^*$ as the number n of patches gets large. Clearly, our formula for $\mathscr{R}_0$ allows us to assess the influence of landscape structure (represented by the matrix M) on metapopulation persistence.

All of the threshold conditions mentioned above involve the quantity ω_M, for which we do not have an explicit expression due to the high dimension of the matrix M (it is

possible to derive a formula for small $n > 1$). For large n we have to compute the value ω_M numerically for a given set of landscape characteristics.

3.2.2. Numerical studies

Our numerical studies focus on the sensitivity analysis of model outcomes to changes of three factors: landscape structure (distribution of patches), species dispersal ability (α) and long-term habitat destruction (d). We consider three hypothetical landscapes that allow us to compare our model results with the results of other models. As pointed out in DeWoody et al. (2005), the SRLM and the model of Keymer et al. (2000) are two extreme cases of our model. That is, our model reduces to the SRLM when $\beta = 0$, and it approaches the model of Keymer et al. (2000) when $\alpha = 0$, $A_i = A$, $i = 1, 2, \ldots, n$ for large n. Some comparisons of predictions of these three models can be found in DeWoody et al. (2005). We extend findings of DeWoody et al. (2005) by comparing landscapes with different patterns. To make the comparison transparent, the landscapes we chose have the same total areas (the sum of areas of all patches), and one of the landscapes has all patches with equal areas. For purposes of illustration we consider the three landscapes shown in Fig. 1 ($n = 50$). In Landscape I

the patches have equal areas and are distributed randomly. Landscape II has the same patch locations as in Landscape I, but the sizes of the patches are randomly produced (with the same total area). Patches in Landscape III occur in clusters. In our numerical simulations, parameters are assigned values comparable to those used by Keymer et al. (2000). For example, we always set $c^* = 1$ and $e^* = 0.1$. Then, for a given value of A we determine values of c and e by using relation (3.14). When patches have different areas, there are various ways to measure metapopulation occupancies at the equilibrium by using different weighs for the components of $\mathbf{p}_2^*$. For example, we can consider the following three weighted average probabilities of occupancy: p_ω (weighted by relative values of individual patches, see (3.10)), $p_A = \frac{1}{\sum_{i=1}^{n} A_i} \sum_{i=1}^{n} A_i p_{i2}^*$ (weighted by areas) and $\hat{p} = \frac{1}{\sum_{i=1}^{n} V_i^R} \sum_{i=1}^{n} V_i^R p_{i2}^*$ (weighted by patch values). In Fig. 2, these three averages are plotted against the expected destroyed habitat d. According to our computations, although both p_ω and $\hat{p}$ tend to yield an overestimate to p_A (which is also observed by Hanski and Ovaskainen, 2000), $\hat{p}$ provides a more accurate approximation to p_A. Based on observations we used $\hat{p}$ for our numerical investigations. Following Keymer et al. (2000),
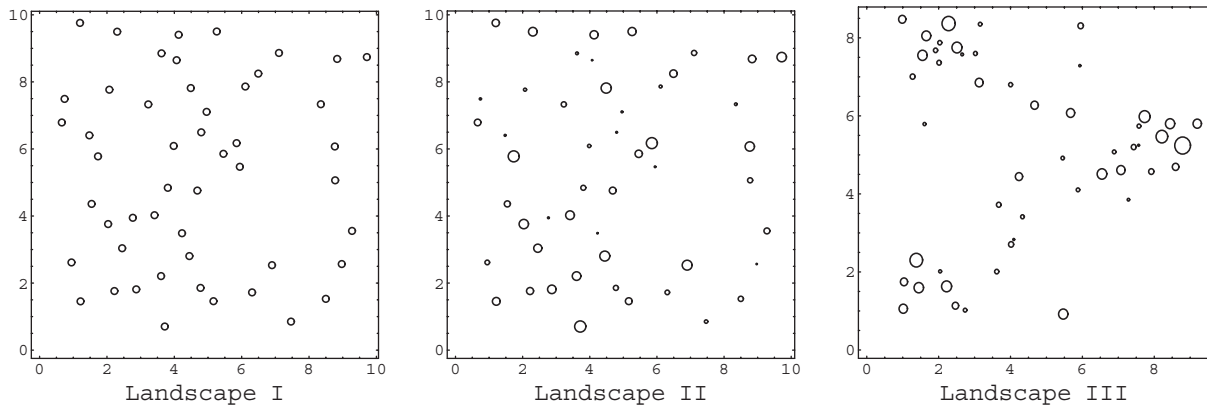

Fig. 1. Three hypothetical landscapes used in numerical simulations: Landscapes I, II, and III. All three landscapes consist of 50 patches with the same total area. Landscape I has all patches with equal areas; Landscape II has the same distribution of patch locations as Landscape I but variable patch sizes; Landscape III has a clustered distribution of patches with variable sizes.
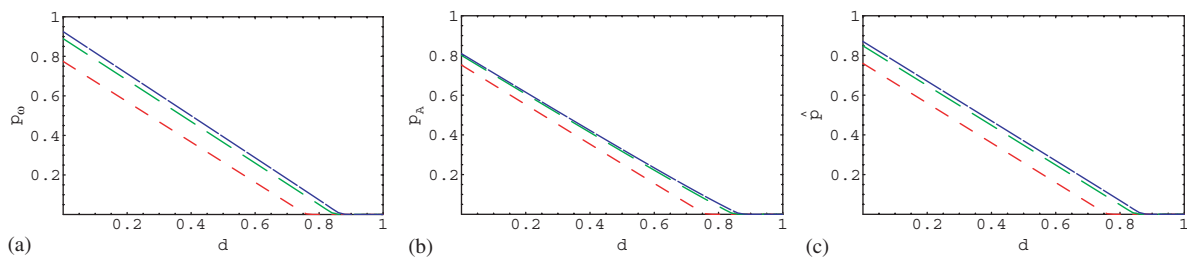

Fig. 2. Graphs of p_ω, p_A and $\hat{p}$ in (a), (b) and (c), respectively, representing the average probability of patch occupancies at the equilibrium weighted by relative values, areas and absolute values of patches, vs the long-term patch destruction d. The short dashed line is for Landscape I, the long dashed line for Landscape II, and the solid line for Landscape III. Here, $\alpha = 0.2$, $c^* = 1$, $e^* = 0.1$, $\beta^* = 0.001$.
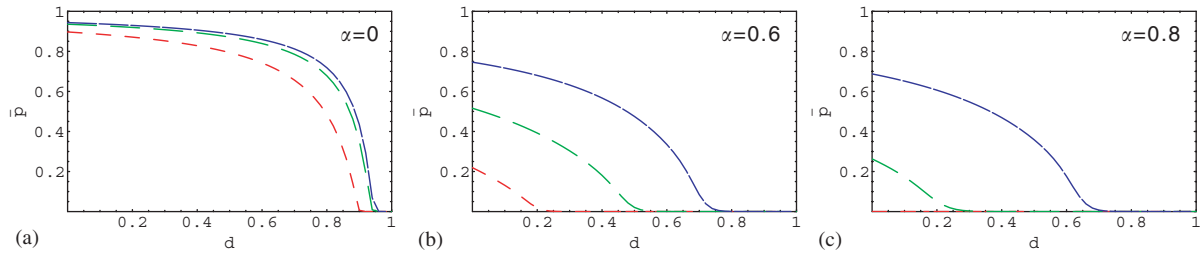
Fig. 3. $\bar{p}$, the long-term proportion of suitable habitat occupied by the focal species, vs the long-term destruction rate d. The patterns of lines in these figures and the following figures have the same meaning as in Fig. 2. In these cases, $c^* = 1$, $e^* = 0.1$, $\beta^* = 0.001$.
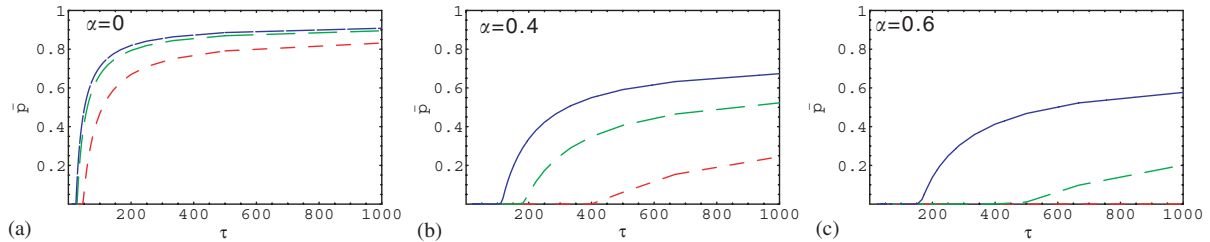

Fig. 4. $\bar{p}$ vs the basic patch lifespan $\tau = 1/\beta$. In these cases, the long-term habitat loss d is fixed at 0.2, and $c^* = 1$.

we also computed $\bar{p} = \hat{p}/(1 - d)$, the long-term proportion of suitable habitat occupied (which we henceforth call weighted occupancy) in the three landscapes for various sets of parameter values.

In Fig. 3, the weighted occupancy $\bar{p}$ is plotted against the habitat loss d for various α and for all three landscapes with other parameter values fixed. The three landscapes exhibit very different outcomes in terms of sensitivities of the weighted occupancy to changes in species dispersal ability (α), with Landscape I being most sensitive (the short dashed curves gets lowered dramatically with increasing α). Landscape III was least sensitive and Landscape II was intermediate. As dispersal ability declines (α increases), the ability to compensate for fragmentation of a landscape declines, and the species becomes increasingly sensitive to the dispersion and connectivity of patches, which can even become predominant determinants of patch occupancies and species persistence. For instance, when $\alpha = 0.8$ (Fig. 3(c)), the weighted occupancy ($\bar{p}$) for Landscape III is much higher than for Landscape II at the same level of habitat loss (d); a metapopulation can endure much greater levels of habitat loss on Landscape III than on Landscape II. No patches are occupied in Landscape I when $\alpha = 0.8$, because the threshold condition for species persistence on Landscape I cannot be satisfied (notice that the threshold condition in terms of how much destruction a species can tolerate is given by $d < \bar{d} = 1 - (e + \beta)/(c\, \omega_M)$ and that, for Landscape I, $\bar{d} < 0$ due to a smaller value of ω_M corresponding to this landscape). The pattern of a landscape thus can greatly affect the persistence of species, and clustered landscapes with heterogeneous patch sizes may support higher occupancy levels, greater persistence, and hence greater tolerance to habitat loss. Fig. 3(a) also shows that when $\alpha = 0$ the species can endure high levels of

habitat loss (d) on all three landscapes. This implies that, for a species with well-developed dispersal ability, the heterogeneity of a landscape contributes little to the species' persistence.

Examining the impact of patch life span, $\tau = 1/\beta$, on the weighted patch occupancy ($\bar{p}$), leads to a similar conclusion. That is, for large α it is more likely for a species to persist in clustered landscapes (type III) with heterogeneous patch sizes, especially when τ is large (see Fig. 4).

3.3. Rescue effect

Section 3.2 considers a special case of our model in which colonization and extinction rates have the forms given in (3.7), where the per-capita local extinction rate is assumed to be independent of the metapopulation size. In some ecological systems density-dependent extinction rates may be more appropriate, such as the rescue effect considered by Hanski (1982, 1983). Here, to illustrate our theorems about multiple interior equilibria, we assume that $e_i(\mathbf{p}_2) = (1 - \theta_i p_{i2})\tilde{e}_i$. That is, we biologically assume that the extinction rate e_i is independent of the populations in the neighborhood of patch i, and high probability of patch occupancy reduces the extinction rate e_i of patch i. In this case, the function $E_i(\mathbf{p}_2)$ in system (3.1)–(3.2) becomes

$$E_i(\mathbf{p}_2) = e_i(\mathbf{p}_2) + \beta_i = \tilde{e}_i(1 - \theta_i p_{i2}) + \beta_i. \quad (3.15)$$

As in Section 3.2, we make the same assumptions on the colonization rate (c_i), extinction rates ($\tilde{e}_i$), and patch dynamics parameters (β_i and λ_i). Suppose that $\theta_i = \theta$ for all patches. Then the right-hand side of system (3.1)–(3.2) is no longer strictly sublinear, and hence, instead of an attracting equilibrium, we may have an attracting basin. In fact, our numerical simulations show that the system may

have two positive equilibria. This confirms the analytic results given in Section 3.1: every solution $(\mathbf{p}_0, \mathbf{p}_2)$ of system (3.1)–(3.2) is attracted to the set $\mathbf{B} \times [\mathbf{p}_2^m, \mathbf{p}_2^M]$ if $\omega_M > \bar{\omega}$, where $\mathbf{p}_2^m$ and $\mathbf{p}_2^M$ are the minimal and maximal equilibria (componentwise) and $\mathbf{p}_2^m$ and $\mathbf{p}_2^M$ may not be equal. Hence, if $\omega_M > \bar{\omega}$ we have metapopulation persistence. Ovaskainen and Hanski (2001) termed $\mathbf{p}_2^M$ the principal equilibrium, however, they did not find a $\mathbf{p}_2^m$ and verify the attractivity.

A difference between assumptions (3.15) and (3.7) on E_i is the case where $\omega_M < \bar{\omega}$. Under assumption (3.7), if $\omega_M < \bar{\omega}$, the trivial equilibrium $(\mathbf{B}, \mathbf{0})$ is globally attractive and hence the metapopulation will definitely disappear. On the other hand, under assumption (3.15), if $\omega_M < \bar{\omega}$, the trivial equilibrium is locally asymptotically stable, there exist attractivity basins of equilibria $\mathbf{B} \times \mathbf{p}_2^m$ and $\mathbf{B} \times \mathbf{p}_2^M$, and hence the metapopulation may still persist, depending on initial values.

In the case of persistence, although we cannot predict the exact size of the metapopulation analytically, we can get a range of the population size by computing $\mathbf{p}_2^m$ and $\mathbf{p}_2^M$ numerically. Consequently we can compute various weighted probabilities of occupancy at $\mathbf{p}_2^m$ and $\mathbf{p}_2^M$ (e.g. $\bar{p}_m$ and $\bar{p}_M$). Our simulations show that the difference between $\bar{p}_m$ and $\bar{p}_M$ is small (see Fig. 5). We have also conducted numerical simulations using other averaged occupancies, and in most cases the maximal and minimal occupancies are not very different (see Fig. 6). Note that the average probabilities of patch occupancy at two equilibria $\mathbf{p}_2^m$, $\mathbf{p}_2^M$ still decrease almost linearly with the increased destruction d when d is not large. We also

observed from the simulations that although the introduction of a rescue effect does not change the threshold condition for species persistence, it greatly increases patch occupancies, especially for species with small dispersal distance (compare Figs. 3 and 5). We also performed simulations for different values of θ, which imply that the patch occupancies increase nonlinearly with increasing ω.

4. Stochastic metapopulation model

A new stochastic metapopulation model is derived that is consistent with model (3.1)–(3.2). In particular, a system of Itô SDEs is derived, where $\mathscr{P}_{i0}$ and $\mathscr{P}_{i2}$ are continuous random variables for the probability that patch i is either uninhabitable or occupied, respectively.

First, we express the differential equations (3.1)–(3.2) in terms of the patch area that is uninhabitable, habitable yet empty, and occupied by the focal species. For a landscape with n patches, assume that a unit area of a patch can be divided into N smaller units or micropatches, where the number of micropatches N can be chosen according to the landscape heterogeneity and the range of the focal species. Then a patch with area A_i units has $N_i = A_i N$ micropatches within patch i. The constant N may be considered a scaling factor. For example, if a unit area of a patch is defined as $1000\,\text{m}^2$, subdivision into smaller units of size $1\,\text{m}^2$ leads to $N = 1000$. Then a patch area $A_i = 1000$ square units has $N_i = (A_i)(N) = (1000)(1000) = 10^6\,\text{m}^2$. On the other hand, if a unit area of patch is defined as $1\,\text{m}^2$ so that $N = 1$, then the patch area $A_i = 10^6$ square units and $N_i = (A_i)(N) = (10^6)(1) = 10^6\,\text{m}^2$. The value of
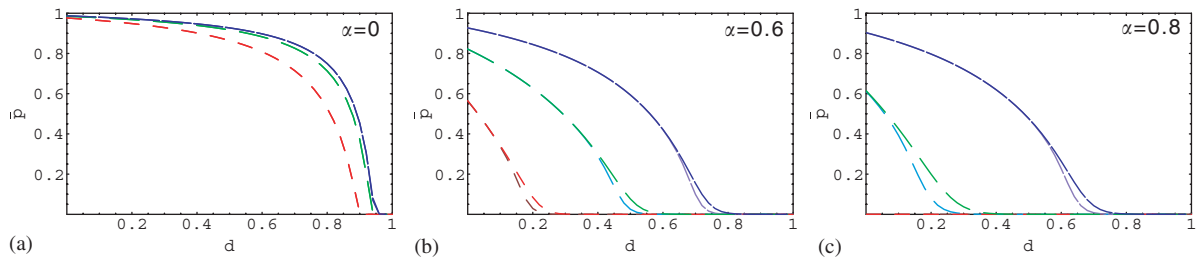

Fig. 5. In the case of rescue effect ($\theta = 0.8$), the weighted occupancies $\bar{p}$ (minimal $\bar{p}_m$ and maximal $\bar{p}_M$) are plotted against the habitat loss (d) for various values of α on three landscapes. Here, $c^* = 1$, $e^* = 0.1$, $\beta^* = 0.001$, the same values as in Fig. 3.
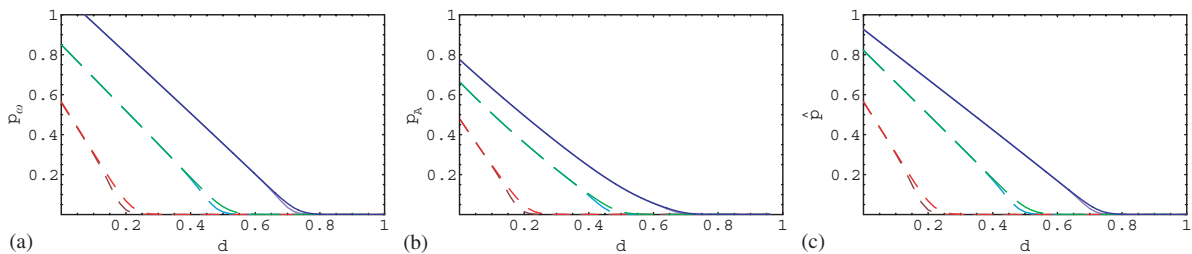

Fig. 6. After introducing the rescue effect ($\omega = 0.8$), the average probabilities of occupancies at the minimal and maximal equilibria first weighted by relative values (a), areas (b) and absolute values (c) of patches decrease almost linearly with increased d. Here, $\alpha = 0.6$, $c^* = 1$, $e^* = 0.1$, $\beta^* = 0.001$.

N_i is the same in either case and equals the area of A_i expressed in the units of the microhabitat size. For the stochastic model to agree with the deterministic model, the units of A_i must be expressed in terms of the microhabitat size. In particular, A_i should be in terms of N_i in the colonization rate and extinction rate for patch i, i.e.,

$$c_i(\mathbf{p}_2) = cN \sum_{j \neq i} e^{-\alpha d_{ij}} A_j p_{j2}(t), \quad e_i(\mathbf{P}_2) = \frac{e/N}{A_i}.$$

The factor N can be included in the coefficients, that is, cN and e/N can be relabeled as c and e, respectively. But notice that the colonization rate increases and the extinction rate decreases with N.

Assume that N, N_i, and A_i are constants. In addition, assume that each of the N_i micropatches can be classified as uninhabitable, habitable yet empty and occupied by the focal species so that $N_{i0} = N_i p_{i0}$, $N_{i1} = N_i p_{i1}$, and $N_{i2} = N_i p_{i2}$. Then N_{i0}, N_{i1}, and N_{i2} are the numbers of micropatches in patch i that are uninhabitable, inhabitable yet empty and occupied, respectively, and $N_i = N_{i0} + N_{i1} + N_{i2}$. It follows from the differential equations (3.1)–(3.2) that

$$\frac{dN_{i0}}{dt} = \beta_i(N_i - N_{i0} - N_{i2}) + \beta_i N_{i2} - \lambda_i N_{i0}, \tag{4.1}$$

$$\frac{dN_{i2}}{dt} = c_i(\mathbf{p}_2)(N_i - N_{i0} - N_{i2}) - (e_i(\mathbf{p}_2) + \beta_i)N_{i2}, \tag{4.2}$$

for $i = 1, 2, \ldots, n$. The destruction rate in model (4.1)–(4.2), $\beta_i(N_i - N_{i0})$, is written as the sum of two rates $\beta_i(N_i - N_{i0} - N_{i2}) + \beta_i N_{i2}$ (destruction rate for a patch in states 1 and 2, respectively). These rates need to be considered separately when formulating the stochastic model. A system of SDEs is derived based on model (4.1)–(4.2).

4.1. Derivation of the stochastic model

Let $\mathcal{N}_{i0}$ and $\mathcal{N}_{i2}$ denote continuous random variables for the number of micropatches in patch i that are in states 0 and 2, respectively. Let the random vectors $\mathcal{N}_0 = (\mathcal{N}_{i0})_{i=1}^n$, $\mathcal{N}_2 = (\mathcal{N}_{i2})_{i=1}^n$, $X = (\mathcal{N}_0, \mathcal{N}_2)$ and $\Delta X = (\Delta \mathcal{N}_0, \Delta \mathcal{N}_2)$, where $\Delta \mathcal{N}_j$ denotes the change in the random vector from time t to $t + \Delta t$, $j = 0, 2$. In addition, define the random variables $\mathscr{P}_{i0} = \mathcal{N}_{i0}/N_i$, and $\mathscr{P}_{i2} = \mathcal{N}_{i2}/N_i$ (N_i is constant), and the random vectors $\mathscr{P}_0 = (\mathscr{P}_{i0})_{i=1}^n$ and $\mathscr{P}_2 = (\mathscr{P}_{i2})_{i=0}^n$. Assume, for small Δt, that ΔX can be approximated by a normal distribution and that the random variability is due to colonization and extinction of species, and destruction and creation of patches.

To derive the system of SDEs, we apply a method developed by Allen (1999). This method is based on a continuous time Markov chain formulation. The infinitesimal transition probabilities for a Markov chain model

based on the differential equations (4.1)–(4.2) satisfy

$\mathrm{Prob}\{(\Delta \mathcal{N}_{i0}, \Delta \mathcal{N}_{i2}) = (j,k)|(\mathcal{N}_{i0}, \mathcal{N}_{i2})\}$

$$= \begin{cases} \beta_i(N_i - \mathcal{N}_{i0} - \mathcal{N}_{i2})\Delta t + o(\Delta t), & (j,k) = (1,0), \\ \beta_i \mathcal{N}_{i2}\Delta t + o(\Delta t), & (j,k) = (1,-1), \\ \lambda_i \mathcal{N}_{i0}\Delta t + o(\Delta t), & (j,k) = (-1,0), \\ c_i(\mathscr{P}_2)(N_i - \mathcal{N}_{i0} - \mathcal{N}_{i2})\Delta t + o(\Delta t), & (j,k) = (0,1), \\ e_i(\mathscr{P}_2)\mathcal{N}_{i2}\Delta t + o(\Delta t), & (j,k) = (0,-1), \\ 1 - [\beta_i(N_i - \mathcal{N}_{i0}) + \lambda_i \mathcal{N}_{i0} + e_i(\mathscr{P}_2)\mathcal{N}_{i2}]\Delta t \\ \quad -[c_i(\mathscr{P}_2)(N_i - \mathcal{N}_{i0} - \mathcal{N}_{i2})]\Delta t + o(\Delta t), & (j,k) = (0,0), \end{cases}$$

$$\tag{4.3}$$

for $i = 1, 2, \ldots, n$. For example, the term $\beta_i \mathcal{N}_{i2}\Delta t + o(\Delta t)$ is the probability an occupied micropatch (state 2) of patch i is destroyed and replaced by an uninhabitable one (state 0). The probabilities for all other transitions are $o(\Delta t)$.

The transition probabilities (4.3) are used to compute the expectation vector and the covariance matrix for the change in the random variables to order Δt (Allen, 1999, 2003; Kirupaharan and Allen, 2004). The conditional expectation to order Δt is

$$\mathbb{E}(\Delta X|(\mathcal{N}_0, \mathcal{N}_2)) \approx (\mathscr{E}_1, \mathscr{E}_2, \ldots, \mathscr{E}_n)\Delta t = \mathscr{E}\Delta t,$$

where

$$\mathscr{E}_i = \begin{pmatrix} \beta_i(N_i - \mathcal{N}_{i0} - \mathcal{N}_{i2}) + \beta_i \mathcal{N}_{i2} - \lambda_i \mathcal{N}_{i0} \\ c_i(\mathscr{P}_2)(N_i - \mathcal{N}_{i0} - \mathcal{N}_{i2}) - (e_i(\mathscr{P}_2) + \beta_i)\mathcal{N}_{i2} \end{pmatrix}$$

$$= \begin{pmatrix} \beta_i(N_i - \mathcal{N}_{i0}) - \lambda_i \mathcal{N}_{i0} \\ c_i(\mathscr{P}_2)\mathcal{N}_{i2}(N_i - \mathcal{N}_{i0} - \mathcal{N}_{i2}) - (e_i(\mathscr{P}_2) + \beta_i)\mathcal{N}_{i2} \end{pmatrix}.$$

The conditional covariance matrix is given by

$$CV(\Delta X|(\mathcal{N}_0, \mathcal{N}_2))$$
$$= \mathbb{E}(\Delta X[\Delta X]^T) - [\mathbb{E}(\Delta X)][\mathbb{E}(\Delta X)]^T,$$

where the expectations are conditional on $(\mathcal{N}_0, \mathcal{N}_2)$. The second term $[\mathbb{E}(\Delta X)][\mathbb{E}(\Delta X)]^T$ is order $(\Delta t)^2$. Thus, applying the transition probabilities (4.3), the covariance matrix to order Δt is

$$CV(\Delta X|(\mathcal{N}_0, \mathcal{N}_2)) \approx \mathbb{E}(\Delta X[\Delta X]^T)$$
$$= diag\{\mathscr{V}_1, \mathscr{V}_2, \ldots, \mathscr{V}_n\}\Delta t = \mathscr{V}\Delta t,$$

where

$$\mathscr{V}_i = \begin{pmatrix} \beta_i(N_i - \mathcal{N}_{i0}) + \lambda_i \mathcal{N}_{i0} & -\beta_i \mathcal{N}_{i2} \\ -\beta_i \mathcal{N}_{i2} & c_i(\mathscr{P}_2)(N_i - \mathcal{N}_{i0} - \mathcal{N}_{i2}) + (e_i(\mathscr{P}_2) + \beta_i)\mathcal{N}_{i2} \end{pmatrix}.$$

Matrix $\mathscr{V}$ is symmetric and positive definite and therefore, has a unique square root, $\mathscr{B} = \sqrt{\mathscr{V}}$, where $\mathscr{B} = diag(\mathscr{B}_1, \mathscr{B}_2, \ldots, \mathscr{B}_n)$ and $\mathscr{B}_i = \sqrt{\mathscr{V}_i}$ (Ortega, 1987).

To order Δt, the mean of ΔX is $\mathscr{E}\Delta t$ and the covariance is $\mathscr{V}\Delta t$ so that $\Delta X \approx \mathbf{N}(\mathscr{E}\Delta t, \mathscr{V}\Delta t)$. Therefore, the following approximation holds:

$$X(t + \Delta t) = X(t) + \Delta X(t)$$
$$\approx X(t) + \mathscr{E}\Delta t + \mathscr{B}\sqrt{\Delta t}\,\sigma,$$

where $\sigma \sim N(0, I)$ and I is the $2n \times 2n$ identity matrix. This latter expression is an Euler approximation to a system of Itô SDEs (Kloeden and Platen, 1992; Kloeden et al., 1997) given by

$$\frac{d\mathcal{N}_{i0}}{dt} = \beta_i(N_i - \mathcal{N}_{i0}) - \lambda_i \mathcal{N}_{i0}$$
$$+ b_{11}^i \frac{dW_{i1}}{dt} + b_{12}^i \frac{dW_{i2}}{dt},$$

$$\frac{d\mathcal{N}_{i2}}{dt} = c_i(\mathcal{P}_2)(N_i - \mathcal{N}_{i0} - \mathcal{N}_{i2})$$
$$- (e_i(\mathcal{P}_2) + \beta_i)\mathcal{N}_{i2} + b_{21}^i \frac{dW_{i1}}{dt} + b_{22}^i \frac{dW_{i2}}{dt},$$

for $i = 1, 2, \ldots, n$. Matrix $\mathcal{B}^i = (b_{jk}^i) = \sqrt{\mathcal{V}_i}$ and W_{i1} and W_{i2} are independent Wiener processes. The preceding system can be simplified by dividing each SDE by the constant total number of micropatches $N_i = A_i N$,

$$\frac{d\mathcal{P}_{i0}}{dt} = \beta_i(1 - \mathcal{P}_{i0}) - \lambda_i \mathcal{P}_{i0}$$
$$+ \frac{\tilde{b}_{11}^i}{\sqrt{A_i N}} \frac{dW_{i1}}{dt} + \frac{\tilde{b}_{12}^i}{\sqrt{A_i N}} \frac{dW_{i2}}{dt}, \qquad (4.4)$$

$$\frac{d\mathcal{P}_{i2}}{dt} = c_i(\mathcal{P}_2)(1 - \mathcal{P}_{i0} - \mathcal{P}_{i2}) - (e_i(\mathcal{P}_2) + \beta_i)\mathcal{P}_{i2}$$
$$+ \frac{\tilde{b}_{21}^i}{\sqrt{A_i N}} \frac{dW_{i1}}{dt} + \frac{\tilde{b}_{22}^i}{\sqrt{A_i N}} \frac{dW_{i2}}{dt}, \qquad (4.5)$$

for $i = 1, 2, \ldots, n$. Matrix $\tilde{\mathcal{B}}^i = (\tilde{b}_{jk}^i) = \sqrt{\mathcal{V}_i / A_i N}$, where matrix

$$\mathcal{V}_i / A_i N = \begin{pmatrix} \beta_i(1 - \mathcal{P}_{i0}) + \lambda_i \mathcal{P}_{i0} & -\beta_i \mathcal{P}_{i2} \\ -\beta_i \mathcal{P}_{i2} & c_i(\mathcal{P}_2)(1 - \mathcal{P}_{i0} - \mathcal{P}_{i2}) + (e_i(\mathcal{P}_2) + \beta_i)\mathcal{P}_{i2} \end{pmatrix}.$$

An explicit expression for the square root of $\mathcal{V}_i / A_i N$ is given by

$$\tilde{\mathcal{B}}^i = \frac{1}{h^i} \begin{pmatrix} \tilde{v}_{11}^i + g^i & \tilde{v}_{12}^i \\ \tilde{v}_{12}^i & \tilde{v}_{22}^i + g^i \end{pmatrix},$$

where $(\tilde{v}_{jk}^i) = \mathcal{V}_i / A_i N$, $g^i = \sqrt{\tilde{v}_{11}^i \tilde{v}_{22}^i - (\tilde{v}_{12}^i)^2}$ and $h^i = \sqrt{\tilde{v}_{11}^i + \tilde{v}_{22}^i + 2g^i}$ (Allen, 1999).

Note that the terms without the Wiener process in model (4.4)–(4.5) have the same form as in model (3.1)–(3.2). However, the terms with the Wiener process have a factor of $1/\sqrt{A_i N}$, that is, the random variables for the probabilities of patches in states 0, 1, and 2 depend on patch areas and the number of microhabitats N in a unit area. The inclusion of N is not necessary in the stochastic formulation if A_j is already expressed in species appropriate units, the microhabitat size. In this case, we let $N = 1$. However, the inclusion of N shows the importance of these units in the stochastic model and in the coefficients of the original model (3.1)–(3.2), where c_i increases with N and e_i decreases with N. The numerical simulations in the next section show close agreement between the deterministic and stochastic models when N is large. The coefficients of the Wiener processes in the system of SDEs become small as the product $A_i N$ increases which result in a decrease in random effects as $A_i N$ increases.

4.2. Numerical simulations of the SDEs

We simulated the SDE and the ODE models and compared their dynamics. All assumptions on the coefficients β_i, λ_i, c_i and e_i were the same as those made in Section 3.2. We simulated models (4.4)–(4.5) and (3.1)–(3.2) with Landscape structure II. The graphs in Fig. 7 illustrate the solutions to the stochastic and the deterministic models with the same initial values and the same parameter values except for N. The top two panels in Fig. 7 are graphs of the probabilities p_{i0} and p_{i2} in one patch vs time t when $N = 1000$ (left) and $N = 5000$ (right), whereas the bottom panels show the average $\hat{p}$ of patch occupancies weighted by absolute values of patches vs time t. The stochastic results matched the deterministic results very well, especially for large N. We also simulated the average $\hat{p}$ at the equilibrium with varying levels of landscape loss d. Fig. 8 illustrates $\hat{p}$ vs d with one realization for each value of d. The average $\hat{p}$ from the SDE model was very close to that from the ODE model.
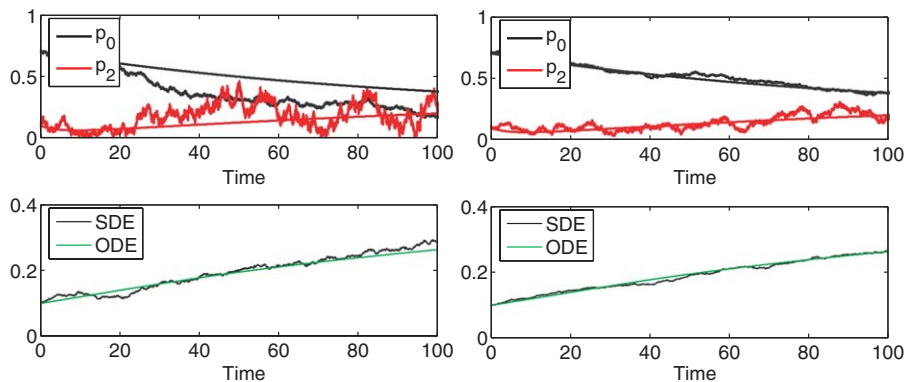

Fig. 7. Solutions to the ODE model (2.3) and two sample paths of the SDE model (4.4)–(4.5) with the same parameters as in Fig. 2, except $d = 0.2$, $N = 1000$ (left), $N = 5000$ (right). The top panels are the graphs of probabilities p_{i0} and p_{i2} for one patch. The bottom panels are the graphs of the corresponding averages $\hat{p}$ for all patch occupancies weighted by absolute values of patches.
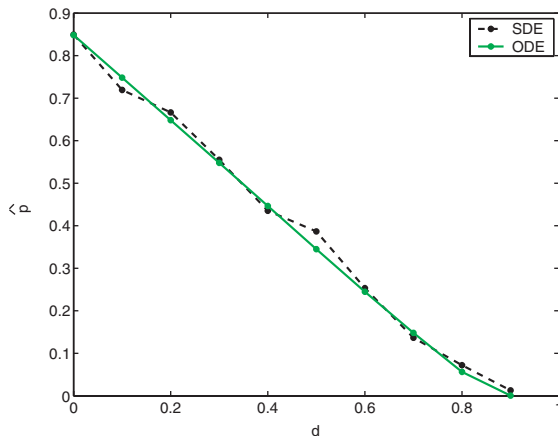
Fig. 8. The weighted occupancy $\hat{p}$ varies with the long-term habitat loss d. The parameters are the same as in Fig. 7 except $N = 1000$. For each value of d, only one realization is performed.

There are several advantages in formulating a SDE model over a Monte Carlo simulation or a continuous time Markov chain model. First, it can be seen that the form of the SDE model (4.4)–(4.5) is consistent with the deterministic model (3.1)–(3.2). Second, the SDE model gives more insight into the stochastic nature of the system. For example, the coefficients of the Wiener process in the SDE model show that variability decreases as the patch area increases. Third, numerical approximations for Itô SDEs are generally more efficient than those for Monte Carlo simulations or for a continuous time Markov chain model.

5. Conclusion

Hanski and Ovaskainen (2000, 2001) termed ω_M the metapopulation capacity of a patch network, with which one may rank different landscapes in term of their capacity to support a viable metapopulation. However, when patch dynamics (characterized by patch destruction rate β and patch creation λ) are considered, ω_M overestimates the ability of a landscape to sustain a metapopulation. Under the traditional assumptions in Section 3.2, $(1-d)\omega_M$ is more appropriate to use as the metapopulation capacity. That is, the long-term habitat loss d of the patches reduces the metapopulation capacity of a landscape. The parameter d also affects the threshold condition for species persistence and patch occupancies. As shown in Section 3.2, the threshold value $\bar{\omega}$ and the weighted occupancies ($\hat{p}$ and p_A) are decreasing functions of d and β.

Our numerical simulations showed that the dispersion of patches and the distribution of patches in a landscape are more important for species with poor dispersal ability, and may be predominant determinants of long-term patch occupancy and species persistence. More precisely, species inhabiting landscapes with clustered and heterogeneous patch sizes have stronger persistence and can tolerate

higher levels of habitat loss. Additional simulations of $\bar{p}$ vs the patch lifespan $\tau = 1/\beta$ for a given level of habitat loss d (Fig. 4) reinforced our conclusions. The pattern of a landscape is of overwhelming importance in determining long-term metapopulation persistence and patch occupancy, except for species with well-developed dispersal ability. These results were also true when rescue effects were considered. Although the rescue effect does not change the threshold condition, $\omega_M > \bar{\omega}$, it may produce multiple nontrivial steady states: the minimal and maximal equilibria. However, for the parameter values we used, the difference between the corresponding minimal and maximal proportion $\bar{p}$ was small for all landscapes considered.

Finally, we developed a new stochastic metapopulation model based on the differential equations (3.1)–(3.2). Our simulations revealed good agreement between the deterministic and the stochastic metapopulation models. Future work can use the stochastic metapopulation model to explore impacts of stochastic factors which cannot be investigated with deterministic models.

Acknowledgements

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